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Cardiovascular Modulation of Selective Attention in Vision

**The Impact of Baroreceptor Activity on
Perceptual Selection and Controlled Distractor Processing**

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General Abstract

Cognitive performance is contingent upon multiple factors. Beyond the impact of environmental circumstances, the bodily state may hinder or promote cognitive processing. Afferent transmission from the viscera, for instance, is crucial not only for the genesis of affect and emotion, but further exerts significant influences on memory and attention. In particular, afferent cardiovascular feedback from baroreceptors demonstrated subcortical and cortical inhibition. Consequences for human cognition and behavior are the impairment of simple perception and sensorimotor functioning. Four studies are presented that investigate the modulatory impact of baro-afferent feedback on selective attention. The first study demonstrates that the modulation of sensory processing by baroreceptor activity applies to the processing of complex stimulus configurations. By the use of a visual masking task in which a target had to be selected against a visual mask, perceptual interference was reduced when target and mask were presented during the ventricular systole compared to the diastole. In study two, selection efficiency was systematically manipulated in a visual selection task in which a target letter was flanked by distracting stimuli. By comparing participants' performance under homogeneous and heterogeneous stimulus conditions, selection efficiency was assessed as a function of the cardiac cycle phase in which the targets and distractors were presented. The susceptibility of selection performance to the stimulus condition at hand was less pronounced during the ventricular systole compared to the diastole. Study one and two therefore indicate that interference from irrelevant sensory input, resulting from temporally overlapping processing traces or from the simultaneous presentation of distractor stimuli, is reduced during phases of increased baro-afferent feedback. Study three experimentally manipulated baroreceptor activity by systematically varying the participant's body position while a sequential distractor priming task was completed. In this study, negative priming and distractor-response binding effects were obtained as indices of controlled and automatic distractor processing, respectively. It was found that only controlled distractor processing was affected by tonic increases in baroreceptor activity. In line with study one and two these results indicate that controlled selection

processes are more efficient during enhanced baro-afferent feedback, observable in diminished aftereffects of controlled distractor processing. Due to previous findings that indicated baro-afferent transmission to affect central, rather than response-related processing stages, study four measured lateralized-readiness potentials (LRPs) and reaction times (RTs), while participants, again, had to selectively respond to target stimuli that were surrounded by distractors. The impact of distractor inhibition on stimulus-related, but not on response-related LRPs suggests that in a sequential distractor priming task, the sensory representations of distractors, rather than motor responses are targeted by inhibition. Together with the results from studies one through three and the finding of baroreceptor-mediated behavioral inhibition targeting central processing stages, study four corroborates the presumption of baro-afferent signal transmission to modulate controlled processes involved in selective attention.

In sum, the work presented shows that visual selective attention benefits from increased baro-afferent feedback as its effects are not confined to simple perception, but may facilitate the active suppression of neural activity related to sensory input from distractors. Hence, due to noise reduction, baroreceptor-mediated inhibition may promote effective selection in vision.

Table of Contents

Acknowledgements	iii
General Abstract.....	iv
Table of Contents	vi
Index of Figures	ix
Index of Tables.....	xi
Index of Abbreviations.....	xii
Index of Publications.....	xiii
Chapter I General Introduction.....	1
1.1 The Arterial Baroreflex	4
1.1.1 Physiology of Arterial Baroreceptors.....	4
1.1.2 Central Projections of Arterial Baroreceptors	6
1.1.2.1 Cardiovascular Branch: Spinal Cord and Brain Stem	6
1.1.2.2 Central Nervous Branch: Mesencephalon, Diencephalon, and Cerebral Cortex	6
1.2 Behavioral Effects of Arterial Baroreceptor Activation	7
1.3 Visual Selective Attention.....	10
1.3.1 Selection Based on Perceptual Features	11
1.3.1.1 Visual Masking.....	12
1.3.1.2 Similarity Effects.....	14
1.3.2 Drawing the Line: Automatic and Controlled Distractor Processing.....	17
1.3.2.1 Negative Priming.....	19
1.3.2.2 Distractor-Response Binding.....	22
1.3.3 Mechanisms of Selective Attention: Locus of Inhibitory Control	24
1.3.4 Approaches to Inhibition	26
1.4 Research Strategies for the Assessment of Baroreceptor-mediated Effects on Human Behavior	27
1.4.1 Experimental Modulation of Arterial Baroreceptor Stimulation.....	28
1.4.2 Natural Variations Within the Cardiac Cycle.....	33
Chapter II Cardiac Cycle Time Effects on Mask Inhibition.....	35
2.1 Abstract	37
2.2 Introduction	37
2.3 Method	42

2.3.1	Participants	42
2.3.2	Physiological Measurements	43
2.3.3	Materials and Apparatus.....	43
2.3.4	Procedure	44
2.3.5	Design.....	46
2.4	Results	47
2.4.1	Target identification	47
2.4.2	Manipulation check	49
2.5	Discussion	50
2.6	Acknowledgements	55
2.7	References	55
 Chapter III Cardiac Cycle Time Effects on Selection Efficiency in Vision		63
3.1	Abstract	65
3.2	Introduction	65
3.3	Method	70
3.3.1	Participants	70
3.3.2	Physiological Measurements	71
3.3.3	Materials and Apparatus.....	71
3.3.4	Procedure	73
3.3.5	Design.....	74
3.4	Results	75
3.4.1	Error Rates.....	75
3.4.2	Response Time	77
3.5	Discussion	78
3.6	Author Notes	83
3.7	References	83
 Chapter IV Baroreceptor Activity Impacts upon Controlled but not Automatic Distractor Processing		94
4.1	Abstract	96
4.2	Introduction	96
4.2.1	Negative Priming and Distractor-Response Binding	99
4.2.2	Tonic manipulation of baroreceptor activity	102
4.3	Method	103
4.3.1	Participants	103

Index

4.3.2 Physiological Measures	104
4.3.3 Materials and Apparatus.....	104
4.3.4 Procedure	105
4.3.5 Design.....	107
4.4 Results	109
4.4.1 Cardiovascular Measures and Manipulation Check	109
4.4.2 Controlled Distractor Processing (Negative Priming).....	110
4.4.3 Automatic Distractor Processing (Distractor-Response Binding).....	113
4.5 Discussion	114
4.6 Acknowledgements	121
4.7 References	121
Chapter V Distractor Inhibition: Evidence From Lateralized Readiness Potentials	135
5.1 Abstract	137
5.2 Introduction	137
5.3 Method	140
5.3.1 Participants	140
5.3.2 Materials and Apparatus.....	141
5.3.3 Procedure	141
5.3.4 EEG Recording and Quantification.....	143
5.3.5 LRP Analysis.....	145
5.3.6. Design.....	146
5.4 Results	146
5.4.1 Behavioral Data	146
5.4.2 LRP Data	148
5.4.3 Control Analyses	149
5.5 Discussion	151
5.6 References	156
Chapter VI General Discussion	163
General References	172
Eidesstattliche Erklärung.....	202

Index of Figures

- Figure 1.** Sequence of events in an experimental trial. The mask stimulus was presented for 17 ms and with high contrast whereas the target stimulus was presented for 50 ms and with low contrast. Fixation time varied with respect to the occurrence of an R wave after the onset of the fixation cross plus a fixed interval of 330 and 30 ms in systolic and diastolic trials, respectively. The mask onset was 170 ms after the R wave for systolic and 470 ms after the R wave for diastolic trials. Stimuli are not drawn to scale. 46
- Figure 2.** Mean sensitivity d' and standard errors (SE) for cardiac systole ($d' = 0.29$) and diastole ($d' = 0.11$). t -Tests revealed significant deviation from zero for stimuli presented during the cardiac systole (R +170 ms), but not for those presented during the diastole (R +470 ms). 49
- Figure 3.** Exemplars of stimulus configurations for correctly displayed and laterally reversed target letters in homogeneous and heterogeneous stimulus conditions. Targets occurred randomly at one of the inner five stimulus positions. 72
- Figure 4.** Sequence of events in an experimental trial. Onset of the stimulus septet was synchronized to the cardiac cycle phase of the participant (180 ms after the R wave for systolic and 480 ms after the R wave for diastolic trials). Feedback was given following erroneous responses only. Stimuli are not drawn to scale. 74
- Figure 5.** Mean selection efficiency (in percentage error) as a function of the cardiac cycle phase. Selection efficiency is indexed by the difference of heterogeneous and homogeneous stimulus condition. Standard errors are depicted. 76
- Figure 6.** Schematic display of the experimental set-up. Half of the participants performed the experimental task head-down with an inclination angle of -6° , half of the participants head-up with an inclination angle of $+6^\circ$ 105
- Figure 7.** Sequence of events in an experimental trial. Middle letters (targets; always depicted in red) had to be identified via the corresponding key press. Flanking letters (distractors; always depicted in green) were to be ignored. An example of an Ignored Repetition trial is depicted. 108
- Figure 8.** Negative Priming effects (in ms; within-subjects comparison) as a function of body position (between-subjects comparison). Averaged RT differences and 95% confidence intervals of the mean are depicted. The NP effect is calculated by subtracting the ignored repetition from control trials. 111

Figure 9. Distractor-response binding effects (in ms; within-subjects comparison) as a function of body position (between-subjects comparison). Averaged RT differences and 95% confidence intervals of the mean are depicted. The DRB effect is calculated by subtracting the mean RT difference of Response Change Distractor Change trials minus Response Change Distractor Repetition trials from the mean RT difference of Response Repetition Distractor Change trials minus Response Repetition Distractor Repetition trials. 114

Figure 10. Schematic display of the trial procedure. Stimuli are not drawn to scale..... 143

Figure 11. (a) Grand averaged S-LRPs of probe responses as a function of distractor-target SOA (0 ms vs. -150 ms) and distractor repetition (repeated vs. changed). The vertical line at time point 0 ms denotes probe target onset (b) probe reaction times in milliseconds as a function of distractor-target SOA (0 ms vs. -150 ms) and distractor repetition (repeated vs. changed). 148

Index of Tables

Table 1. Mean error rates (in percentage) as a function of cardiac cycle phase, stimulus condition, and letter orientation. Standard deviations are provided in parantheses.	75
Table 2. Mean RTs (in ms) as a function of cardiac cycle phase, stimulus condition, and letter orientation. Standard deviations are provided in parantheses.	78
Table 3. Mean heart rate (HR; in bpm), systolic blood pressure (SBP; in mmHg), and diastolic blood pressure (DBP; in mmHg) (standard deviations in parentheses) for initial (baseline) measurement and the experimental phase (during tilt procedure) as a function of body position.	109
Table 4. Mean Reaction Times (RTs) for responses to the probe display (in ms; standard deviations in parentheses) and Percentages of Errors (PEs) as a function of body position and the response and distractor relations between prime and probe display.	112
Table 5. Mean reaction times in milliseconds and error rates in percentage (in brackets) as a function of Distractor Repetition (repeated vs. changed) x Response Repetition (repeated vs. changed) and Distractor-Target SOA (0 ms vs. -150 ms).	147
Table 6. Mean S-LRP onset latencies of probe responses (standard deviations in brackets) as a function of Distractor Repetition (repeated vs. changed) x Response Repetition (repeated vs. changed) and Distractor-Target SOA (0 ms vs. -150 ms).	150

Index of Abbreviations

AR	Attended repetition
LGN	Lateral geniculate nucleus
CNS	Central nervous system
CNV	Contingent negative variation
ECG	Electrocardiogram
EEG	Electroencephalogram
EOG	Electrooculogram
ERP	Event-related potential
fMRI	Functional magnetic resonance imaging
IR	Ignored repetition
LRP	Lateralized readiness potential
N _T	Target negativity
P _D	Distractor positivity
PFC	Prefrontal cortex
PRES	Phase Related External Suction
R-LRP	Response-locked lateralized readiness potential
SDT	Signal Detection Theory
S-LRP	Stimulus-locked lateralized readiness potential
SNS	Sympathetic nervous system
SOA	Stimulus onset asynchrony
S-R binding	Stimulus-response binding

Index of Publications

Chapters II through V of the doctoral dissertation represent original research articles published in (Chapter II, IV, and V) or submitted to (Chapter III) the international peer-reviewed journals *Biological Psychology*, *Brain and Cognition*, and *Psychophysiology*. The original content of these articles has been retained. The format of the articles was adapted and differs from that of the original articles.

Chapter II

Pramme, L., Larra, M. F., Schächinger, H., & Frings, C. (2014). Cardiac cycle time effects on mask inhibition. *Biological Psychology*, *100*, 115-121. doi: 10.1016/j.biopsycho.2014.05.008

Chapter III

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Chapter IV

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Chapter V

Pramme, L., Dierolf, A. M., Naumann, E., & Frings, C. (2015). Distractor inhibition: Evidence from lateralized readiness potentials. *Brain and Cognition*, *98*, 74-81. doi: 10.1016/j.bandc.2015.06.003

Chapter I

General Introduction

The autonomic and the central nervous system (CNS) are extensively interconnected. The efferent transmission from the brain via neural and endocrine signalling pathways to the periphery controls, among others the body fluid volume, and regulates the blood flow and blood pressure. Complementarily, information on the state of the organism is transferred via neural, hormonal, and physiochemical ascending pathways to widespread structures within the brain (Jänig, 2003, 2006; Saper, 2002; Vaitl, 1996). Afferent signals from the viscera are, in particular, processed within the spinal cord, brain stem, and hypothalamus. In addition, several forebrain structures serve the control and integration of visceral information with somatosensory and sensory signals from the body and its environment (Berntson & Cacioppo, 2007; Dalgleish, 2004; Jänig, 2006).

In everyday life, a glance at the significance of integrative central and autonomic functioning beyond the regulation of autonomic processes can be gained when the homeostasis of the organism is challenged, i.e., when the maintenance of an optimally balanced state of the organisms' physiological systems is perturbed. For instance, stressful situations reveal the behavioral relevance of the autonomic nervous system as increased autonomic activity can be associated with a strongly limited attentional focus and working memory capacity (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & Van Ijzendoorn, 2007; Bishop, 2008; Schmader & Johns, 2003) or the inability to focus attention effectively (Eysenck, Derakshan, Santos, & Calvo, 2007; Fox, 1993; Wine, 1971). Despite an incomplete understanding of the underlying mechanisms, the corticopetal and inter-cortical transmission of visceral and somatosensory information is assumed to mediate the influence of bodily states on non-autonomic behaviour (e.g., Aziz, Schnitzler, & Enck, 2000; Berntson, Sarter, & Cacioppo, 2003; Critchley & Harrison, 2013; Saper, 2002).

However, not only in extreme environments, but also under non-stressful conditions have cognition, emotion, and the perception of the self been found to depend on the central

processing of bodily signals (Cameron, 2002; Critchley, 2005, 2009; Critchley & Harrison, 2013). For instance, memory processes have widely been acknowledged to be influenced by the arousal state of the body, with higher sympathetic activation associated with enhanced memory consolidation (Cahill, Gorski, & Le, 2003; Kensinger & Corkin, 2004). Furthermore, vigilance, in the sense of attentional alertness (compare Petersen & Posner, 2012), is linked to circulatory parameters like heart rate, arterial blood pressure, and cerebral blood flow (Duschek, Heiss, Schmidt, Werner, & Schuepbach, 2010). Furthermore, with regard to afferent feedback from the cardiovascular system, indices of attentional capacity have been found to be correlated with the gain of the baroreflex (Duschek, Muckenthaler, Werner, & Reyes del Paso, 2009b) and several studies found simple perceptual performance to fluctuate with the concurrent level of baroreceptor activity (e.g., Edwards, Ring, McIntyre, Carroll, & Martin, 2007b).

In this dissertation the effect of baroreceptor activity on visual selective attention is examined. As will be discussed in the following chapters, research on the impact of baroreceptor activity on cognition has thus far mostly been confined to the modulation of basic sensory and sensorimotor functions. Therefore, the dissertation is centered on four studies in which different measures of selection were implemented and effects of naturally occurring and systematically induced variations in baroreceptor activity on early visual selection, as well as controlled distractor processing are reported. The general structure is as follows, a general introduction in Chapter I provides an overview of the theoretical background. Details of the method, results and a discussion of the empirical studies are given individually in Chapters II to V which represent the empirical work contributing to this dissertation. At the end of each introductory section in Chapter I, the reader is guided by a short summary of the relevance of the content for the respective study. A separate chapter providing a general discussion of the results concludes the dissertation. As each empirical chapter itself places the

individual results in a wider theoretical context, this last chapter is kept short, provides a synopsis of the results and comments on prospective research.

1.1 The Arterial Baroreflex

A crucial regulatory mechanism under central autonomous control is constituted by the arterial baroreflex. This reflex controls the short-term regulation of arterial blood pressure to maintain an optimal perfusion of tissues and organs. In response to changes in blood pressure, for instance due to body movement, changes in body position or enhanced perfusion of skeletal muscles, myocardial contractility, heart rate, and peripheral resistance of the vasculature are adjusted via sympathetic and parasympathetic efferent output (Berntson, Quigley, & Lozano, 2007; Eckberg & Sleight, 1992; Mancina & Mark, 1983; Smith & Kampine, 1990). Mainly, controlled by a brain stem-based reflex circuitry, feedback from higher CNS structures, namely the hypothalamus, amygdala, and prefrontal cortex (PFC), modulates the gain of arterial baroreflex control in order to meet current metabolic demands (McCloskey, 1981; Mitchell, Reeves, Rogers, Secher, & Victor, 1989; Waldrop, Eldridge, Iwamoto, & Mitchell, 1996). Accordingly, baroreflex sensitivity is inversely related to physiological and mental stress (Duschek, Werner, & Reyes del Paso, 2013).

1.1.1 Physiology of Arterial Baroreceptors

Changes in blood pressure are sensed by arterial baroreceptors mainly located within the vessel walls of the vasculature. Although large arteries like the subclavian and innominate arteries contain nerve endings classified as baroreceptors, evidence shows that the baroreflex is almost entirely controlled by those located within the carotid sinus and the aortic arch

(Nonidez, 1937; Shin, Hulbert, & Biggs, 1987). Carotid baroreceptors are located within the tunica adventitia externa of the carotid sinus. They are activated by and respond with increased firing rates to deformations of the tunica due to changes in pressure acting on the vessel. Its signals are conveyed to the nucleus tractus solitarius (NTS) via the carotid sinus branch of the glossopharyngeal nerve (Angell-James, 1971; Brown, 1980; Fidone & Sato, 1969). Aortic baroreceptors are primarily sited within the vessel walls of the aortic arch, presumably between the tunica media and tunica adventitia, with afferents comprised within the vagus nerve (Davos, Davies, & Piepoli, 2002; Kirchheim, 1976). Endings of both aortic and carotid baroreceptors are connected to myelinated A-fibers and unmyelinated C-fibers that vary in conduction velocity (Coleridge, Coleridge, & Schultz, 1987; Coleridge & Coleridge, 1980; Fidone & Sato, 1969). The receptors are classified as mechanoreceptors, which do not respond to pressure changes as such but to deformations of the vessel walls due to increases in intravascular pressure. The discharge pattern of the afferents is thereby determined by the base level of the arterial pressure as well as the rate and amplitude of pressure change. Under resting conditions and normal blood pressure, baroreceptors display an increased firing rate with each systolic upstroke and plateau of the arterial pressure wave with interleaved intervals of silence during the diastole (Adrian, 1926; Angell-James, 1971; Bronk & Stella, 1932, 1934; Coleridge, Coleridge, Poore, Roberts, & Schultz, 1984; Landgren, 1952). Along the glossopharyngeal and vagus nerve baroreceptor, afferents proceed to and terminate at cardiovascular centers within the medulla oblongata. In response to an increase in arterial blood pressure, higher firing frequency of the receptors provokes the excitation of vagal output to the heart and the inhibition of sympathetic control of the vasculature. Simultaneous parasympathetic excitation and sympathetic withdrawal result in a reduction in heart rate. In addition, sympathetic withdrawal leads to a decrease in the myocardial contractility, and vasomotor tone

(Benarroch, 1993; Dembowsky & Seller, 1995; Mancina & Mark, 1983; Smith & Kampine, 1990).

1.1.2 Central Projections of Arterial Baroreceptors

1.1.2.1 Cardiovascular Branch: Spinal Cord and Brain Stem

With their cell bodies housed in the lower ganglia of the glossopharyngeal and vagus nerve, the ascending nerve fibers of the arterial baroreceptors proceed to the caudal part of the medulla oblongata where they converge to the NTS (Berger, 1979; Gabriel & Seller, 1970; Kalia & Welles, 1980; Palkovits & Záborszky, 1977; Wallach & Loewy, 1980). The NTS exhibits extensive inhibitory and excitatory connections to other brain stem structures as part of the brain stem-based reflex circuitry. For instance, efferent connections to the nucleus ambiguus and the rostral ventrolateral medulla enclose parasympathetic and sympathetic motor neurons, respectively, that mediate the chronotropic baroreflex responses (Barman & Gebber, 1985; Bieger & Hopkins, 1987; Brown & Guyenet, 1985; Hopkins, 1987; McAllen & Spyer, 1978). Of relevance for the cardiovascular regulation are further the caudal ventrolateral medulla, dorsal motor nucleus of the vagus, several reticular nuclei and the A5 cell group which themselves receive input from and give rise to projections to several structures of the CNS (Beckstead, Morse, & Norgren, 1980; Byrum & Guyenet, 1987; Palkovits & Záborszky, 1977).

1.1.2.2 Central Nervous Branch: Mesencephalon, Diencephalon, and Cerebral Cortex

Neuroanatomical studies in rodents show that besides projections at the brain stem level, adrenergic and noradrenergic neurons of the NTS and dorsal vagal nucleus provide projections to extended parts of the CNS that include the bed nucleus of the stria terminalis, the

thalamus, hypothalamus, and amygdala (Palkovits & Záborszky, 1977; Ricardo & Koh, 1978). A major part of the afferents to the forebrain is relayed over the parabrachial nucleus and thalamus, but there are also direct connections to the insula, the septal nuclei, limbic system, and the PFC (Loewy & Spyer, 1990; Ricardo & Koh, 1978; Saper, 1982b). For instance, with regard to insular cortex, studies in the rat show that arterial baroreceptor input is transferred directly from the parabrachial nucleus and indirectly via the thalamus to the anterior and posterior insula (Cechetto & Saper, 1987; Zhang & Oppenheimer, 2000). The functional significance of the reciprocal connections between brain stem nuclei and the insula is considered to primarily lie within the integration of visceral, behavioral, and emotional responses of the organism (Dembowsky & Seller, 1995; Saper, 1982a; Sawchenko, 1983). Furthermore, all forebrain connections being reciprocal, they provide the basis for an integrative top-down control of the baroreflex (Jänig, 2006; McCloskey, 1981; Waldrop et al., 1996). In addition to these rather distinct projections, signals originating from arterial baroreceptors are extensively distributed along ascending pathways from the formation reticularis, which receives direct input from the NTS (Dembowsky & Seller, 1995; Koepchen, Langhorst, Seller, Polster, & Wagner, 1967; Langhorst, Schulz, Schulz, Lambertz, & Krienke, 1983).

1.2 Behavioral Effects of Arterial Baroreceptor Activation

Ensuing from animal testing in the first half of the 20th century, evidence accumulated that baroreceptor stimulation by (mimicked) changes in blood pressure not only affects cardiovascular parameters like heart rate and peripheral resistance, but is further associated with behavioral changes not primarily linked to the regulation of the cardiovascular system. In his studies on circulatory reflexes in dogs and monkeys, German physiologist Eberhard Koch (1932), observed reductions in motion, skeletal muscle tone and overt responses to external

stimuli when stimulating the carotid baroreceptors by an inflating balloon within the carotid sinus. Subsequent animal studies found modulatory effects of baroreceptor activation or the stimulation of the bulbar cardiovascular centers on sleep onset (Baust & Heinemann, 1967; Koch, 1932), the dampening of pain perception (Dworkin, Filewich, Miller, Craigmyle, & Pickering, 1979; Randich & Maixner, 1984), the impairment of sensorimotor functioning (Coleridge, Coleridge, & Rosenthal, 1976; Gahery & Vigier, 1974) and cortical inhibition (Bonvallet & Bloch, 1961; Bonvallet, Dell, & Hiebel, 1954; Kreindler, 1946; Magnes, Moruzzi, & Pompeiano, 1961). Behavioral effects of baroreceptor activation were largely replicated in human studies. This is true for the latency of sleep onset (Cole, 1989), pain perception (Al'Absi et al., 2005; Dworkin et al., 1994; Rockstroh et al., 1988), sensorimotor functioning (Birren, Cardon, & Phillips, 1963; Edwards et al., 2007b) as well as indices of cortical inhibition (Rockstroh et al., 1988; Walker & Walker, 1983). For instance, whereas baroreceptor stimulation exerts detrimental effects, a reduction in baroreceptor activation enhances sensorimotor functioning (Pauli, Hermsdörfer, Marquardt, Birbaumer, & Rau, 1993; Rau & Elbert, 2001). With respect to cortical measures, the contingent negative variation (CNV), an acknowledged index of response preparation (Birbaumer, Elbert, Canavan, & Rockstroh, 1990), has been found to be markedly reduced during external carotid baroreceptor stimulation (Elbert, Roberts, Lutzenberger, & Birbaumer, 1992; Rau, Pauli, Brody, Elbert, & Birbaumer, 1993). In addition, neurophysiological research indicates that baroreceptor activation exerts a general inhibitory influence on the CNS (Dembowsky & Seller, 1995; Duschek, Mück, & Del Paso, 2007; Duschek et al., 2009b; see also Bonvallet & Bloch, 1961). A more detailed delineation of previous findings relevant for the studies reported in this dissertation can be found in the introductory sections of Chapters II through IV.

Yet, several studies conducted in the 1960s and 1970s in which the natural variation in baroreceptor activity served as independent variable reported null effects for the modulation

of sensory and sensorimotor processes, which lead to a preliminary rejection of the hypothesis that baroreceptor stimulation effectively impacts on behavior (for reviews see, Carroll & Anastasiades, 1978; Velden & Juris, 1975). As most of these early studies lacked sufficient statistical power, no inferences can be drawn on the basis of these results alone (compare Edwards, Ring, McIntyre, Winer, & Martin, 2009). Furthermore, recent studies using higher sample sizes and improved timing techniques predominantly reported influences of naturally occurring variations in baroreceptor activity within the cardiac cycle of both reflex responsiveness (Edwards et al., 2007a; Schulz et al., 2009a) and response latencies of simple stimulus detection (Edwards et al., 2007b).

Recent attempts to investigate baroreceptor-related modulation of higher cognitive functions have, however, produced rather ambiguous results. In line with an inhibitory effect of baro-afferent transmission, increased baroreceptor activity was associated with lower intensity ratings regarding reflex-eliciting and affective stimuli (Garfinkel et al., 2014; Schulz et al., 2009b). However, whereas facilitating effects on decision making in the Sternberg short-term memory task (Martins, McIntyre, & Ring, 2014), and improved long-term memory performance (Moor et al., 2005) have been reported for naturally occurring increases in baroreceptor activation and pharmacologically increased baroreceptor activation during retrieval and encoding, respectively, detrimental effects on long-term memory have also been found (Garfinkel et al., 2014). Owing to the fact that study designs do not allow direct comparison, to date, no clear indications can be drawn. On the whole, studies examining the impact on higher cognition are rare and, in part, leave room for alternative explanations. Differences in memory performance associated with varying baroreceptor activity during stimulus presentation, for instance, could also be explained by impaired perceptual processing, rather than by a direct impact on the encoding process. In particular, whereas the impact on basal sensorimotor functions has been put to test by using single stimulus presentations (e.g., Edwards et al.,

2009; Saxon, 1970), so far, no studies have investigated a potential impact on those processes that control perceptual input, i.e., selection processes. Yet, considering the general dampening effect of baroreceptor activation on the CNS, direct projections from the NTS to the thalamus and PFC as well as the reticular formation (e.g., Langhorst et al., 1983; Loewy & Spyer, 1990), it is tempting to conjecture that selective attention may be modulated as well. The effective processing of relevant visual information under conditions of multiple sensory input, e.g., due to cluttered visual displays, has been associated with the inhibition of neural activity elicited by irrelevant sensory input and the amplification of processing traces associated to the relevant input (e.g., Duncan, Humphreys, & Ward, 1997). According to this model, a general inhibitory influence in phases of enhanced baroreceptor feedback might facilitate selection processes through the suppression of neural activity related to irrelevant information. Consequently, it might be reasoned that perceptual performance may be differentially affected depending on the attentional demands a given task requires.

1.3 Visual Selective Attention

Selectivity of human's perception of the outer world has long been a relevant topic in philosophy and later in psychology. In ancient times, Aristotle noted that the most intense stimulus will expel all concurrent stimuli of the same sense from conscious perception (Aristotle, trans. 1931) and in the early 19th century, Dugald Stewart reasoned that the allocation of attention to a certain object or event by suspending all other information from the mind determines the availability of information for further processing and conscious retrieval (Stewart, 1822). Already acknowledging the behavioral relevance of selectivity, Stewart's approach heralded the start of experimental research on attention and can be ranked among one of the first theories which emphasize the functionality of selective attention, rather than a

deficit due to limitations in processing capacity (see Neumann, 1991). From this perspective, selectivity of perceptual input permits goal-oriented initiation of motor responses from among a multitude of possible actions without interference from irrelevant sensory information. Thus, stimulus selection forms an important prerequisite for goal-directed and effective behavior (Allport, 1987; Rizzolatti, Riggio, & Sheliga, 1994). However, selection in everyday life as well as in laboratory tasks appears to be imperfect. This is especially apparent for situations in which deliberate behavior premises the extraction of stimuli from a complex environment followed by an adequate response out of a variety of possible actions. Here, the efficient detection and differentiation of relevant from irrelevant information is often characterized by slowed information processing and a more error-prone behavior as compared to unambiguous stimulus conditions. Research suggests that irrelevant input can interfere with the processing of target information on perceptual, conceptual, and executive processing stages (e.g., Allport, Tipper, & Chmiel, 1985; Eriksen & Eriksen, 1974). As outlined above, so far, no studies have investigated the impact of baroreceptor activity on selection. Chapters II and III cover this issue by assessing the participants' perceptual performance under conditions of high and low interference. Two distinct approaches have been implemented which are discussed in the following paragraph.

1.3.1 Selection Based on Perceptual Features

Interference on a perceptual level is classically demonstrated by congruency effects of the similarity between target and distractor information (Eriksen & Eriksen, 1974; Yeh & Eriksen, 1984). Although typically small in size compared to compatibility effects from distractors that additionally interfere on a response level, varying degrees of similarity between relevant and irrelevant information, in general, impose different requirements on the precision of selection. For instance, responses to targets are slowed when surrounded by physically dif-

ferent, as compared to identical stimuli. In addition, distractors interfere to a greater or lesser extent the more features they share with the distractor or target set, respectively (e.g., Banks & Prinzmetal, 1976; Eriksen & Eriksen, 1974; Eriksen & Schultz, 1979; Estes, 1974; Flowers, 1990; Keren, O'Hara, & Skelton, 1977; Stoffels & van der Molen, 1988; Yeh & Eriksen, 1984; but see Sanders & Lamers, 2002).

1.3.1.1 Visual Masking

Selection is further required when the perceptibility of a target stimulus is impaired by a second stimulus that follows or precedes the target in close contiguity. This reduction in the effectiveness of a visual stimulus by the presentation of a temporally and/or spatially contiguous stimulus (a *mask*) is referred to as *visual masking*. Different types of visual masking can be distinguished. Pattern masking, that is, masking by a spatially overlapping stimulus, may be performed by a mask composed of random patterns (masking by noise; Kinsbourne & Warrington, 1962), or composed of patterns resembling the target features in contour, orientation or other pictorial features (masking by structure; Breitmeyer & Ganz, 1976). By using a patterned forward mask, for instance, the perception of a second stimulus in a sequence is hampered with masking effects being most pronounced for simultaneous stimulus onsets abating monotonically with an increase in the stimulus onset asynchrony (SOA) of mask and target (Breitmeyer & Ögmen, 2006; Kolers, 1962). It is assumed that the mask interferes with the early sensory representation of the target stimulus by adding noise due to an overlap of the processing streams and the integration of both representations into a single percept (Enns & Di Lollo, 2000; Kahneman, 1968; Scheerer, 1973). In general, the neurophysiological basis of masking by pattern is assumed to be located along the retino-geniculo-cortical pathway of the visual system. That is to say, effects of masking are caused by interactions in the retina and at central sites such as the lateral geniculate nucleus (LGN), the striate and extra-striate cortex.

Masking by structure, in particular, is thought to impinge on form processing within the striate and extra-striate cortex (e.g., Breitmeyer & Ganz, 1976; Michaels & Turvey, 1979; Schiller & Wiener, 1963; Turvey, 1973). In accordance with an action site early in the visual processing stream, the degree of pattern masking is a function of the contrast of the mask, but is independent of task manipulations that target later processing stages, like the allocation of attention by variations in set size (e.g., Spencer & Shuntich, 1970). However, spatial overlapping is not a necessary precondition for masking to occur. Forms of lateral masking can be achieved by the presentation of masks that proximate but do not overlap the contours of a target stimulus. When the mask precedes the target, this masking is referred to as paracontrast (Kahneman, 1968; Stigler, 1910). Corresponding to patterned forward masking, the efficiency of paracontrast increases with enhanced mask and decreased target contrast (Breitmeyer & Ganz, 1976) and is similarly assumed to interfere with early feedforward processing of the target. In contrast to forward masking by pattern, paracontrast probably results from the inhibition of neural activity related to the target by concurrent activity from the mask input (Breitmeyer & Ganz, 1976; Kondo & Komatsu, 2000).

Chapter II utilizes interference imposed by a structured forward mask to investigate whether the efficiency of early perceptual selection is affected by baro-afferent signal transmission. In the study, a target stimulus is preceded by a patterned forward mask. Mask characteristics were adjusted in order to allow for adequate task performance, which means that masking strength was imperfect. On the basis of a pilot study (own unpublished data), the contrasts and spatial position of the stimuli were adapted in order to provide correct responses in approximately two thirds of trials (i.e., an overall accuracy of ~ 0.66) irrespective of baroreceptor activity. In the study, mask and target sequence were presented during phases of high and low baroreceptor activity. If the ability of the visual system to select between two temporally overlapping processing streams is sensitive to baro-afferent signal transmission, the de-

tection performance in response to the target stimulus should vary as a function of the level of baroreceptor activation.

1.3.1.2 Similarity Effects

A different approach on selection processes is taken in the study reported in Chapter III. As stated above, selection is also required when a target is embedded in an array of simultaneously presented distractors. Accordingly, interference was engendered by presenting a target stimulus horizontally flanked by stimuli of different figural similarity to the target and of different homogeneity to each other. It is an established finding in attention research that the similarity between targets and distractors as well as the similarity among distractors correlates with the degree of interference distractors impose. On the one hand, stronger interference is imposed by distractors that are similar to the target and less interference is evoked by distractors that can easily be distinguished from the target (e.g., Bjork & Murray, 1977; Estes, 1972).¹ On the other hand, interference from distractors being highly similar to one another is negligible compared to interference imposed by physically diverse distractors (e.g., Beck, 1966; Gordon, 1968).

According to the *attentional engagement theory* (Duncan & Humphreys, 1989, 1992) both forms of similarity affect the efficiency of target selection by determining the match with a target template (*interalternative similarity*) and by facilitating perceptual grouping (*within-display similarity*). A target template denotes an internal image or description of target-relevant stimulus information. With regard to the interalternative similarity, it is suggested

¹ On a semantic level, however, similarity can also provide facilitation of target processing and retrieval processes. Here, non-targets that are semantically related to the target item can cause semantic priming. As the distractors in Chapter III only vary in the degree to which they correspond perceptually, but not semantically, a facilitation effect of dissimilar distractors is not to be expected.

that the more similar members of the same category, target or distractor are, and the more dissimilar members of different categories are, the more straightforward the comparison of the display stimuli with the target template proceeds in order to detect or identify the target (see also Shepard & Podgorny, 1986). In a second step, within-display similarity determines whether perceptual grouping of presented stimuli facilitates or hampers the suppression of distractors and hence whether selection can proceed efficiently. In detail, whether stimuli are consciously processed and control behavior is determined by selection weights assigned to each stimulus in a display. Selection weights are assigned in dependence of the stimulus' match or mismatch to the target template. Due to a linkage of selection weights, weights of perceptually grouped stimuli are propagated among a group of stimuli. In the case of the classification of a stimulus as distractor its selection weight is reduced to zero, which prevents the stimulus from reaching behavioral relevance. Via weight linkage, the suppression of one distractor can be disseminated among the perceptual group and hence distractors can be suppressed in parallel (*spreading suppression*). The degree to which suppression is spread directly relates to the similarity among distractors and consequently the strength of distractor grouping. Furthermore, it is assumed that a change of selection weights in one perceptual group leads to an inverse change in stimuli not clustered to the same group. As a consequence of a reduction in selection weights assigned to perceptually grouped distractors, the relative amount of weights of non-suppressed stimuli increases and the probability of target detection or identification accrues accordingly. The degree of selection weight increase is inversely related to the similarity between the target and distractors, i.e., the strength of perceptual grouping of the target to the distractors. In summary, according to the attentional engagement theory, selection efficiency is influenced by the strength of perceptual grouping between distractors as compared to the strength of grouping between targets and distractors. In a search display, selection can operate on a large group of stimuli in parallel when targets and distrac-

tors are unambiguously organized into different groups resulting in fast reaction times (RTs) and high accuracy rates. When grouping strength is reduced, however, efficiency of the target search is hampered as increasingly smaller groups have to be processed separately. In other words, search has to proceed in a serial manner which results in longer RTs and a higher rate of incorrect responses.

Chapter III investigates the effect of natural variations in baroreceptor activation on selection efficiency required by stimulus conditions under which task-relevant information is encompassed by task-irrelevant information by manipulating stimulus similarity in an adapted visual search task. Adjustments to classic search tasks (compare Treisman, Sykes, & Gelade, 1977; Wolfe, 1994) were twofold. First, in order to systematically align the stimulus presentation to phases of high and low baroreceptor stimulation within the cardiac cycle (see Chapter 1.4.2) the display size, i.e., the number of stimuli presented simultaneously, was held constant, and the presentation duration was fixed and reduced to a minimum (see Chapter 3.3 for a detailed description of the experimental design). Second, in order to warrant that selection is based on focal attention, the visual search task was further modified. Whereas the mere detection of a stimulus does not require the allocation of attention, focused attention is necessary for the discrimination and identification of stimuli (e.g., Sagi & Julesz, 1985a; Sagi & Julesz, 1985b). Successful task performance, therefore, required the identification and classification of a target. Based on the attentional engagement theory (Duncan & Humphreys, 1989, 1992), selection efficiency was operationalized as the difference in performance between homogeneous and heterogeneous distractor conditions. Heterogeneous distractors were defined by a high similarity between targets and distractors and a low similarity between distractors. By contrast, homogeneous distractors were characterized by a low similarity between targets and distractors and a high similarity between distractors. Search was expected to be maximally difficult with heterogeneous distractors. Furthermore, selection efficiency was assessed as a

function of baroreceptor activity within the cardiac cycle. If selection is sensitive to baroafferent signal transmission, selection efficiency should vary between phases of high and low baroreceptor stimulation.

1.3.2 Drawing the Line: Automatic and Controlled Distractor Processing

Whereas Chapters II and III attend to early selection processes, boundary conditions of baroreceptor-mediated effects are still to be defined. For this purpose, the study reported in Chapter IV investigates whether baroreceptor activity impacts on selective attention when interference not only operates on a perceptual, but also on a response-related processing stage. More importantly, by comparison of controlled selection, as indexed by the Negative Priming effect, with automatic distractor processing, indexed by distractor-response binding, the generalization of baroreceptor-mediated effects on the processing of irrelevant information as such is examined.

Stringent to varying degrees, a range of theoretical approaches and empirical studies address a qualitative distinction between cognitive processes according to the automaticity with which they are executed. A strong distinction of automatic and controlled processes was made in a seminal paper by Shiffrin and Schneider (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). According to their approach, automatic and controlled processes can be differentiated by a dichotomy of certain features characterizing the information processing. Whereas controlled processing of stimuli, for instance, the search for a particular object, can deliberately be initiated and modified by the acting person, it also demands attentional capacity and is dependent on the stimulus load, i.e., the mathematical product of targeted and distracting stimuli that are presented to the visual system. Controlled processing, further, occurs in a serial manner and is hence limited in the quantity of items that can be processed simulta-

neously. In contrast, automatic processing, for instance the detection of an arbitrary stimulus event, can neither be easily ignored nor prevented as it is based on routines stored in long-term memory. Automatic processes only bind attention in case a task relevant stimulus is presented and requires further processing, are independent of stimulus load and allow the parallel processing of multiple stimuli. Currently a total of nine features distinguishing automatic from controlled processes has been identified. These are the intention to initiate a process, its goal directedness, goal dependency, as well as the controllability and autonomy of a process and, further, its dependency on stimulus conditions, the degree of consciousness about a process, as well as its efficiency and speed of execution (Moors & De Houwer, 2006). The clear distinction between automatic and controlled cognitive processes follows James (1890/1950), who categorized attention processes as those that work non-voluntarily (i.e., stimulus-driven or *reflex-like* processes) and are completed effortless, and those requiring active and voluntary initiation. Considered a conceptual simplification, more recent approaches, however, endorse a gradual or relative approach that views automaticity as a continuum and characterizes processes by its relative degree to which relevant features like goal-relatedness or intention, awareness, efficiency and control are met. Furthermore, different functional trajectories of the features and conceptual distinctions have been acknowledged. Several authors therefore recommended to consider features of automaticity separately and to describe them in relation to standards like other processes or states of practice (Logan, 1985; Moors & De Houwer, 2006; Shiffrin, 1988).

Chapter IV not only tries to manifest previous findings of baroreceptor modulation of selection by using a prime-probe paradigm, but further investigates whether a line may have to be drawn between the impact on relatively controlled and automatic processes. For this purpose, two measures representing the processing of distractor information which vary in the extent to which they are executed automatically were implemented within a single paradigm.

On the one side of the continuum Negative Priming (NP) was assessed, representing the after-effect of previous selection processes, and on the other side of the continuum distractor-response binding (DRB), representing the encoding and retrieval of stimulus-response (S-R) bindings. As will be outlined in the following two paragraphs, previous research shows that NP and DRB differ with respect to those features that distinguish between controlled and automatic processes. Whereas NP predominates in controllability, the encoding of distractor-response bindings displays a relatively autonomous process which proceeds unintentionally and is mainly stimulus-driven in that it does not require the allocation of attention to or the conscious processing of distractor stimuli to be integrated into S-R bindings.

1.3.2.1 Negative Priming

The NP effect constitutes a widely used and robust measure of selective attention (for reviews see Fox, 1995; Frings, Schneider, & Fox, 2015; May, Kane, & Hasher, 1995; Tipper, 2001). First observed by Dalrymple-Alford and Budayr (1966), who used a modified Stroop task (Stroop, 1935), the NP effect denotes slower and less accurate responses to previously presented but formerly irrelevant stimuli compared to stimuli that have not been encountered before. In the NP paradigm a prime-probe sequence of simultaneously presented target and distractor stimuli is employed. In the ignored-repetition (IR) condition distractor stimuli of the prime correspond to the target of the probe. Probe responses of the IR condition are compared to responses within a control condition which is characterized by a complete alternation of stimuli between prime and probe (Tipper, 1985). The detrimental performance on IR trials is assumed to index direct consequences of the target selection in the prime. Originally attributed to the outlasting inhibition of the former distractor representation (Tipper, 1985, 1992) or its response (Neill, 1977; Tipper & Cranston, 1985), later accounts regarded retrieval processes as underlying mechanism. Especially, by referring to the *instance theory of automaticity*

(Logan, 1988), the reencounter of a previous distractor has been suggested to retrieve previously encoded information attached to the internal representation of the stimulus classifying the stimulus as a distractor (Neill & Valdes, 1992; Neill, Valdes, Terry, & Gorfein, 1992) or of the previously executed but probe-incompatible response (Rothermund, Wentura, & De Houwer, 2005). Furthermore, slowed responses in IR trials have been accounted for by an incompatibility between the information processes required in the prime and in the probe (Leboe, Whittlesea, & Milliken, 2005; Neill & Mathis, 1998) or a partial match between the representation of the prime encounter in memory and the perceptual representation of the probe, which necessitates a controlled, and as such more time consuming processing of the probe display in comparison to a completely new or completely repeated stimulus configuration in the control condition (Milliken, Joordens, Merikle, & Seiffert, 1998). However, a synopsis of the empirical evidence suggests that the NP effect likely reflects the interaction of several processes including inhibition-based and retrieval-based mechanisms (Fox, 1995; Frings et al., 2015; Mayr, Buchner, & Dentale, 2009; Neill, 2007). Accordingly, the inhibition of irrelevant information in the prime may facilitate the selection of the prime target. Additionally, retrieval processes due to the subsequent presentation of the distractor within the probe may trigger the reactivation of its previous processing as distractor stimulus (Tipper, 2001). Hence, by accounting for the functional complexity of selection processes involved, the NP effect constitutes a suitable measure for action control by selective attention (Frings et al., 2015).

A review of the research literature further shows that the manifestation of the NP effect underlies a certain degree of controllability as it can actively be altered by the implementation of cognitive strategies with regard to context information of a task as well as characteristics of the probe response. Particularly, selection processes operating during probe processing may be altered or terminated when expendable or detrimental to efficient task perfor-

mance. For instance, when the processing of the probe is easy and rapidly executed no decrement in performance on IR compared to a control condition is observed (Allport et al., 1985; Lowe, 1979; Milliken et al., 1998). Hence, controlled selection might be replaced by fast and automatic analysis of the probe display when processing difficulty of the probe is low (Frings & Spence, 2011; Moore, 1994). Furthermore, context information of a task which makes cognitive strategies applicable influences NP. This is the case when the prime and the probe responses are probabilistically related as can be seen by a larger NP effect when contingencies between the prime and probe prompt to a repetition of the prime response to enhance performance in the probe. In other words, a lower portion of IR trials or a higher portion of trials with targets repeated from prime to probe (attended repetition, AR) have been found to be associated with increased NP (Frings & Wentura, 2008; Kane, May, Hasher, Rahhal, & Stoltzfus, 1997; Lowe, 1979). In addition, an increase in the proportion of IR trials, i.e., an increase in repetitions of prime distractors as probe targets, is associated with an absence of NP effects when participants are aware of the contingency (Frings & Wentura, 2006; Milliken & Rock, 1997). Several experiments demonstrated even a positive priming effect when participants were able to report a clear contingency between the prime distractor and the probe target, whereas participants who were unaware showed a regular slowing of RTs in IR trials (Driver & Baylis, 1993; Hasher, Stoltzfus, Zacks, & Rypma, 1991; Milliken, Lupianez, Debner, & Abello, 1999). To date, it is not clear, however, if contingency information has to be consciously represented, although it seems that contingency information does not necessarily have to be explicitly verbalized in order to modulate NP (Frings & Wentura, 2006; Miller, 1987). Taken together, contingency effects on NP demonstrate that just like selective attention in other tasks, processes underlying the NP effect can actively be controlled by the build-up of expectancies (Driver & Baylis, 1993; Frings & Wentura, 2006; for expectancy effects in other selective attention tasks see also Logan & Zbrodoff, 1979; Miller, 1987;

Neely, Keefe, & Ross, 1989). Consequently, by defining control over a mental process as the existence of a causal relation between an aspired behavioral goal and its effect (see Dennett, 1984; see also Bargh, 1994), the NP effect qualifies as a suitable measure for controlled processing of distracting information.

1.3.2.2 Distractor-Response Binding

Automatic information processing in general is assumed to be achieved with progressing practice in consistent settings (e.g., Schneider & Fisk, 1982). More precisely, it is assumed that by the accumulation of the same sensory encounter, traces in episodic memory are established that can later be retrieved when a part of those representations is encountered again. The automatic retrieval as a substitute of initial algorithmic stimulus processing and response selection permits fast and efficient responding (Logan, 1988). Sensory features of an encounter are sketched as to become integrated and stored into an *object file* (Kahneman, Treisman, & Gibbs, 1992). The instantaneous integration of visual features includes the temporal linkage between representations of low level visual features and has been attributed to the temporal synchronization in the gamma frequency range of neuron populations controlled by the muscarine-cholinergic neurotransmitter system (Colzato, Erasmus, & Hommel, 2004; Colzato, Raffone, & Hommel, 2006). Furthermore, when motor information is available, stimulus and action features are integrated into an *instance* (Logan, 1988) or *event file* that will be retrieved as a whole as soon as a part of the representation is reencountered (Hommel, 2004; Hommel, Müssele, Aschersleben, & Prinz, 2001). The formation of S-R bindings can be achieved after a single encounter with a stimulus (e.g., Hommel & Colzato, 2009; Horner & Henson, 2009) and is assumed to be mediated by the dopaminergic neurotransmitter system (Colzato & Hommel, 2008). S-R bindings can be demonstrated by the interaction of stimulus and response repetitions. In a prime-probe paradigm the repetition of a stimulus feature com-

pared to non-repetitions leads to benefits in RT when the same response as during the first stimulus encounter is executed. Slowed responses, on the other hand, occur when a stimulus is repeated while a different response is demanded (Hommel, 1998, 2004).

The integration of stimulus information into an event file does not necessarily proceed in a goal-directed, intentional or controlled manner as even response-irrelevant stimuli, i.e., distractors, are bound (Frings, Rothermund, & Wentura, 2007; Rothermund et al., 2005). *Distractor-response binding* (DRB), indexed by the interaction of distractor and response repetitions, is a robust finding. For instance, responses are integrated with distractors of different modalities (e.g., Frings et al., 2007; Mayr et al., 2009; Moeller & Frings, 2011) as well as cross-modally (Frings, Moeller, & Rothermund, 2012).

Furthermore, the encoding of stimuli and its integration into an event file is assumed to operate mainly stimulus-driven in that the allocation of attention to the encoded stimuli is not a necessary precondition for neither S-R bindings of task-relevant nor task-irrelevant stimuli to evolve (e.g., Hommel, 2005; Hommel & Colzato, 2004; Moeller & Frings, 2014). Rather, temporal contiguity, the spatial overlap of features or perceptual grouping into an object are sufficient parameters for the S-R bindings to be formed (Frings & Rothermund, 2011; Moeller et al., 2012; van Dam & Hommel, 2010). Furthermore, when the task prompts the classification into valence categories, the integration of affective words is confined to distractors matching the target word in valence (Giesen & Rothermund, 2011). As valence opposed to other semantic categories is processed and matched unintentionally (Klauer & Musch, 2002), this finding does not contradict the large portion of research indicating that the binding of features proceeds automatically. However, the finding suggests that at least the binding of affective stimuli is not merely stimulus-driven but further driven by affective congruency. The extent of event-file retrieval, however, is modulated by the task relevance of potential retrieval cues. For instance, binding effects tend to be larger when integrated stimulus features vary

within task-relevant stimulus dimensions. This modulatory effect emerges irrespective of whether a task set is construed before or after the formation of S-R bindings and is therefore likely to affect the retrieval, but not the formation of S-R bindings (Hommel, 1998; Hommel, Memelink, Zmigrod, & Colzato, 2014). Similarly, when relevant and irrelevant information is not presented to form a strong perceptual group or are even part of different tasks, the allocation of attention to the distractor is a necessary precondition for the event file retrieval but not the encoding (Moeller & Frings, 2014). In contrast, when targets and distractors can easily be grouped together, such as when they are aligned horizontally with minimal inter-contour distance, task-relevant and task-irrelevant distractors elicit comparably strong binding effects (Giesen, Frings, & Rothermund, 2012). This suggests that when stimulus conditions are given that allow for perceptual grouping to occur, S-R bindings emerge irrespective of the strategic value a stimulus might have and that DRB is insensitive to the degree of interference distractors induce. Following Frings et al. (2007) and Giesen et al. (2012), the study presented in Chapter IV measured DRB in a prime-probe paradigm with letter stimuli presented horizontally in order to promote perceptual grouping of the stimuli.

1.3.3 Mechanisms of Selective Attention: Locus of Inhibitory Control

The research reported in Chapter V of the dissertation is distinct from the previous since modulatory effects on selection processes are not in the focus. Instead, the study focuses on electrocortical correlates of distractor processing. In that the study attempts to locate the source of distractor inhibition within the information process by separating primarily sensory from response-related processing stages. This line of research forms an organic part of the topic of the impact of baroreceptor activity on perceptual selection and controlled distractor processing as previous research implied different processing stages to be targeted by baroreceptor-mediated inhibition and inhibition as underlying mechanism of attention.

The results reported in Chapters II through IV indicate the impact of distractors on performance to be contingent on transient changes in baroreceptor activity. Nevertheless, so far, only a few studies have been investigating which processing stage(s) are affected by baro-afferent signal transmission. Yet, two studies on the processing of simple stimuli of different modalities as well as on the magnitude of the startle eye-blink reflex point to the localization of attenuating effects of baro-afferent transmission on a sensory processing level (Edwards et al., 2007b; Schulz et al., 2009b). The locus of interference control by distractor inhibition within the information process, however, remains undetermined. Namely, inhibition on a response level has been demonstrated for the execution of overt and covert shifts of attention (Kingstone & Pratt, 1999), but whereas there is distinct evidence for the suppression of motor responses, findings on the suppression of perceptual or semantic stimulus processing are rather mixed and have sometimes been dismissed entirely (MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003).

With regard to the studies reported in this dissertation, the manipulations of selection difficulty reported in Chapters II and III are very likely to act upon early visual selection, rather than upon response-related conflicts (see above). Within the visual system, neurophysiological foundations have been identified for both the facilitation of relevant and the inhibition of irrelevant sensory input. For instance, in primates, neurons within the occipital (V4) and temporal (IT) cortex that represent stimuli at unattended locations display reduced activity compared to identical sensory information at attended locations (Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999). The contribution of inhibition within the occipital cortex to selective attention was later confirmed for human participants (Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000). Yet, with regard to the inhibitory processes underlying NP operationalized as a measure of controlled distractor processing in Chapter IV the situation is less clear. Inhibition is, in addition to other processes like episodic retrieval during the

probe, very likely to play a major role in selection during the prime (Frings et al., 2015), but may be limited to a response-related processing stage. For instance, differential effects for IR and control trials on early sensory event-related potentials (ERPs) have been ambiguous (Gibbons, 2006; Gibbons, Rammsayer, & Stahl, 2006). The same is true for later ERP components like the P3 (Behrendt et al., 2010; Kathmann, Bogdahn, & Endrass, 2006). On these grounds, Chapter V tries to separate perceptual from response-related processing stages related to distractor inhibition as an integral component of selective attention. For baroreceptor-mediated effects on controlled distractor processing to potentially operate on the same stage of the information process like the inhibition of irrelevant information tapped by NP, distractor inhibition would have to be present on a pre-motor, i.e., perceptual or semantical, processing stage.

1.3.4 Approaches to Inhibition

As outlined above, NP reflects cognitive control processes involved in selective attention but is not qualified as a selective measure of distractor inhibition (Frings et al., 2015). Nevertheless, pure effects of distractor inhibition can be captured by performance benefits associated with the repetition of distractor stimuli. The repetition of distractors from the prime to the probe display provokes small benefits in RTs (Neumann & DeSchepper, 1991). This effect is independent of the relationship between the distractor and the target and cannot be explained by alternative mechanisms like perceptual priming or feature mismatch. The effect of distractor repetition can be studied by implementing the distractor relationship (repetition or change) independently of the target relation (repetition or change) between the prime and the probe (Frings & Wühr, 2007; Giesen et al., 2012). The benefit of distractor repetitions may be explained according to inhibition theories of selective attention (Houghton & Tipper, 1994; Tipper & Cranston, 1985). Accordingly, outlasting inhibition of the distractor represen-

tation facilitates the selection of the target in the probe, but appears to be independent of the retrieval of S-R bindings (e.g., Giesen et al., 2012; also see chapter V for a discussion).

In order to obtain a specific index of distractor inhibition, a prime-probe design was used to assess the impact of distractor repetitions on overt manual responses and the lateralized readiness potential (LRP) of the EEG. In order to separate influences on a pre-motor processing level from the response-related processing level, LRPs were divided into a sensory portion of the LRP, i.e., stimulus-locked LRP (S-LRP), and the motor component of the LRP, i.e., response-locked LRP (R-LRP). According to the assumption of selective attention via the inhibition of distractor representations, a shorter stimulus processing time, reflected by the S-LRP associated with distractor repetitions was predicted to be observed.

1.4 Research Strategies for the Assessment of Baroreceptor-mediated Effects on Human Behavior

A multitude of methodological strategies has been utilized since the outset of investigations into baroreceptor-mediated effects on human behavior approximately five decades ago. In this, two broad main lines of research can be distinguished. They comprise, on the one hand, the experimental manipulation of baroreceptor stimulation which employs superficial, i.e., exogenous force on baroreceptors and, on the other hand, the utilization of natural variations in strain exerted on the baroreceptors within the course of the cardiac cycle (for reviews, see Elbert & Rau, 1995; Rau & Elbert, 2001; Vaitl & Gruppe, 1991). The latter will henceforth be denoted as cardiac cycle time paradigm.

1.4.1 Experimental Modulation of Arterial Baroreceptor Stimulation

Subsumed under the first category is, among others the application of pharmacological substances impinging on vasoconstriction and vasodilatation. For instance, the effects of sympathomimetics like phenylephrine and midodrine on the processing of painful stimulation (Duschek, Heiss, Buechner, & Schandry, 2009a; Larbig, Elbert, Rockstroh, Lutzenberger, & Birbaumer, 1985; Rockstroh et al., 1988) and long-term incidental visual memory (Moor et al., 2005) have been investigated. Conditions of increased sympathetic nervous system (SNS) activity can then be compared to the infusion of a placebo such as saline, or of vasodilators like sodium nitro-prusside (e.g., Moor et al., 2005; see also Chamberlain, Müller, Blackwell, Robbins, & Sahakian, 2006). Furthermore, neck suction devices have widely been used to directly stimulate baroreceptors located in the carotid sinus by exerting extra-cervical pressure. In the context of the Phase Related External Suction (PRES) technique, transmural pressure of the carotid sinus is manipulated by the application of brief volleys of either negative or positive pressure (Eckberg, Cavanaugh, Mark, & Abboud, 1975; Rau, Elbert, Geiger, & Lutzenberger, 1992). As baroreceptors do not respond to changes in blood pressure as such, but rather to variations in strain exerted on the vessel wall (Angell-James, 1971; Eckberg & Sleight, 1992), the application of negative pressure is suitable for the amplification of intra-cycle oscillations in blood pressure. In the experimental condition, the variation in baroreceptor stimulation within the cardiac cycle is augmented by the exertion of negative pressure during the ventricular systole, simulating a steep rise and large amplitude of an arterial blood pressure increase, and positive pressure during the diastole to reinforce the inhibition of the receptors. As control serves the reverse application scheme in that negative pressure is applied during the diastole and positive pressure during the systole (Rau et al., 1992). As outlined above, with this technique differential effects have been found for spinal and brain stem-based reflexes (Nyklíček, Wijnen, & Rau, 2005; Rau, Brody, Brunia, Damen, & Elbert, 1993), the

processing of pain (Al'Absi et al., 2005; Droste et al., 1994; Rau et al., 1994) as well as sub-cortical and cortical activity (Basile et al., 2013; Brody et al., 1997; Elbert, Rockstroh, Lutzenberger, Kessler, & Pietrowsky, 1988).

Both techniques discussed so far have several deficits with regard to its specificity, its durability, as well as to its secondary effects. On the one hand, the application of neck pressure via the PRES device provides a high level in specificity as only carotid baroreceptors, but no other circulatory parameters are targeted directly. At the same time, however, the omission of other baroreceptor sites from stimulation can concomitantly be seen as one of the technique's major weakness. Specifically, whereas carotid baroreceptor activity is controlled effectively, delayed alterations in aortic baroreceptor activity due to carotid baroreflex-induced changes in circulation, i.e., heart rate deceleration and vasodilatation, can neither be controlled, nor accounted for (Rau & Elbert, 2001). In addition, application of the PRES technique precludes the evocation of long-term effects. As a consequence, behavioral effects qualified as object of investigation are noticeably constrained. On the other hand, the investigation of long-term effects can be considered a valuable asset of pharmacological agents, but its binding sites are rather unspecific. This is true for norepinephrine, which affects various organ sites due to its affinity to different receptor (sub-)types (Guimarães & Moura, 2001). For instance, the administration of SNS-activating substances may not only elevate the arterial blood pressure level, but also activate the peripheral SNS and, as a consequence, cause physical symptoms like palpitations (Schächinger, Weinbacher, Kiss, Ritz, & Langewitz, 2001). Furthermore, although the cerebral vasculature is sparsely populated by α -adrenoceptors and the extent of sympathetic innervations is lower than that of the systemic vasculature (Bevan et al., 1998), cerebral arteries exhibit, even if limited in its extent, clear changes in tonus due to increases in SNS activity (Bevan, Bevan, & Duckles, 1980; Toda, 1983). In addition, sympathetic cerebral influences may act indirectly through interactions with other neuronal systems

(Guimarães & Moura, 2001). Nitric oxide, for example, besides passing the blood-brain barrier (Lawther, Kumar, & Krovvidi, 2011; Thiel & Audus, 2001) increases its permeability when released by the vasodilator sodium nitroprusside (Bates, Baker, Guerra Jr, & Harrison, 1991; Lipton et al., 1993), and regulates capillary blood flow through its affinity to chemoreceptors of brain vascular pericytes (Ballabh, Braun, & Nedergaard, 2004; Bergers & Song, 2005). As a consequence, effects induced by pharmacological substances may interfere with task performance irrespective of changes in baroreceptor activity. It needs to be acknowledged at this point that confounds may in part be overcome by elaborate study designs. Moor et al. (2005), for instance, successfully separated the effects of peripheral SNS and blood-pressure induced baroreceptor activity by comparative administration of epinephrine, esmolol hydrochloride, norepinephrine, and nitroprusside sodium. Nonetheless, strict pharmacological controls require a complex study protocol and may not always be feasible in view of ethical constraints (Rau & Elbert, 2001).

In contrast, the systemic manipulation of body position offers a non-invasive technique that reliably alters circulatory parameters without simultaneously affecting central nervous functions (Vaitl, 1989). Contingent upon the organism's alignment in space, blood flow is differentially exposed to gravitational pull. In order to continuously preserve perfusion of peripheral and central tissues, in response to pressure changes, autonomic and central nervous structures as well as humoral factors interact through complex pathways. In particular, changes in stimulation of arterial and cardiopulmonary baroreceptors lead to modifications in vagal activity and sympathetic tone, which cause direct adjustment of blood pressure by targeting the heart rate and peripheral resistance (Sandler, 1980). Accordingly, Vaitl (1989) introduced the passive tilting-technique for the examination of extra-cardiovascular effects of baroreceptor activation which provokes relatively long-lasting changes in blood pressure and

heart rate. Variations in body orientation are obtained via a pneumatically controlled tilt table, which permits changing the participants' body posture without any active movement.

Long known among researchers interested in the effects of orthostatic stress, previous reports demonstrated marked cardiovascular changes when placed in perpendicular, as compared to supine body position. Notably, due to venous pooling (the accumulation of blood in the veins of the buttocks, pelvis, and lower extremities) extreme tilt angles provoke a decrement in systolic pressure (Katkov & Chestukhin, 1980), stroke volume, and consequently in cardiac output (Bestler, Schandry, Weitkunat, Keller, & Bader, 1989; Tuckman & Shillingford, 1966; Wieling, 1988; Witzleb, 1993). Importantly, a reduction in cardiac output evokes baroreceptor unloading, causing an inhibition and activation of parasympathetic and sympathetic influence on the sinus node, respectively (Bestler et al., 1989; Stafford, Harris, & Weissler, 1970; Tuckman & Shillingford, 1966; Wieling, 1988). Alterations in baroreceptor activity and subsequent reduction in afferent signal transmission can therefore be indexed by a counter-regulatory increase in heart rate, which further down-regulates initial changes in arterial blood pressure (Rushmer, 1976; Sandler, 1980). Considering the opposite spectrum while aiming at enhanced baroreceptor stimulation, head-down tilting leads to a shift of venous blood from peripheral vessels to the torso. As a consequence, increased left ventricular pre-load, mainly due to circulatory changes within the capacity vessels, accelerates pre-contractile stretching of the myocardium. The subsequent enhancement in stroke volume leads to a greater stimulation of arterial baroreceptors as is indexed by a primarily vagally mediated decrease in heart rate and peripheral resistance (Bestler et al., 1989; Robinson, Epstein, Beiser, & Braunwald, 1966; Sandler, 1980; Smith & Kampine, 1990).

In a series of experiments, Vaitl (1989) confirmed stable changes in blood pressure and heart rate in response to a passive head-up tilt of +45° for a duration of 30 minutes; distinguishing the method suitable for the investigation of long-term effects of changes in baro-

receptor activation. Taking this idea further, Vaitl and Gruppe (1990, 1992) found increased power within the theta band of the spontaneous EEG at occipital, parietal and central sites associated with higher levels of baroreceptor activity induced by head-down tilt. An inverse relationship between heart rate and theta power further strengthens the involvement of baroreceptor activation in this effect. Considering a lack of the modulation of other frequency spectra as well as functional and behavioral correlates of theta (see Schacter, 1977), the results again implicate an inhibitory impact of baroreceptor loading on cortical excitation.

An advantage of the modulation of baroreceptor stimulation by the tilting procedure lies within the non-invasive utilization of physiological regulatory mechanisms of the human organism which can neither be achieved by pharmacological interventions nor by neck suction (Vaitl, 1989). Nevertheless, the application of extreme tilt angles provokes significant secondary effects like markedly diminished venous return from cerebral and facial circulation during head-down tilt, comparably large pressure changes as well as reduced ejection periods during head-up tilt (Bestler et al., 1989; Katkov & Chestukhin, 1980; Naylor, Chow, McLean, Heard, & Avolio, 2005; Stafford et al., 1970). On this account, it is advisable that researchers apply small inclination angles whenever possible. Along these lines, Iida et al. (1999) demonstrated alterations in baroreflex gain for a $+6^\circ$ head-up and a -6° head-down tilt.

In summary, subtle inclination angles provided, the application of positive and negative tilting angles on the reclined participant represents a qualified tool for the systematic reduction and increase in baroreceptor activity, respectively, and was therefore also implemented in the study reported in Chapter IV.

1.4.2 Natural Variations Within the Cardiac Cycle

During rest, arterial baroreceptors display an alternating activation pattern. More precisely, with the upstroke and during the plateau of the arterial pressure wave with each ventricular systole, vessel walls of the arteries are stretched, causing the deformation and hence activation of arterial baroreceptors (Angell-James, 1971; Bronk & Stella, 1932, 1934). The time interval of baroreceptor activation within each cardiac cycle can be estimated by means of the pulse transit time and the firing characteristics of the baroreceptors. The pulse pressure wave arrives at the aortic arch and carotid sinus at approximately 90-100 and 140-150 ms after the R wave of the electrocardiogram (ECG), respectively, and prevails at a systolic pressure level for approximately 250 ms (Hill & Merrifield, 1976; Kroeker & Wood, 1955; Ring, Liu, & Brener, 1994; Stafford et al., 1970). The temporal firing pattern of the baroreceptors parallels the pulse pressure wave. Hence, it is characterized by an immediate receptor activation when the systolic pressure threshold is reached and an immediate firing cessation when the pressure wave levels off (Bronk & Stella, 1932; Eckberg & Sleight, 1992; Landgren, 1952). In sum, the aortic and carotid baroreceptor activation interval ranges from approximately 90 to 390 ms after the R wave, with compound activity from 140 to 340 ms after the R wave (see also Edwards et al., 2009).

Pulsatile discharge patterns of the receptors are further relayed to brain stem neurons of the NTS and forwarded to the reticular formation as well as the amygdala with neurons of the latter two structures displaying a decrease in the discharge frequency with increases in baroreceptor activity (Dembowsky & Seller, 1995; Lambertz, Schulz, & Langhorst, 1995; Langhorst et al., 1983; but see Koepchen et al., 1967). As a consequence, the impact of natural oscillations in baroreceptor activity provides a suitable technique for the investigation of baroreceptor-mediated effects on cognition whenever paradigms with brief stimulus durations

can be utilized. Furthermore, although weaker effects than for exogenous baroreceptor stimulation are to be expected (see Rau et al., 1992), differential effects on carotid and aortic baroreceptors not under the control of the experimenter, as would be the case with artificial stimulation, can be circumvented. Accordingly, the cardiac cycle time paradigm was implemented in the studies reported in Chapters II and III.

Chapter II

Cardiac Cycle Time Effects on Mask Inhibition

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2.1 Abstract

Research on the interaction of the cardiovascular and the central nervous system has demonstrated inhibitory effects associated with baroreceptor stimulation. One way of examining baroreceptor influence on behavior and central nervous processes is by making use of naturally occurring variations in baroreceptor stimulation in the course of the cardiac cycle. In terms of perceptual and sensorimotor processes, until today, research has focused primarily on cardiac cycle time effects on the perception of and reaction to simple stimuli. The present study is the first to investigate modulatory effects of variations in baroreceptor activity in the context of a more complex stimulus configuration using a visual masking task in which a target has to be selected against an interfering mask. The results suggest that baroreceptor stimulation enhances inhibitory processes needed to solve perceptual interference.

2.2 Introduction

Ever since animal experimentation revealed inhibitory effects of carotid sinus stimulation not only on the autonomic but also on the central nervous system (e.g., Bonvallet, Dell, & Hiebel, 1954; Koch, 1932; Kreindler, 1946) several ways of research on circulation-brain interaction in humans have been pursued (for a review, see Vaitl & Schandry, 1995). The loading and unloading of carotid and aortic baroreceptors and its neural connectivity was identified as a mechanism mediating effects on cognition (Elbert & Rau, 1995; Rau & Elbert, 2001). In particular, it could be shown that, by and large, baroreceptor activation exerts inhibitory effects on cortical structures and diverse functions of the organism (Dembowsky & Seller, 1995). Accordingly, stimulation of the baroreceptors does not only reduce cardiovas-

cular parameters, i.e., heart rate, heart contractility, peripheral resistance (Brownley, Hurwitz, & Schneiderman, 2000; Davos, Davies, & Piepoli, 2002), but also dampens sensory and motor functions, such as pain perception, reflexes and sensorimotor control. A reduction in baroreceptor activation, on the other hand, results in an enhancement of sensorimotor functioning (e.g., Dworkin et al., 1994; Pauli, Hermsdörfer, Marquardt, Birbaumer, & Rau, 1993; Rau, Brody, Brunia, Damen, & Elbert, 1993). One way of examining central influences of arterial baroreceptors is by making use of naturally occurring variations in baroreceptor stimulation during the course of the cardiac cycle. Arterial baroreceptors, located within the vessel walls of the aortic arch and the carotid sinus show a pulsatile excitation pattern which parallels the pulse pressure wave, and peaks as the systolic pressure wave reaches the aortic and carotid sinus, respectively (Dembowsky & Seller, 1995; Mancia & Mark, 1983). Several studies demonstrated variations in cortical activity associated with different cardiac cycle phases (e.g., Cohen, Lieb, & Rist, 1980; Lacey & Lacey, 1970; Sandman, Walker, & Berka, 1982; Walker & Sandman, 1982). Furthermore, effects of stimulus presentation time within the cardiac cycle on sensorimotor functions could be shown for different sensory modalities and measures. For instance, simple reaction times in response to auditory stimuli were faster for stimuli presented during the P wave of the electrocardiogram (ECG), i.e., during the ventricular diastole, as compared to stimuli presented during earlier phases of the cardiac cycle (cardiac systole; Birren, Cardon, & Phillips, 1963). Similar results were found for visual and tactile stimuli. Again, stimulation at early phases of the cardiac cycle, i.e., during systolic stimulation of the baroreceptors, lead to an increase in total and pre-motor reaction times by comparison with the late phase (Edwards, Ring, McIntyre, Carroll, & Martins, 2007; McIntyre, Ring, Edwards, & Carroll, 2008). Additionally, higher sensory sensitivity thresholds were observed for visual and auditory stimulation during the cardiac systole compared to an enhanced perceptual sensitivity at the end of the cardiac cycle (Requin & Brouchon, 1964; Saxon, 1970; but see

Edwards, Ring, McIntyre, Winer, & Martin, 2009). In the same vein, a study conducted by Sandman, McCanne, Kaiser, and Diamond (1977) showed that accuracy rate for the identification of shortly presented visual stimuli (6 ms) during the P wave exceeded that of stimuli presented during R or T wave. The modulation of visual perception by cardiac cycle phase was further substantiated by a study, which also analysed cortical potentials evoked by the stimuli. It was found that averaged right hemispheric evoked potentials, especially the P1 component, which can be linked to early spatial attention processes (e.g., Clark, Fan, & Hillyard, 1995; Clark & Hillyard, 1996), proved to be smaller during the systole in contrast with the diastole (Walker & Sandman, 1982). Moreover, several studies indicate that changes in baroreceptor stimulation have an impact not only on the sensorimotor level but also on higher order central processes. For example, baroreceptor activation affected the evaluation of intensities of startle stimuli shown in a cardiac cycle time paradigm (Schulz et al., 2009). Also, long-term visual recognition memory seems to be influenced as indicated by the systematic manipulation of baroreceptor activity via the administration of either peripheral resistance and blood pressure increasing drugs (norepinephrine) or a vasodilatation drug (sodium nitroprusside) (Moor et al., 2005). Further, performance on various cognitive tests associated with chronic hypertension have been shown to be impaired (e.g., Blumenthal, Madden, Pierce, Siegel, & Appelbaum, 1993; Harrington, Saxby, McKeith, Wesnes, & Ford, 2000). However, a chronic increase in blood pressure as it is the case in chronic hypertension is not necessarily associated with increased baroreceptor activity (e.g., Eckberg & Sleight, 1992; McCubbin, Green, & Page, 1956). The relationship between hypertension and baroreceptor functioning is still not fully disclosed (e.g., Heusser et al., 2010; Lohmeier, Hildebrandt, Warren, May, & Cunningham, 2005). Taken together, these studies suggest that differential baroreceptor activation across the cardiac cycle, impacts cortical activity, simple reaction time, sensory sensitivity, as well as higher cognitive processes. The present study was designed to further inves-

investigate the impact of circulatory mechanisms on sensory and cognitive functions. In particular, we analysed the impact of baroreceptor activity on early visual selection. That is, we used a visual detection task in which a perceptually degraded target (presented near the sensory threshold) had to be identified against a visually strong distracting stimulus presented before the target (i.e., a forward mask)². Visual masking refers to the presentation of two stimuli in spatial and/or temporal contiguity to each other, one stimulus (mask) impairing the visibility of the other (target) (Enns & Di Lollo, 2000). In order to detect a target in the presence of interfering stimuli, selection can take place at different levels of processing (Kiesel, Kunde, & Hoffmann, 2007). In the case of a forward mask, spatially overlapping stimuli and a close temporal relationship between mask and target impede perceptual selection processes within the visual system and hence prohibit a clear separation of the mask and the target stimulus (Enns & Di Lollo, 2000). At the level of early perceptual processing different attentional processes are considered to be involved in resolving conflicts due to the exposure to multiple stimuli indicating different modes of behavior (e.g., Kiesel et al., 2007; Kunde, Kiesel, & Hoffmann, 2003; Lingnau & Vorberg, 2005). The suppression of irrelevant information has been shown to be an important factor (e.g., Machado, Wyatt, Devine, & Knight, 2007). As early as on the level of sensory processing, sensory selection is accomplished by reciprocal suppression of the neural activations elicited by each stimulus presented at the same time (Kastner & Ungerleider, 2000). Moreover, the inhibition of response tendencies, elicited by distracting stimuli, seems to be a crucial factor, allowing the organism to select relevant from irrelevant information and therefore to interact effectively with the environment (e.g., Frings, Wentura, & Wühr, 2012; Wühr & Frings, 2008). That is, when both, the distracting and the target stimulus, are assigned to a response, early activation of the neural activity elicited by

² Note that we conducted a pilot experiment ($N = 10$) as to ensure that the chosen stimulus presentation parameters lead to near threshold identification performance of the average participant.

the distractor is inhibited in order to avoid any reaction in response to the distractor but to allow a correct response indicated by the target stimulus (e.g., Eimer & Schlaghecken, 1998, 2003; Lingnau & Vorberg, 2005; Schlaghecken & Eimer, 1997). In our experiment, the direction of a target arrow had to be identified and mask-target sequences were presented with mask-onset either 170 ms after the R wave, that is, during the systolic stimulation of the baroreceptors, or 470 ms after the R wave of the ECG, that is, during the cardiac diastole. Presentation times were based on the time course of the systolic pressure wave subsequent to the R wave (e.g., Kroeker & Wood, 1955) and the firing characteristics of the baroreceptors in response to a distension of the vessel walls (e.g., Bronk & Stella, 1932, 1934; Landgren, 1952). As, for example, pointed out by Edwards et al. (2009), an increase in baroreceptor firing rate in the course of the cardiac cycle at both aortic and carotid vessels prevails approximately 90-390 ms after the R wave. As we used a sequence of stimuli we adapted the stimulus presentation times accordingly in order for both mask and target to be presented during the same cycle phase. The presentation times chosen were further validated by the delay between the R wave and systolic upstroke at the earlobe measured to control for inter-individual differences in the progression of the pressure wave. The mean transmission time from R wave to the right earlobe was $M = 183$ ms ($SD = 13$ ms; ranging from $M = 162$ - 217 ms) and can be seen as approximation for the arrival of the systolic upstroke at the carotid sinus. Furthermore, difficulty of the perceptual processing of the target was increased both by displaying it in low contrast to the background and by using a visually strong forward mask while using a short ISI of 100 ms. As the direction of the mask was statistically unrelated to the direction of the target (i.e., the mask's direction was orthogonally varied to the target's direction), the mask hampered the target identification. Participants were informed that the mask could not be used for predicting the target stimulus and hence were instructed to completely ignore the mask. Within the framework of heart-brain interaction, the target-identification should be easier when the inter-

ference of the mask is reduced. That is, if the postulated inhibitory effect of baroreceptor activation during systolic upstroke in the cardiac cycle holds true, inhibition of the mask should be increased during the cardiac systole and as a result target identification should increase. Therefore, the identification rate of the target should be higher with the mask presented 170 ms after the R wave (cardiac systole) in comparison to its presentation with a delay of 470 ms after the R wave (cardiac diastole).

2.3 Method

2.3.1 Participants

Twenty-eight healthy right-handed students from the University of Trier (12 female) with a mean age of $M = 24.07$ (range 19-30 years; $SD = 2.98$ years) years participated in the study. Prior to their participation the physical health status was assessed using a health questionnaire. Exclusion criteria were any actual health complaints, abuse of illicit drugs within the last six months, medication other than occasional pain killers and oral contraceptives, confirmed somatic or psychiatric diseases within the last six months other than banal infections or minor injuries. Heart rate and blood pressure of the participants were within normal range. Mean resting heart rate was $M = 69.83$ ($SD = 6.16$) bpm, mean systolic blood pressure was at $M = 113.78$ mmHg ($SD = 13.49$), and mean diastolic blood pressure was at $M = 65.73$ mmHg ($SD = 6.07$). Mean BMI was $M = 22.79$ kg/m² ($SD = 2.28$). All participants signed written informed consent and were made aware of their right to discontinue participation in the study at any time. They received 15 € expense allowance for their participation.

2.3.2 Physiological Measurements

Electrocardiogram (ECG) was continuously recorded using standard Ag/AgCl electrodes (ECG Tyco Healthcare H34SG Ag/AgCl electrodes of 45 mm diameter). Attachment sites were prepared using 96% ethanol and electrodes placed according to standard lead II configuration. ECG was recorded by Biopac MP150 system and ECG100C amplifier modules with highpass filter set to 0.5 Hz. The signal was stored to disk with a sampling rate of 1 kHz at 16 bit resolution. Artifacts were corrected and heart rate calculated offline using WinCPRS software. A standard cuff oscillometric Dinamap monitor (Dinamap SX 1846, Critikon, US) was used to measure systolic, diastolic, and mean blood pressure. Online R wave detection was performed with a modified analog circuit from a Gould Biotach Amplifier (Gould Inc., Instruments Division) producing TTL pulses.

2.3.3 Materials and Apparatus

The experiment was conducted using the E-prime software (E-prime 2.0). Stimuli were presented on a standard color TFT-monitor (48.3 cm (19"), FlatronL1942PK, LG) with a 60 Hz refresh rate. The colors of the stimuli were defined by the RGB color model with a color component range from 0 to 255. In the following, the amount of the three primary colors (red, green, blue) will be stated for each stimulus. Furthermore, luminance of the stimuli was measured by a digital luminance meter (Gossen GmbH). The stimuli were two adjacent arrows pointing either to the right or left (<< ; >>); presented in the font Calibri) in the middle of a grey rectangle (RGB-triplet 217, 217, 217; width 4.39°, height 2.29°; luminance: 106.1 cd/m²). Each arrow was about 0.96°, in width and 0.48° in height. Target stimuli were depicted in a slightly darker grey than the color of the rectangle (RGB-triplet 191, 191, 191; luminance: 78.3 cd/m²) and always shown in the screen center. Mask stimuli were dark grey in

color (RGB-triplet 64, 64, 64; luminance: 7.32 cd/m²). The position of the mask stimulus was varied randomly above or below the screen center (2.29° eccentricity so that it did not overlap with the target's location). The remainder of the display was black. Responses had to be given on a standard QWERTZ keyboard.

2.3.4 Procedure

Each participant was tested individually in a quiet room. After the experimental procedure had been explained and a health questionnaire completed, ECG electrodes were attached to the chest and a brachial cuff to the left arm. Before the beginning of the experimental procedure participants underwent a total of a six minute resting period during which ECG and blood pressure were assessed. The assignment to one of two experimental groups was set before each session on a rotating basis. As cardiac cycle phase was manipulated within subjects the two groups did only differ in the sequence implemented. Participants in one group underwent a first block of 120 trials with stimuli presented during cardiac systole and subsequently a second block of 120 trials with stimuli presented during cardiac diastole. For the other group the reverse order was realized. At the beginning of the experiment the participants were seated in a comfortable chair in front of the monitor. Instructions were given on the computer display. Participants were instructed to concentrate on the second (the *target*) of two consecutively appearing arrow stimuli and to ignore the first (the *mask*). The task was to identify the direction of the target arrow by typing their answer (“links” [left] for a left pointing arrow and “rechts” [right] for a right pointing arrow). It was made clear that the mask did not give any information about the target direction and should be ignored. If they were not able to distinguish the direction of target stimulus, they should respond according to their intuition. The sequence of an experimental trial was as follows (cf. Figure 1). The trial started with a fixation cross, which appeared at the screen centre for a mean duration of $M = 965$ ms

($SD = 325$ ms); that is $M = 953$ ms ($SD = 282$ ms) for systolic and $M = 978$ ms ($SD = 362$ ms) for diastolic trials. The mean fixation time was determined by the detection of an R wave after a fixed interval of 330 and 30 ms of fixation for systolic and diastolic trials, respectively. 170 ms following an R wave for systolic and 470 ms following an R wave for diastolic trials the mask was presented for 17 ms. Mean fixation time did not differ significantly between the two cardiac cycle conditions ($p = 0.114$). Subsequent to the mask, a black screen followed for 100 ms, before the target was presented for 50 ms, which was overwritten by a black screen shown for 1000 ms. At the end of each trial the participants were requested to type the direction of the target arrow into a text box by using the computer keyboard. By pressing the enter key, each trial could be terminated. Simultaneously a new trial was started. Pairings of mask and target arrows for each trial were randomly selected and appeared with the same frequency. The participants completed two blocks consisting of 120 trials each. The two experimental blocks differed in the time point the mask was presented in the cardiac cycle. The mask stimulus presentation time within the cardiac cycle was either set 170 ms after the R wave (cardiac systole) or 470 ms after the R wave (cardiac diastole). The sequence was counterbalanced. Half of the participants first worked through 120 trials with the mask starting during the systole before they completed 120 trials with mask onset during the diastole and the other half vice versa. Prior to the experimental trials the task was practiced within 16 trials. For each block the mask-target relation concerning the arrows direction was completely uncorrelated; that is in half of the trials the mask pointed to the left (right) while the target pointed to the left (right) whereas in the other half the mask pointed to the left (right) while the target pointed to the right (left).

2.4 Results

Three participants were excluded from the statistical analysis as their overall accuracy was much too good (given that target stimuli were intended to be presented at participants' perceptual threshold). These participants were outliers with respect to their target identification performance when compared to the sample (Tukey, 1977).

2.4.1 Target identification

A measure for analyzing differences in detection performance is the sensitivity index d' originating from the *Signal Detection Theory* (SDT), an approach widely used in psychophysics (e.g., Green & Swets, 1966). This index is typically used for various tasks in which stimuli are to be classified by an unequivocal response and has been applied to perceptual priming tasks as well (e.g., Frings & Neubauer, 2005; Greenwald, Klinger, & Schuh, 1995). The index d' is defined as the difference between the z -standardized hit rate (H, the proportion of correctly identified stimuli) and the z -standardized false-alarm rate (F, the proportion of incorrectly classified stimuli) as computed by the formula $d' = z(H) - z(F)$ (cf. Macmillan & Creelman, 2005). As in the present task participants had to respond to a single stimulus by categorizing it into one of two stimulus classes (left-pointing arrow versus right-pointing arrow) this rationale applies here in like manner. We calculated the d' for each participant and each cardiac cycle phase over all trials. Implementing the standard calculation of d' in the present study, false alarms were defined as participants' response "right" on trials with a left-pointing arrow displayed. Hits, on the other hand, were defined as participants' response "right" when the actual target showed a right-pointing arrow. Resulting d' -values were submitted to a 2×2 multivariate analysis of variance (MANOVA) with cardiac cycle phase as within subject factor and sequence as between subject factor. The main effect for cardiac cy-

cle phase was significant, $F(1,23) = 9.87$, $p = 0.005$, $\eta_p^2 = 0.30$, whereas the main effect of sequence was not, $F(1,23) = 1.11$, $p = 0.30$, revealing a higher discriminability rate of the target arrow with the mask presented during the cardiac systole. In fact, while identification performance with masks and targets presented during the cardiac systole significantly differed from zero, $t(24) = 4.24$, $p < 0.001$, this was not true for mask and targets shown during cardiac diastole, $t(24) = 1.71$, $p = 0.10$ (see Figure 2). In addition, the interaction effect of cardiac cycle phase and sequence, $F(1,23) = 4.29$, $p = 0.05$, $\eta_p^2 = 0.16$, was marginally significant. To account for a potential sequence effect, a comparison of d' was performed, considering only those responses given in the first experimental block. Still, d' was significantly larger in cardiac systole trials as compared to the diastole trials, $t(24) = 3.01$, $p < 0.01$. Identification performance during the cardiac systole significantly differed from zero, $t(12) = 3.28$, $p < 0.01$, which was, again not true for mask and targets shown during cardiac diastole, $t(11) = -0.45$, $p = 0.66$. Analysis of participants' response criteria revealed no significant differences for cardiac cycle phase. As it is statistically independent of the sensitivity index d' (Macmillan & Creelman, 2005) we calculated the criterion location c as response bias measure. Participants displayed an equal proportion of left and right responses in both cardiac cycle phases as was indicated by c -values statistically equal to zero for both conditions; $t(24) = -0.55$, $p = 0.59$ for the cardiac systole and $t(24) = -0.54$, $p = 0.59$ for the cardiac diastole. A 2×2 MANOVA with cardiac cycle phase as within subject factor and sequence as between subject factor further showed that the response criterion did not vary as a function of cardiac cycle phase, $F(1,23) = 1.29$, $p = 0.267$, and was not modulated by sequence ($F < 1$). The interaction was also not significant, $F(1,23) = 1.28$, $p = 0.269$. Note that we also checked in a 2 (cardiac cycle) $\times 2$ (sequence) $\times 2$ (mask-target congruency: congruent vs. incongruent) MANOVA whether the d' in the diastole or systole was modulated by mask-target congruency; this was not the case, as the interaction of cardiac cycle and congruency was not significant, $F < 1$.

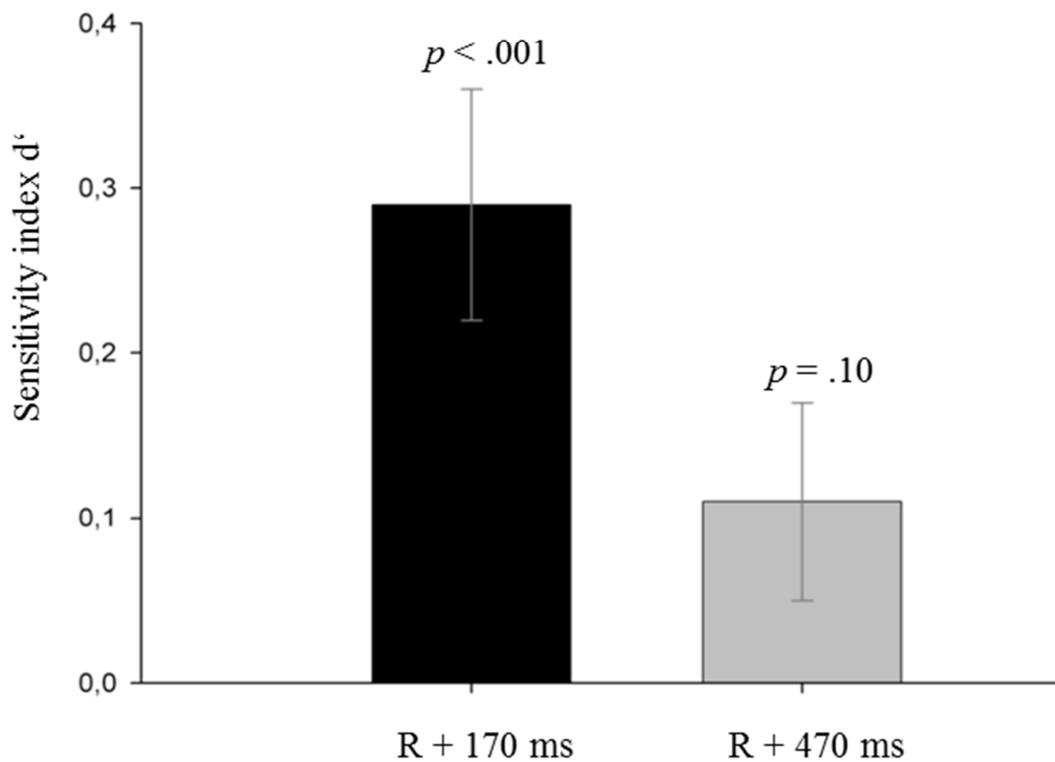


Figure 2. Mean sensitivity d' and standard errors (SE) for cardiac systole ($d' = 0.29$) and diastole ($d' = 0.11$). t -Tests revealed significant deviation from zero for stimuli presented during the cardiac systole (R +170 ms), but not for those presented during the diastole (R +470 ms).

2.4.2 Manipulation check

We also checked whether participants had a tendency to use the mask for identifying the target (against the given instructions). Accuracy rates were subjected to a $2 \times 2 \times 2$ MANOVA with the within subjects factors mask-target relation (congruent versus incongruent) and cardiac cycle phase (R wave +170 ms versus +470 ms), and with sequence as between factor. The main effect for mask-target relation was significant, $F(1,24) = 14.755$, $p = 0.001$, $\eta_p^2 = 0.39$, showing that participants had a tendency to use the mask information to identify the target. Yet, this effect was neither modulated by the cardiac cycle ($F < 1$), nor by the sequence of the cardiac cycle conditions, $F(1,23) = 1.14$, $p = 0.30$.

2.5 Discussion

In the current study we used a target discrimination task in which a visually dominant mask interfered with target detection to shed further light on inhibitory processes exerted by baroreceptor afferents. Studies concerned with baroreceptor effects on sensorimotor functions have been constricted to the presentation of single simple stimuli (e.g., Edwards et al., 2007; Sandman et al., 1977). In the present study we used a visual detection task in which a perceptual degraded target (presented near the sensory threshold) had to be identified against a visually strong distracting stimulus preceding the target (i.e., a forward mask). Detection rate for mask-target sequences presented during the cardiac systole (R +170 ms) was improved compared to a presentation during cardiac diastole (R+470 ms). What is more, perceptual sensitivity during the cardiac diastole was equivalent to chance level, whereas detection rate was above chance for stimulus sequences presented during the cardiac systole. In other words, when mask and target are presented during phases of low baroreceptor activity, participants were not able to identify the direction indicated by the target arrow. On the contrary, when mask and target are presented during high baroreceptor activity, detection rate of the target was significantly improved. Our study is the first to demonstrate a cardiac cycle time effect on inhibitory processes in visual selection. In the present visual detection task the inhibitory influence during the systolic upstroke helps to inhibit the perceptual interference of the mask and in doing so facilitates target processing. Put differently, it is more feasible to separate the neural activation of the strong mask from that of the target, when its presentation falls into a phase of reduced cortical excitability, i.e., the cardiac systole. Note that the effect of the cardiac cycle affects the reduction of interference due to the mask and not – as one might muse – the processing of the target stimulus per se. If the target stimulus would have been presented without a mask, the task would have been much easier. In fact, presenting a stimulus for 50

ms without masking would probably lead to supraliminal perception in every trial (e.g., Frings, Bermeitinger, & Wentura, 2011; Frings & Neubauer, 2005) and thus the performance would be nearly perfect for each cardiac cycle. Yet, presented together with a strong mask, target detection was near threshold due to the interference of the mask. The effects of the cardiac cycle could be attributed to the impact on the interference between the mask and the target. Furthermore, studies which applied simple detection tasks using single visual or auditory stimuli demonstrated compromised performance in the detection of the stimuli during systolic upstroke compared to the cardiac diastole (Requin & Brouchon, 1964; Sandman et al., 1977; Saxon, 1970), that is, the simple discrimination performance for targets presented without masks should have led to exactly the opposite result pattern. Thus, the present findings yield strong evidence for a reduction of mask-interference during the cardiac systole, leading to an enhancement in detection performance and not for an influence of the cardiac cycle on the target alone. Nevertheless, to preclude any impact of target inhibition accountable for an ease of selectivity with certainty, experimental designs in which mask and target are presented in cardiac systole and diastole separately are desirable for future studies. In doing so the suggestion of an inhibitory impact of baroreceptor activation exerted predominantly on the mask as put forward by our study could be tested indirect manner. From a neurophysiological view different points of application vulnerable to inhibition by baroreceptor activation are conceivable although for the present results still theoretical in nature. Corticopetal projections of the baroreceptors incorporate pathways over the solitary tract and the cardiovascular regulatory centres within the brain stem to the reticular formation, limbic structures, the thalamus, hypothalamus, and insular cortex (for an overview, see Dembowsky & Seller, 1995). The modulatory influence of baroreceptor activation on behavioral and electrocortical parameters is thought to be mediated both by its specifically directed connections with subcortical and cortical brain structures as well as by diminishing cortical excitability more globally by its inhibi-

tory effects on neurons in the reticular formation (Dembowsky & Seller, 1995; Elbert & Rau, 1995). As stated in the introduction, baroreceptor activity in the course of systolic upstroke is to be expected from approximately 90 to 390 ms after the R wave (e.g., Edwards et al., 2009) an interval consistent with the arrival of the systolic upstroke at the earlobe as measured in the current sample. In systole trials the mask-target sequence was presented from 170 to 337 ms after the R wave warranting increased baroreceptor activity. In diastole trials the mask-target sequence was presented from 470 to 637 ms after the R wave when decreased baroreceptor activity has to be expected. In addition, signal transmission time from baroreceptors to the central nervous system has to be considered in order to elaborate what kind of neurologically based mechanisms underlie the current findings. Findings from animal studies can be consulted. That is, while impulses from cat's carotid sinus nerve stimulation arrive at the hypothalamus within 10-20 ms (Adair & Manning, 1975), the inhibition of neurons of the reticular formation of the dog can be seen approximately 100 ms after the R wave (Lambertz & Langhorst, 1995). Considering the time course of baroreceptor transmission and visual processing, inhibitory influences on mask perception might work on feedforward connections of visual processing including ascending pathways from subcortical structures like the superior colliculus and medial dorsal nucleus to the frontal eye fields or over the lateral geniculate nucleus to V1 (Ferster, Chung, & Wheat, 1996; Lamme & Roelfsema, 2000; Sommer & Wurtz, 2000). Further, connectivity mediating recurrent stimulus processing might be affected. Whereas inhibition of feedforward connections would affect the representation of single-neuron receptive fields, inhibitory influences on connectivity mediating recurrent stimulus processing would presumably impair the contextual modulation of those initial responses (for a review on different processing stages in vision see Lamme & Roelfsema, 2000). Feedforward processes in the visual system are completed within 100 ms or less (e.g., Lamme & Roelfsema, 2000). That is for example the frontal eye fields can be reached by 45 ms (Kirch-

ner, Barbeau, Thorpe, Régis, & Liégeois-Chauvel, 2009; Lamme & Roelfsema, 2000). Contextual modulations by recurrent processing, however, call on longer time intervals depending on the task and stimulus properties (e.g., Motter, 1994; Roelfsema, Lamme, & Spekreijse, 1998). Note, that we were able to eliminate any confounding of the response with subsequent cardiac cycle phases as might be the case by using reaction time as dependent measure. That is, reaction time paradigms measure differences in the latency of motor responses following an imperative stimulus. However, while the presentation of the stimulus might be locked to a certain cardiac event (e.g., cardiac systole or diastole), the execution of the response falls inevitably in a succeeding cardiac cycle phase not controlled for by the experimenter. By asking our participants to indicate the direction of the target arrow by typing (“left” or “right”), we chose a response modality which takes place in a timescale beyond a certain cardiac cycle phase. That is, keying the word “left” or “right” very likely exceeds the duration of the ventricular systole or diastole which, under normal heart rate of 75 bpm, lasts approximately 250-300 ms and 500-550 ms, respectively (Smith & Kampine, 1990). The mean latency of the response was 2061 ms ($SD = 485$ ms). What is more, the response does solely rely on the detection of the target, which takes place early during perceptual processing. This time point is, other than a conglomerate of sensory and motor processes by measuring reaction time, orchestrated to a short interval of the respective cycle. The present results are in line with earlier studies demonstrating cardiac cycle time effects for the perception of simple sensory stimuli. For example, in a study conducted by Sandman et al. (1977) accuracy rate for the identification of tachistoscopically presented visual stimuli during the P wave was significantly improved compared to stimuli presented during R or T wave. Furthermore, right hemispherically, more pronounced cortical potentials evoked by short light flashes were associated with intervals of low carotid pressure within the cardiac diastole compared to phases of high carotid pressure during the cardiac systole. This effect was especially distinct for the P1 component

(Walker & Sandman, 1982), an early positive deflection reflecting early spatial attention processes on sensory evoked potentials (e.g., Clark et al., 1995; Clark & Hillyard, 1996). In comparison with our results, a reduced P1 component during phases of high carotid pressure suggests that similar processes might be involved. One could hypothesize that both the results of Walker and Sandman (1982) as well as our current findings reflect reduced gain control due to attention allocated to the location of upcoming stimuli. In other words, the amplification of sensory potentials evoked by visual stimulation elicited at attended locations (for a review on sensory gain control in selective attention, see Hillyard et al., 1996; Hillyard, Vogel, & Luck, 1998) might be reduced in phases of increased baroreceptor stimulation. This is, although at this point highly speculative, conceivable as the amplitude of P1 is thought to reflect the amount of attention paid to allocation where a stimulus emerges (e.g., Anllo-Vento, 1995; Eimer, 1997; Heinze, Luck, Mangun, & Hillyard, 1990; Luck et al., 1994). As baroreceptor activity is associated with reduced cortical excitability (cf. Elbert & Rau, 1995) increases in baroreceptor stimulation during the systolic upstroke might counteract facilitating effects caused by attentional processes. Considering the vast quantity of studies on cognition making use of subliminal or close-to-threshold sensory input (cf. Eimer & Schlaghecken, 2003; Schmidt, Haberkamp, & Schmidt, 2011), our results might also hold implications for the determination of perception thresholds of to-be-subliminally presented stimuli. That is, performances as well as sensory thresholds could be varying due to stimuli unintentionally presented at different time points within the cardiac cycle, i.e., in phases with different states of cortical inhibition. Controlling for cardiac cycle effects in masked priming experiments might therefore be an intriguing way as to ensure truly subliminal presentation of the prime. In particular, in many masked priming experiments a sequence of mask-prime-mask is presented before the target stimulus. The question is then, whether the prime is accessible; considering our results it seems that the detection of a prime stimulus in such a priming experiment de-

depends on the point in time during the cardiac cycle at which this mask-prime-mask sequence is delivered. To conclude, our results demonstrated variations of cortical inhibition in the course of the cardiac cycle. Visual detection performance was improved during the cardiac systole compared to the diastole. The study therefore yields evidence for the modulation of visual selection by differences in baroreceptor activity.

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Chapter III

Cardiac Cycle Time Effects on Selection Efficiency in Vision

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3.1 Abstract

The effect of cardiac cycle time on attentional selection was investigated in an experiment in which participants classified target letters in a visual selection task. Stimulus onsets were aligned to the R wave of the electrocardiogram (ECG) and stimuli presented either during the ventricular systole or diastole. Selection efficiency was operationalized as difference in target selection performance under conditions of homogeneous and heterogeneous distractors. Differences in performance, i.e., the impact selection difficulty had on the ability to select the target, were attenuated for stimuli presented during the ventricular systole compared to the diastole. Increased baro-afferent signal transmission during the systole appears to reduce interference of highly distracting stimuli on visual selection efficiency.

3.2 Introduction

Afferent signals from the viscera conveyed to the central nervous system (CNS) contribute to the regulation of physiological and behavioral processes in order to maintain homeostasis and the adequate provision of the organism with nutrients and oxygen (Loewy & Spyer, 1990; Vaitl, 1996). Along with its significance for the perception of the physical self and emotion (Craig, 2002; Wiens, 2005) the central processing of visceral information is indicated in effects on cognition like memory, attention, and empathy (Critchley & Harrison, 2013; Menon & Uddin, 2010; Uddin, Kinnison, Pessoa, & Anderson, 2014). Focusing on the cardiovascular system, activity of arterial baroreceptors is suggested to affect perception, sensorimotor processes, and higher cognitive functions (e.g., Duschek et al., 2013; Edwards et al., 2007; Garfinkel et al., 2013). Arterial baroreceptors, mechanoreceptors primarily located within the vessels of the carotid sinus and the aortic arch are essential for the sensing and

short-term regulation of blood pressure and heart rate (Eckberg & Sleight, 1992; Stauss, 2002). Afferent fibers pass the glossopharyngeal and vagus nerve to the nucleus tractus solitarius (NTS) and determine the output of autonomic brain stem centers like the rostral ventrolateral medulla and nucleus ambiguus, thereby regulating myocardial contractility, peripheral vasomotor tone and heart rate by sympathetic as well as parasympathetic efferents (Davos et al., 2002; Levy, Ng, Lipman, Zieske, & Nelson, 1966; Schreihofner & Guyenet, 2002). Baro-afferent signals are forwarded by the NTS to the reticular formation, and higher-order CNS structures like the thalamus, hypothalamus, amygdala and cortex (Henderson et al., 2004; Manning, 1975; Zhang & Oppenheimer, 2000). These direct and indirect pathways are assumed to exert a general inhibitory influence of baroreceptor activation on the CNS (e.g., Dembowski & Seller, 1995; Rau et al., 1993b; Vaitl & Gruppe, 1991).

Arterial baroreceptors fire during the upstroke and plateau of the arterial pressure wave elicited by systolic ventricular ejection of the stroke volume, and silence during the diastolic phase (Angell-James, 1971; Bronk & Stella, 1932; Mancia & Mark, 1983). Therefore, an alternating pattern of baroreceptor activity results which provides the basic principle of a method to examine naturally occurring CNS effects of arterial baroreceptor activity. In fact, variations within the course of the cardiac cycle have been found for early sensory potentials of the electroencephalogram (Cohen, Lieb, & Rist, 1980; Sandman, McCanne, Kaiser, & Diamond, 1977; Walker & Sandman, 1982). For instance, early event-related cortical potentials evoked by simple auditory and visual stimuli have been indicated to be more pronounced during the diastole compared to the ventricular systole (Sandman, Walker, & Berka, 1982). The same is true for the visually evoked P1 component (Walker & Sandman, 1982) associated with early processes of spatial attention (Clark, Fan, & Hillyard, 1994; Clark & Hillyard, 1996).

In the same line, behavioral studies of visual and auditory perception indicated increased sensory thresholds for stimuli presented during the systole compared to those presented later in the cardiac cycle (Requin & Brouchon, 1964; Saxon, 1970; but see Velden & Juris, 1975). Furthermore simple and choice reaction times (RTs) in response to visual, auditory, and tactile stimulation during the systole are indicated to be prolonged in comparison to the diastole (Birren et al., 1963; Edwards et al., 2007; McIntyre, Ring, Edwards, & Carroll, 2008; but see Thompson & Botwinick, 1970). For example, in a study conducted by Edwards et al. (2007) RTs to auditory, visual, and tactile stimuli speeded up linearly within the course of the cardiac cycle. Recently, Pramme, Larra, Schächinger, and Frings (2014) reported early visual selection being related to the timing within the cardiac cycle. In their study, the discrimination of a perceptually degraded target against a forward mask was enhanced when the stimulus sequence was presented during the cardiac systole compared to the diastole; suggesting inhibitory effects on mask interference at the time of increased baroreceptor activation that facilitate the separation of the neural processing of the target from that of the mask.

In sum, research on the effects of baroreceptor activation on behavioral and electrocortical measures strongly suggests that basic sensory processing is affected by increased baroreceptor signal transmission. Yet, whether baroreceptor activity also modulates visual selection remains less clear. In fact, the paper of Pramme et al. (2014) provides only a first hint. The purpose of the present study was therefore to further investigate the effect of natural variations of baroreceptor activity on visual selective attention. Whereas in the masking paradigm applied by Pramme et al. (2014) selection difficulty arises from a reduction in the target's visibility due to a temporal conflict of overlapping processing streams originating from a short succession of mask and target stimulus (cf. Enns & Di Lollo, 2000), in the present study participants had to actively scan an array of potentially relevant stimuli in order to detect and classify the target correctly. The identification of the target stimulus and its classification ne-

cessitated a search of the stimulus set by focal attention (cf. Bonnel, Possamai, & Schmitt, 1987; Sagi & Julesz, 1985a, b).

For this purpose, participants performed a letter search task in which a target stimulus had to be selected from among a set of irrelevant stimuli (distractors). Selection difficulty was manipulated by the variation of the similarity between target and distractors as well as the similarity between the distractors in order to measure the participant's efficiency of selecting the relevant target stimulus. In accordance to the attentional engagement theory of visual search (Duncan & Humphreys, 1989; Duncan & Humphreys, 1992; Watson & Humphreys, 1997) selection efficiency is determined by similarity. That is, the similarity of the distractors to the target and the similarity between distractors. Duncan and Humphreys (1989) delineate that stimuli in a visual search display have to be compared to a target template that is stored in memory. The more the target contrasts with the distractors the easier the target can be selected and compared to the template as the distractors are automatically discarded from further analyses; reflected in shorter RTs and reduced error rates (e.g., Bauer, Jolicoeur, & Cowan, 1996; Duncan & Humphreys, 1989; Scialfa, Esau, & Joffe, 1998). Likewise slower responses and higher error rates result from low similarity between distractors (e.g., Bergen & Julesz, 1983; Bundesen & Pedersen, 1983; Farmer & Taylor, 1980) as the perceptual grouping of similar distractors facilitates its simultaneous suppression, whereas the rejection of separate distractor representations impedes target selection (Duncan & Humphreys, 1989).

In the present study, selection efficiency was operationalized as the difference in performance for conditions of high and low selection difficulty. Therefore, targets were displayed within the context of homogeneous and heterogeneous distractor stimuli. In the homogeneous stimulus condition the detection of a target letter under uniform distractors was required. The letter was enclosed by six distracting stimuli that were made out of two identical subcomponents of the target. For example, the capital letter *N* was enclosed by six stimuli

comprising only the two outer vertical lines of the letter *N*. In this condition the distractors shared only minimal features with the target but the distractors were highly similar to each other. In the heterogeneous stimulus condition, however, the task of the participants required complex perceptual discrimination as the target had to be discriminated from complex distractors showing a strong overlap with the target features and a considerable variability among each other. In the heterogeneous condition, the target was enclosed by six distractors that were made out of two different subcomponents of the target. For example, the capital letter *N* was enclosed by one vertical and the diagonal line. Stimuli were presented for a short time interval in order to vary the timing of the stimulus onset with respect to the cardiac cycle phase. Onset times were selected according to the time course of the systolic pressure wave subsequent to the R wave of the ECG (e.g., Kroeker & Wood, 1955) and the pattern of baroreceptor activation in response to a distension of the arteries (Bronk & Stella, 1932, 1934; Landgren, 1952). As, for instance, described by Edwards et al. (2009) the firing rate of the arterial baroreceptors is increased in a time interval ranging from approximately 90 to 390 ms after the R wave with joint activation at carotid and aortic sites present from approximately 140 to 340 ms after the R wave.

With regard to experimental findings pointing to the localization of baro-afferent effects on a sensory processing level (e.g., Edwards et al., 2007) and the particular susceptibility of the response latency as dependent variable to uncontrolled effects from subsequent cardiac cycle phases, the percentage of error was analysed as primary dependent variable. That is, whereas the timing of stimulus presentation and hence early phases of its processing may be controlled for, subsequent response preparation and peripheral motor processes might systematically fall within the complementary cycle phase. What is more, the unintended alignment of response-related processes to the cardiac cycle may be confounded to the experimental manipulation as, depending on the task characteristics, the duration of the central stimulus pro-

cessing will vary according to the experimental condition. In the current task, necessary requirements for the analysis of errors were therefore achieved by degrading the perceptibility of the stimuli by means of a relatively low contrast to the background and by limiting the stimulus duration to 133 ms (cf. Duncan & Humphreys, 1989; Kleiss & Lane, 1986; Shiffrin & Gardner, 1972). For the execution of saccades requires a longer time interval (Fischer & Weber, 1993), the size of the possible target positions were scaled in order to allow for the target perception without eye movements (Motter & Simoni, 2007).

3.3 Method

3.3.1 Participants

22 students and employees from Trier University (7 male) with a mean age of 22 (range 18-30; $SD = 3$) years participated in the study. Prior to experimentation the physical health status of the participants was assessed with a health questionnaire. Exclusion criteria were current somatic diseases or health complaints, impaired vision, confirmed psychiatric diseases within the last six months, medication other than occasional mild analgesics and oral contraceptives, the consumption of more than five cigarettes and more than three servings of alcohol (i.e., three times 300 ml of beer, 200 ml of wine, or 20 ml of spirits) per day, and the abuse of illicit drugs within the last six months. Participants were of normal weight with a mean BMI of 22.1 kg/m² ($SD = 2.3$). Heart rate and blood pressure of the participants were within normal range with a mean resting heart rate of 70.6 bmp ($SD = 9.2$), mean systolic blood pressure of 110.2 mmHg ($SD = 13.3$), and mean diastolic blood pressure of 65.9 mmHg ($SD = 7.0$). All participants signed written informed consent and were made aware of their

right to discontinue participation in the study at any time. Participants received an expense allowance of 10 € or partial course credit for their participation.

3.3.2 Physiological Measurements

An ECG was continuously recorded using Ag/AgCl ECG electrodes (45 mm in diameter, Kendall H34SG, Covidien). Attachment sites were cleansed using 96% ethanol and electrodes placed according to standard lead II configuration. The ECG signal was recorded by a MP150 data acquisition unit and ECG100C amplifier modules (Biopac Systems) and stored to hard disk with a sampling rate of 1 kHz at 16 bit resolution. The ECG was high-pass filtered by 0.5 Hz, artifacts corrected and heart rate calculated offline using WinCPRS software (WinCPRS, 1.160). An oscillometric blood pressure monitor (Dinamap SX 1846, Critikon) with a brachial cuff (UltraCheck 2635, Statcorp Medical) was used to measure systolic, diastolic, and mean arterial blood pressure. Online R wave detection was performed with a modified analog circuit from a Gould Biotach Amplifier (Gould Instrument Systems) producing TTL pulses.

3.3.3 Materials and Apparatus

The experiment was programmed and behavioral data recorded with E-prime software (E-prime 2.0, Psychology Software Tools). Stimuli were presented on a standard color TFT-monitor (48.3 cm (19"), Flatron L1942PK, LG Electronics) with a 60 Hz refresh rate. The colors of the stimuli were defined by the RGB color model with a color component range from 0 to 255. In the following, the amount of the three primary colors (red, green, blue) will be stated for each stimulus. Furthermore, luminance of the stimuli was measured by a digital luminance meter (Mavo-Monitor USB, Gossen). The targets comprised capital letters (*E*, *N*, *L*, and *Z*), resembling in style the sans serif typeface Arial, which could either be aligned cor-

rectly, i.e., written from left to right, or laterally reversed, that is in mirror writing. Each letter was 0.29° in width and 0.48° in height. Each target was enclosed by six distractors which comprised two subcomponents of the respective letter. The subcomponents could either be identical or different. See Figure 3 for an example. For the letters *N* and *Z* each stimulus condition was realized twice; once the orientation of the diagonal corresponded to the diagonal of the correctly displayed and once to the laterally reversed target letter.

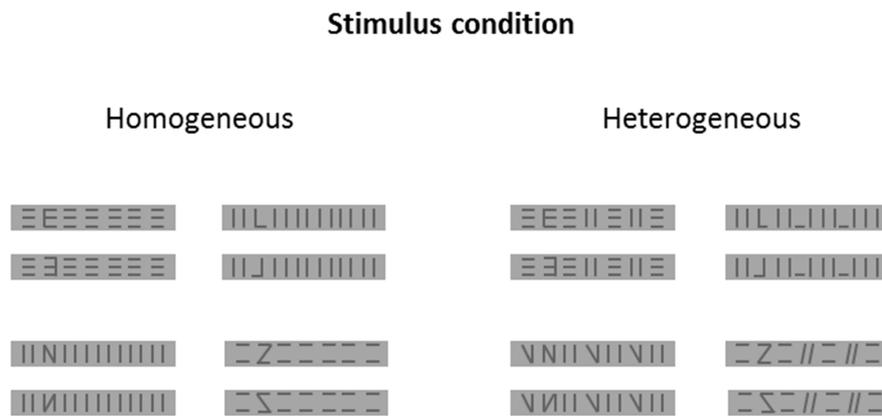


Figure 3. Exemplars of stimulus configurations for correctly displayed and laterally reversed target letters in homogeneous and heterogeneous stimulus conditions. Targets occurred randomly at one of the inner five stimulus positions.

All stimuli were colored in dark gray (RGB-triplet 100, 100, 100; luminance: 19.8 cd/m²) superimposed on a background of light gray (RGB-triplet 166, 166, 166; luminance: 53.3 cd/m²). Stimuli were presented as a horizontally aligned septet (width: 3.15°) with an inter-contour distance of 0.19° in the center of the screen consisting of one target and six distractor stimuli with the target being located at one of the five inner positions. Responses were given via a Serial Response Box (Psychology Software Tools).

3.3.4 Procedure

Each participant was tested individually in a quiet room seated in a comfortable chair with a viewing distance of approximately 60 cm to a computer monitor. After the experimental procedure had been explained and a health questionnaire completed, a brachial cuff was attached to the left upper arm and three ECG electrodes to the chest. Before the beginning of the experimental procedure participants underwent a six minute resting period during which ECG, pulse wave, and blood pressure were assessed. For the experimental procedure, the brachial cuff was removed. Subsequently, instructions for the experimental task were given on the computer monitor. Responses were given by a key press with the left or right index finger after releasing an initial key. The participant's task was to classify the depiction of a letter (target stimulus) as correctly or laterally reversed. Speed and accuracy were accentuated. An experimental trial was initialized by a set of seven fixation crosses matching the spatial positions of the sequencing stimuli. The fixation display appeared for a mean duration of $M = 930$ ms ($SD = 104$) with $M = 928$ ms ($SD = 108$) for systolic and $M = 932$ ms ($SD = 108$) for diastolic trials. The mean fixation time was determined by the detection of an R wave after a fixed interval of 320 and 20 ms of fixation for systolic and diastolic trials, respectively. 180 ms following an R wave for systolic and 480 ms for diastolic trials the stimulus septet was displayed. After 133 ms a blank display was inserted until a response was made. In case of an erroneous response a display informing the participant about the mistake and instructing them to respond as fast and accurately as possible appeared for a further 2000 ms. Before the next trial started, a blank screen of 1000 ms was displayed. With its offset a new trial commenced (see Figure 4).

Participants underwent 480 experimental trials with a 30 and 60 second break after each 80 and 240 trials, respectively. All combinations of stimulus condition (homogeneous, heterogeneous) and letter orientation (correct, laterally reversed) were realized 30 times for

each onset time within the cardiac cycle (R+180, R+480). Stimulus condition, letter orientation, and cardiac cycle time were randomly selected for every trial as was the position of the target stimulus. Preceding the experimental trials, participants practiced the task for 20 trials. During practice, the timing of the stimulus onsets was not synchronized to the cardiac cycle and participants received feedback about the correctness of the given responses on each trial. After the experimental procedure the brachial cuff was attached for a final blood pressure measurement.

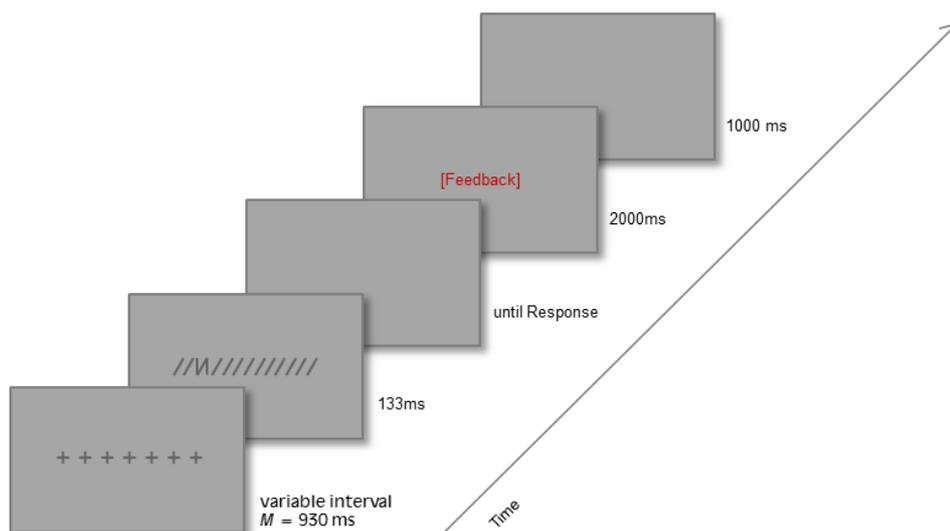


Figure 4. Sequence of events in an experimental trial. Onset of the stimulus septet was synchronized to the cardiac cycle phase of the participant (180 ms after the R wave for systolic and 480 ms after the R wave for diastolic trials). Feedback was given following erroneous responses only. Stimuli are not drawn to scale.

3.3.5 Design

The design comprised three within-subjects factors, stimulus condition (homogeneous versus heterogeneous), letter orientation (correct versus laterally reversed), and cardiac cycle phase (R wave +180 ms versus +480 ms). Percentage of errors and RTs as control analysis

were analyzed via a 2 x 2 x 2 MANOVA, respectively. For follow-up analyses, Bonferroni-corrected t tests for dependent samples were calculated.

3.4 Results

3.4.1 Error Rates

On average participants responded incorrectly on 20.7% ($SD = 7.4$; range 8.0 to 34.0) of all trials. Mean percentage of errors are depicted in Table 1.

Table 1. Mean error rates (in percentage) as a function of cardiac cycle phase, stimulus condition, and letter orientation. Standard deviations are provided in parentheses.

	Systole		Diastole	
	homogeneous	heterogeneous	homogeneous	heterogeneous
correctly oriented	18.0 (9.8)	22.4 (9.5)	14.4 (7.9)	25.2 (10.9)
laterally-reversed	14.7 (6.2)	27.3 (11.6)	13.6 (8.9)	29.9 (12.3)

Overall erroneous responses were more frequently made on heterogeneous ($M = 26.2\%$, $SD = 8.5$) compared to homogeneous ($M = 15.2\%$, $SD = 6.8$) trials, $F(1, 21) = 132.11$, $p < .001$, $\eta_p^2 = .863$. Stimulus condition was modulated by cardiac cycle phase, $F(1, 21) = 8.50$, $p = .008$, $\eta_p^2 = .288$, in that the difference between homogeneous and heterogeneous stimulus conditions was more pronounced for the diastole ($M = 13.6\%$, $SD = 6.8$) than systole ($M = 8.5\%$, $SD = 5.2$) with both differences deviating significantly from zero; for diastole:

$t(21) = 9.35, p < .001$, and systole: $t(21) = 7.59, p < .001$ (Figure 5). Furthermore, the interaction of letter orientation and stimulus condition was significant, $F(1, 21) = 7.55, p = .012, \eta_p^2 = .265$. Namely, the difference in selection efficiency was more pronounced for laterally reversed ($M = 14.5\%$, $SD = 9.0$) than for correctly displayed ($M = 7.6\%$, $SD = 5.4$) letters; $t(21) = 7.57, p < .001$ and $t(21) = 6.57, p < .001$, respectively. Percentage of errors did not differ between laterally reversed and correctly displayed letters; neither for the homogeneous $t(21) = 1.75, p = .327$, nor the heterogeneous, $t(21) = 1.87, p = .271$, stimulus condition. No further effect was significant, all $F_s < 1$. A control analysis using signal detection indices instead of simple error rates as dependent variable yielded essentially the same results.

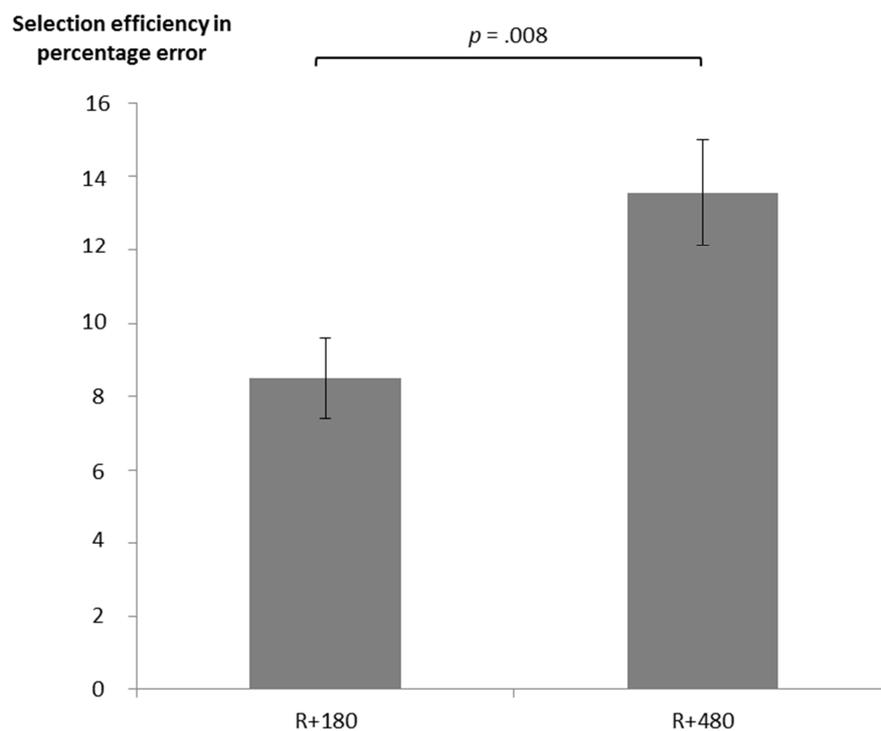


Figure 5. Mean selection efficiency (in percentage error) as a function of the cardiac cycle phase. Selection efficiency is indexed by the difference of heterogeneous and homogeneous stimulus condition. Standard errors are depicted.

3.4.2 Response Time

For the sake of completeness we analyzed RTs. For RT analyses only trials with correct responses and response times exceeding 200 ms but that did not surmount three interquartile ranges of the third quartile of the participant's RT distribution (Tukey, 1977) were incorporated into the analyses. Due to these constraints 21.3% ($SD = 7.3$) of trials were discarded from analyses. Mean RTs are depicted in Table 2. Overall RTs were slower on heterogeneous ($M = 987$ ms, $SD = 198$) compared to homogeneous ($M = 932$ ms, $SD = 191$) trials, $F(1, 21) = 29.37$, $p < .001$, $\eta_p^2 = .583$. Furthermore participants responded slower to laterally reversed ($M = 981$ ms, $SD = 209$) than correctly oriented ($M = 937$ ms, $SD = 180$) target letters, $F(1, 21) = 12.80$, $p = .002$, $\eta_p^2 = .379$. Neither the main effect of cardiac cycle phase nor the first order interactions were significant, all $F_s < 1$. The first order relations were however qualified by a three-way interaction, $F(1, 21) = 6.83$, $p = .016$, $\eta_p^2 = .245$. Inspection of the three-way interaction revealed that whereas for stimuli presented during the systole selection efficiency profited from homogeneous distractors irrespective of letter orientation, this advantage was limited to correctly displayed stimuli during the diastole. In more detail, for stimuli presented during the systole, facilitation of stimulus selection on homogeneous trials was equally present for laterally reversed and correctly displayed letters with the former being impeded to a greater extent by heterogeneous distractors. For the same stimulus configurations presented during diastole, however, responses to correctly displayed but not laterally reversed letters profited from homogeneous distractors with the latter being associated with RTs on an equally high level as for heterogeneous distractors.

Table 2. Mean RTs (in ms) as a function of cardiac cycle phase, stimulus condition, and letter orientation. Standard deviations are provided in parentheses.

	Systole		Diastole	
	homogeneous	heterogeneous	homogeneous	heterogeneous
correctly oriented	915 (174)	960 (179)	903 (178)	974 (200)
laterally-reversed	950 (203)	1015 (211)	961 (218)	1009 (223)

3.5 Discussion

The present study used a visual selection task within a cardiac cycle time paradigm to differentiate selection efficiency for stimuli presented during the ventricular systole and diastole. Targets and distractors were presented simultaneously with the onset either 180 ms or 480 ms after the R wave of the ECG. Selection efficiency was operationalized as difference score of the performance between conditions of heterogeneous and homogeneous distractors. Heterogeneous distractors evoked larger error rates than homogeneous distractors. Yet, this effect was modulated by the time the stimulus set was presented with respect to the cardiac cycle phase of the participant. The difference in selection efficiency for easy and difficult selection conditions was less pronounced when the stimulus display was presented during the ventricular systole (i.e., 180 to 313 ms after the R wave) compared to the presentation during the ventricular diastole (i.e., 480 to 613 ms after the R wave). The results demonstrate that the onset of stimulus presentation with regard to the cardiac cycle affects attentional abilities to select a target stimulus from distractors in a way that selection efficiency is enhanced during phases of baroreceptor activation (systole) compared to baroreceptor inactivation (diastole). In

other words, increased interference due to context conditions that hamper selection (cf. Duncan & Humphreys, 1989) are of less consequence in phases of increased baroreceptor activation.

This finding is in line with a previous study that suggested less mask interference when mask and target are presented during the systole compared to the presentation during the diastole (Pramme et al., 2014). Here, increased baroreceptor activation during the systole seemed to dampen interference of the irrelevant mask by facilitating the separation of temporally overlapping sensory representations of mask and target. Together the results implicate that baroreceptor-mediated inhibition of subcortical and cortical structures bolsters selective attention by withdrawing activity from sensory subsystems that are currently processing interfering input (i.e., the distractors).

From this perspective, the pattern of results can further be reconciled with and adds to previous studies that report decrements in sensory and sensorimotor performance for stimuli presented during the systole compared to the diastole (e.g., Birren et al., 1963; McIntyre, Ring, Hamer, & Carroll, 2007; Walker & Sandman, 1982). As neurophysiological and neuropsychological studies suggest baroreceptor activation to evoke a general inhibitory influence on subcortical and cortical structures (e.g., Dembowsky & Seller, 1995; Vaitl & Gruppe, 1990, 1992), its impact on performance may depend on the attentional requirements set by the task at hand. In particular, behavioral consequences of baroreceptor-mediated inhibition may be relative to whether selective attention or alertness/vigilance predominate the task demands (cf. Petersen & Posner, 2012; Posner & Petersen, 1990). To be precise, as the detection or localization of a target, like in the cardiac cycle time studies on sensory motor performance, does not require focal attention, as parallel processing of the sensory input suffices, baroreceptor activation is associated with a decrement in performance, because sensory processing as a whole is slowed or suppressed as activation thresholds of sensory input are in-

creased by baroreceptor-mediated inhibition. The identification of a letter and its classification as correctly displayed or laterally reversed in the ongoing task or the separation of mask and target representation in Pramme et al. (2014), on the contrary, necessitate serial processing of the stimuli by focal attention (cf. Bonnel et al., 1987; Sagi & Julesz, 1985a; Sagi & Julesz, 1985b). In this latter case, the alignment of the attentional focus to the relevant information is critical for an effective task performance and the suppression of ongoing neural activity may be conceptualized as noise suppression reducing crosstalk from conflicting information. Hence, following this line of reasoning, diminished detection accuracy and raised sensory thresholds during the ventricular systole should predominate in mere detection tasks, whereas tasks requiring focal attention are expected to benefit from stimulus presentations in phases of increased baroreceptor activation. In line with models that conceptualize attention as resource fluctuating with respect to neural activation patterns within the CNS, i.e., as determined by activation patterns within multiple brain systems (e.g., Desimone & Duncan, 1995; Duncan et al., 1997), our results demonstrate that attention is not a constant resource. On the contrary, besides being modulated by contextual factors like the perceptual grouping of distractors (Tipper, 1985; Wühr & Frings, 2008), distractor features (Bjork & Murray, 1977; Duncan & Humphreys, 1989; Frings & Wühr, 2007b), sequence effects (Frings & Wühr, 2007a; Gratton, Coles, & Donchin, 1992; Neumann & DeSchepper, 1991), task instructions (Jonides & Gleitman, 1972), and cognitive load (Forster & Lavie, 2008; Lavie, 2010), attentional selection efficiency is dependent on states of the autonomic and central nervous system (cf. Porges, 1992; Thayer & Lane, 2000).

Fluctuations in attention capacity in a time frame of several milliseconds may stabilize behavior, by maintaining a homeostatic activation level of the brain and provide a basis for the integration and coordination of multiple behaviorally relevant systems of the CNS (see for example, Komisaruk, 1977; Lambertz & Langhorst, 1995; Langhorst, Schulz, Lambertz,

Schulz, & Camerer, 1980; Perlitz et al., 2004). Furthermore, changes in vagal output due to environmental factors may serve the acute adaptation to the (task) demands at hand by adjustment of baro-afferent signal transmission. In stressful situations, whether triggered by physiological or psychological stressors, the baroreflex will be suppressed allowing an increase in cardiac output, and, thus, sufficing metabolic supply without counter-regulation by the baroreflex (Duschek et al., 2013; Gianaros, Onyewuenyi, Sheu, Christie, & Critchley, 2012; for a review, see Duschek, Muckenthaler, Werner, & Reyes del Paso, 2009). As a consequence, increased baroreceptor-mediated inhibition of the CNS may facilitate the allocation of attentional focus to a currently behaviorally relevant stimulus or demanding mental operations as well as adequate response systems mobilized (cf. Porges, 2001; Thayer & Lane, 2000). Research on heart rate changes evoked by stimulus presentation or response initiation (e.g., Jennings & Van der Molen, 2005; Lacey & Lacey, 1974, 1978; Somsen, Jennings, & Van der Molen, 2004) as well as correlational studies on baroreflex sensitivity and cognitive performance (e.g., Reyes Del Paso, González, & Hernández, 2004; Reyes Del Paso, González, Hernández, Duschek, & Gutiérrez, 2009; Yasumasu, Reyes del Paso, Takahara, & Nakashima, 2006), support this assumption by arguing that cardiac deactivation (e.g., heart rate deceleration) in response to a warning signal facilitates subsequent stimulus detection and motor response by reducing baroreceptor-afferent feedback to the CNS, but that cardiac activation (e.g., heart rate acceleration) supports complex cognitive processing, e.g., mental arithmetic, by reducing environmental input which could otherwise lead to interference with the primary task. To conclude, baroreceptor mediated inhibition of CNS structures involved in selective attention may support the ability of the organism to efficiently detect and select behaviorally relevant from irrelevant information and, thus, contribute to efficient response selection and goal-directed behavior.

On a neural level, the inhibitory influence of baro-afferent transmission may add to the suppression of distractor representations within the visual cortex (cf. Desimone & Duncan, 1995; Duncan et al., 1997). The impact on a sensory processing level is supported by Edwards et al. (2007) and Schulz and colleagues (Schulz et al., 2009a; Schulz, Wager, Romer, & Schächinger, 2009b) who demonstrated that baroreceptor activation does not primarily affect the motor component of response execution; or does so differentially. The inhibitory effect of baro-afferent transmission on subcortical and cortical structures beyond the NTS is likely to be conferred by widespread afferent fibers of the *formatio reticularis* which receives direct efferent input from the NTS and exhibits pulsatile activation patterns corresponding to the progression of the cardiac cycle (e.g., Lambertz & Langhorst, 1995; Lambertz et al., 1995). Alterations in discharge patterns can reach the reticular formation within 80 to 230 ms after the R wave of the ECG; the exact timing depending on the discharge level of the neurons and other rhythmical influences at brain stem level, e.g., respiration (Lambertz & Langhorst, 1995; Lambertz, Vandenhouten, Grebe, & Langhorst, 2000). The visual cortical area V1 contributes to object-based selective attention by enhanced firing rates in response to attended (compared to unattended) objects (Roelfsema, Lamme, & Spekreijse, 1998). This enhancement occurs approximately 235 ms after stimulus onset. That is, whereas the first visual response in V1 has a latency of approximately 35 ms object-based selective attention mechanisms commence with an additional latency of 200 ms. Similarly in choice tasks the firing rate to distracting stimuli of cells within the inferior temporal cortex of the macaque, a hierarchically higher area of the visual cortex involved in object recognition, is inhibited 200 ms after stimulus onset (Chelazzi, Miller, Duncan, & Desimone, 1993; Moran & Desimone, 1985). With regard to a stimulus onset of 180 ms after the R wave in the current study it could be speculated that concurrent inhibition by ascending transmission of the reticular formation to the extrastriate cortex contributes to facilitated target selection. On the other hand, pulsatile

discharge patterns within the thalamus (Oppenheimer et al., 1998) that might affect sensory gating mechanisms or direct corticopetal connections to the insula and PFC may be involved (Henderson et al., 2004; Kimmerly, O'Leary, Menon, Gati, & Shoemaker, 2005). Future studies using electrocortical or imaging techniques may shed light on the underlying neural mechanisms.

In conclusion, the current results suggest that baro-afferent signal transmission facilitates visual selection of task relevant information. Baroreceptor-mediated inhibition during the cardiac systole may reduce interference imposed by highly distracting stimuli.

3.6 Author Notes

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Chapter IV

Baroreceptor Activity Impacts upon Controlled but not Automatic Distractor Processing

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4.1 Abstract

Changes within the cardiovascular system have been shown to alter sensorimotor and memory performance, pain perception as well as cortical arousal. This influence is assumed to be mediated by afferent feedback of baroreceptors that when stimulated exert inhibitory effects on cortical structures. Mainly responsible for short-term regulation of blood pressure, afferents of the baroreceptors are widely connected to subcortical and cortical structures like the insular cortex. A putative impact on cognitive control processes remains an open question, however. Using a sequential distractor priming task, the present study investigated whether inhibitory influences of baroreceptor activation apply to selective information processing in the presence of irrelevant information. In particular, we assessed distractor-response binding and Negative Priming as indices of automatic and controlled distractor processing, respectively. Baroreceptor activation was experimentally manipulated by the systematic variation of body position. The results showed that only Negative Priming but not distractor-response binding was modulated by body position suggesting that controlled but not automatic processing of distractors is affected by baroreceptor activity.

4.2 Introduction

The inner organs of the body are interconnected with the central nervous system (CNS) via distinct neuronal pathways (Jänig, 1995, 2006). Those communication pathways comprise the spinal cord and brain stem that are directly involved in the regulation and adaptation of inner organ functions. Visceral information is further transferred to higher CNS structures like the insular cortex (e.g., Aziz, Schnitzler, & Enck, 2000) allowing for distinct representations and the integration of bodily sensations, emotional awareness, and conscious-

ness of the self (Craig, 2003; Damasio, 2003; Gray, Harrison, Wiens, & Critchley, 2007; Dworkin, 2000). Vegetative information from baroreceptor afferents concerning changes in systemic blood pressure for example is relayed both to brain stem structures that mediate reflexive effects on vasomotor control (Aicher, Kurucz, Reis, & Milner, 1995; Masuda, Terui, Koshiya, & Kumada, 1991; Ross, Ruggiero, & Reis, 1985) as well as to other CNS structures like the reticular formation, the hypothalamus, limbic structures, and cortical areas (e.g., Cechetto & Saper, 1987; Grindstaff, Grindstaff, Sullivan, & Cunningham, 2000; Henderson et al., 2004). Arterial baroreceptors are located within the vessel walls of the aortic arch and the carotid sinus and respond to deformations of the vessel walls due to changes in intra-arterial pressure (Dembowsky & Seller, 1995). In the case of a rise in arterial blood pressure a drop in heart rate and peripheral resistance can be observed down-regulating the blood pressure (Davos, Davies, & Piepoli, 2002). The transmission of cardiovascular information to CNS structures is also involved in cognition and emotion (Craig, 2002; Critchley & Harrison, 2013; Menon & Uddin, 2010) with widespread associations of the reticular formation assumed to mediate extra-cardiovascular effects associated with the activation of baroreceptors (Dembowsky & Seller, 1995). That is, the activation of baroreceptors has been found to induce a general inhibitory influence on the CNS (Dembowsky & Seller, 1995; Rau & Elbert, 2001) reflected in decreased cortical activation (e.g., Elbert et al., 1988; Rau & Elbert, 1991; Sandman, Walker, & Berka, 1982; Walker & Sandman, 1982), the attenuation of brain stem-based reflexes (e.g., Schulz et al., 2009a; Edwards et al., 2003; Edwards, Ring, McIntyre, & Carroll, 2001), pain perception (e.g., Apkarian, Jyväsjärvi, Kniffki, Mengel, & Stiefenhofer, 1989; Dworkin et al., 1994; Edwards et al., 2003), sensory (Requin & Brouchon, 1964; Saxon, 1970), and sensorimotor processes (e.g., Birren, Cardon, & Phillips, 1963; Edwards, Ring, McIntyre, Carroll, & Martin, 2007; Stewart, France, & Suhr, 2006; but see Jennings & Wood, 1977; Thompson & Botwinick, 1970). In addition, the cortical processing of nociception as

indexed by pain-evoked potentials (e.g., Brody et al., 1997; Edwards, Inui, Ring, Wang, & Kakigi, 2008; Gray, Minati, Paoletti, & Critchley, 2010), the evaluation of reflex-eliciting (Schulz et al., 2009b) and affective stimuli (Garfinkel et al., 2014; Gray et al., 2012), meta-cognitive judgment (Garfinkel et al., 2013) as well as short- (Martins, McIntyre, & Ring, 2014) and long-term memory (Garfinkel et al., 2013) have been shown to underlie the influence of variations in baroreceptor loading during the course of the cardiac cycle or due to externally induced baroreceptor stimulation. Thus, to date literature on extra-cardiovascular effects of baroreceptor activation implies that those are not confined to simple sensory and sensorimotor processes (for reviews, see Elbert & Rau, 1995; Rau & Elbert, 2001) but might even impinge on more complex cognitive processes. The present study aimed at investigating potential effects of baroreceptor activation on cognitive control processes. In particular, when humans encounter relevant and irrelevant information in a specific situation, selection processes have to take place in order to coordinate actions effectively and to choose and perform the most adequate response (e.g., James, 1890; Neumann, 1987; Styles, 2006). At least two mechanisms have been discussed as to how humans process irrelevant information in such selection situations. On the one hand, selective attention towards the relevant information and additionally selective ignoring of irrelevant information has been suggested for cognitive control of actions (e.g., Cowan, 1988; Neill, 1977; Neumann, Cherau, Hood, & Steinnagel, 1993; Houghton & Tipper, 1994). In particular, it has been argued that selective inhibition of distracting objects facilitates responding in a selection situation in which interference arises. On the other hand, irrelevant information is also processed in a more automatic fashion; that is, even irrelevant objects retrieve previous entries in memory (for example, they can retrieve action that was encoded together with them; Frings, Rothermund, & Wentura, 2007) and thereby influence behavior. We argue that by stimulating baroreceptor activity we infringe cognitive inhibition used for selective attention processes while at the same time automatic

retrieval of stimulus-response (S-R) routines should not be influenced. To this end, we used a sequential distractor priming paradigm, in which indices for both types of distractor processing can be simultaneously measured. In particular, Negative Priming (NP) effects can be seen as indices for controlled distractor processing while distractor-response binding (DRB) effects are pure retrieval effects that are more or less independent from selective attention. We will shortly introduce both effects before we outline how we manipulated baroreceptor activity.

4.2.1 Negative Priming and Distractor-Response Binding

A typical task that necessitates cognitive control processes involved in selective attention is the NP task (Allport, Tipper, & Chmiel, 1985; Tipper, 1985; see Fox, 1995 for a review). Participants respond to a target object while ignoring irrelevant or distracting stimuli. Usually studied in a prime-probe sequence, NP occurs when a previously ignored prime stimulus is repeated as the probe target (Ignored Repetition, IR) leading to slowed reaction times (RTs) and higher error rates compared to prime-probe sequences without stimulus repetitions (Dalrymple-Alford & Budayr, 1966; Neill, 1977). This slowing of participants' responses is assumed to reflect an after-effect of ignoring the distracting prime item. Thus, there appears to be a general consensus in the literature that NP taps into selective control mechanisms (see Tipper, 2001). However, the exact nature of these control processes is still being debated. A coarse-grained taxonomy of theories of NP differentiates between inhibition- (Houghton & Tipper, 1994; Tipper, 1985) and retrieval-based accounts (Milliken, Joordens, Merikle, & Seiffert, 1998; Neill, 1997; Rothermund, Wentura, & De Houwer, 2005). According to the inhibition theory, the representation of the distractor stimulus is thought to be actively suppressed by mechanisms of selective attention during the processing of the prime episode, and that this inhibition persists until the presentation of the next display. Thus, when the ignored

distractor from the previous trial becomes the target in the current trial (IR), the recently inhibited representation now has to be activated in order for the participant to respond correctly, and hence NP occurs. By contrast, according to retrieval theories, NP is caused by the fact that perceiving a target activates memory traces associated with that particular stimulus. In the IR condition, the last memory trace of the current target stimulus may contain information like ‘distractor’ or ‘do-not-respond’, and it is this information that interferes with the execution of rapid and accurate responses to the current target. Although this debate continues until today, most researchers and NP theories agree that it is the selective ignoring of the prime distractor leading to NP (e.g., Frings & Spence, 2011). As a result, the NP effect can be seen as an after-effect of cognitive control in the prime display and hence as an index for measuring controlled distractor processing. However, not each and every aspect of our behavior can be intentionally controlled. Other mechanisms that do not tap onto cognitive resources are therefore necessary. The retrieval of previous S-R episodes might play an important role for automatic and less resource-demanding guidance of behavior. In particular, the binding of stimulus and response features into an ‘instance’ (Logan, 1988) or ‘event file’ (Hommel, 1998, 2004) in episodic memory affects behavior by automatic retrieval of responses (Henson, Eckstein, Waszak, Frings, & Horner, 2014; for a review on S-R binding). Reencountering the stimulus of such an event file leads to a retrieval of the entire episode from memory, including the associated response (e.g., Denkinger & Koutstaal, 2009; Hommel, 1998, 2004; Logan, 1988; Pösse, Waszak, & Hommel, 2006). This retrieval of previous actions operates fast and automatically, exerting efficient bottom-up control of behavior by establishing stimulus-driven behavioral routines. In addition, the storage and retrieval of event files is not restricted to relevant stimulus features. Even distractors can be integrated with responses, so that subsequent presentations of a distractor stimulus can also lead to a retrieval of the response that was executed during a previous encounter with the distractor (Rothermund et al.,

2005; see also Frings et al., 2007; Gibbons & Stahl, 2008; Mayr & Buchner, 2006; Mayr, Buchner, & Dentale, 2009); this distractor-based retrieval of previous responses has been labelled distractor-response binding (DRB). DRB can be operationalized by the interaction of response and distractor relation in a sequential prime-probe distractor priming task. Specifically, the repetition of a distractor from prime to probe should improve performance if the to-be-executed response is repeated as well. In this case the prime response retrieved by the distractor is compatible to the currently demanded response and will therefore facilitate responding to the probe. In case of a response change, on the other hand, the prime response retrieved by the distractor is incompatible to the currently demanded response and will lead to response interference, hence, hamper responding to the probe. Distractor along with response repetition therefore leads to faster responses to the probe display whereas distractor repetition along with response changes leads to a slowing of probe responses (Frings et al., 2007). Distractor-response bindings appear to operate on an automatic level. That is, the allocation of attention to a stimulus is not a necessary precondition for DRB to occur (Rothermund et al., 2005; Hommel, 2005; but also see Hommel & Colzato, 2004; Moeller & Frings, 2014). Further, no repeated exposure or practice is needed, as bindings can emerge even after a single exposure (e.g., Horner & Henson, 2009). In short, for S-R bindings to be formed and retrieved, temporal contiguity and perceptual grouping have become apparent as the only necessary and sufficient framework conditions (Frings & Rothermund, 2011; Hommel, 2005) Finally, Giesen et al. (2012) showed that DRB is independent from controlled distractor inhibition. Taken together, the binding of distractors and responses can therefore be seen as a measure of automatic processing of distracting information.

4.2.2 Tonic manipulation of baroreceptor activity

Rather long-term, tonic effects of increased versus decreased baroreceptor activity can be studied by manipulating circulatory parameters via variations in body position. For this purpose, participants are positioned on a tilt table aligned with different inclination angles (Vaitl, 1989). Physiological parameters under orthostatic compared to supine body position can be assessed. Previous reports demonstrated pronounced cardiovascular changes in human organisms under orthostatic demands; that is, a decrement in stroke volume, and consequently in cardiac output, due to venous pooling in the lower limbs. Further, counter-regulatory mechanisms like an increase in diastolic blood pressure and heart rate can be observed (e.g., Tuckman & Shillingford, 1966; Wieling, 1989; Witzleb, 1983). Changes in heart rate and blood pressure set in within a few seconds and remain at a stable level for at least 30 minutes (Vaitl, 1989), making the method suitable for the investigation of long-term effects of changes in baroreceptor activation (Vaitl, 1989; Vaitl & Gruppe, 1991). During head-down tilt, ventricular preload, stroke volume as well as pressure within the vessels of the pulmonary and the thoracic part of the systemic circuit are augmented and accompanied by a decrease in heart rate (Bestler, Schandry, Weitkunat, Keller, & Bader, 1989; Katkov & Chestukhin, 1980; Nixon, Murray, Leonard, Mitchell, & Blomqvist, 1982); the latter indicating increased baroafferent feedback as means of the counter-regulation of blood pressure change (Eckberg & Sleight, 1992; Iida et al., 1999). In the present study, participants worked through a sequential distractor priming paradigm consisting of a target letter flanked on either side by a distractor letter. The DRB and NP effect as indices of automatic and controlled distractor processing, respectively, were assessed. In order to manipulate long-term baroreceptor activation, participants were either positioned with their upper body tilted upwards by $+6^\circ$ or downwards by -6° . The chosen inclination angles allowed us (1) to minimize physiological side effects, like for instance hampered return of venous blood from the brain, face, and neck, or pronounced

inner organ (e.g., brain, eye, heart, lung) pressure changes, that would be expected for more extreme inclination angles (cf. Katkov & Chestukhin, 1980; Naylor, Chow, McLean, Heard, & Avolio, 2005) and (2) to minimize non-targeted physiological effects confounded with the different body positions by realizing comparable conditions. Furthermore, while sufficient to affect baro-afferent transmission (Iida et al., 1999) the implementation of relatively small inclination angles makes the method more suitable for the study of cognitive phenomena as it is more comfortable for the participant (Vaitl & Gruppe, 1992) and therefore less prone to unwanted effects on psychological parameters like mood or well-being. Given the bottom-up nature of binding processes we expected an impact of increased baroreceptor activity during head-down tilt on effects of controlled distractor processing (NP) while effects of automatic distractor processing (DRB) should be independent of baroreceptor-induced impairments of cognitive functioning.

4.3 Method

4.3.1 Participants

67 students from the University of Trier (40 female) aged between 19 and 31 years ($M = 23.90$, $SD = 2.74$) participated in the study. Prior to their participation the physical health status was assessed using a health questionnaire. Exclusion criteria were any actual health complaints, abuse of illicit drugs within the last six months, medication other than occasional pain killers and oral contraceptives, confirmed somatic or psychiatric diseases within the last six months other than standard infections or minor injuries. All participants reported normal or corrected-to-normal vision. Four further participants were not included in the data analysis. Two data sets were incomplete due to technical problems during data acquisition, one partici-

part did not follow the instructions of the experimental task, and the fourth had to be discarded due to outlier heart rate values during the resting state (heart rate > 100 bpm). Heart rate and blood pressure of the valid participants were within normal range. Mean resting heart rate was $M = 70.3$ ($SD = 9.9$), mean systolic blood pressure was at $M = 113.1$ mmHg ($SD = 11.8$), and mean diastolic blood pressure was at $M = 68.1$ ($SD = 6.3$). Mean BMI was $M = 22.3$ kg/m² ($SD = 2.1$). All participants signed written informed consent and were made aware of their right to discontinue participation in the study at any time. They received 10 € for their participation.

4.3.2 Physiological Measures

Blood pressure and heart rate were recorded at two minute intervals via a standard brachial cuff oscillometric Dinamap monitor (Dinamap SX 1846, Critikon, US) attached to the left arm during initial resting baseline, the practice, adaptation, and experimental phase, as well as during the post experimental resting phase.

4.3.3 Materials and Apparatus

For the resting phases participants were seated on a comfortable chair, during practice, and the experimental block they reclined on an upholstered tilt table that could be tilted by the experimenter by 0° (horizontal), -6° (head-down tilt), and +6° (head-up tilt). A standard colour monitor was attached to a wall-mounted swivel arm that could be adjusted to warrant a standardized distance of 60 cm from the participant's forehead in each tilting condition. The experiment was conducted using E-prime software (E-prime 2.0, Psychology Software Tools, Inc., US). The stimuli shown on the display were the letters D, F, J, and K in the font Courier New. Each letter was about 0.86° in width and height and assigned to one of four response keys. During the practice block a paper tag on the monitor frame with the correct assignment

of letters was visible and feedback about the correctness of the response was given. Prime and probe displays consisted of a horizontal row of three adjacent (width of stimulus triplet 2.67°) letters, with the two outer letters (distractors) being always identical and depicted in green, while the centred stimulus (target) was depicted in red. Participants responded via key presses using a self-made response pad, i.e., four computer keys were attached on a horizontal axis on a light board that was placed on the participant's lower torso so that the keys could be reached easily. Arms of the participants rested on the tilt table to either side of the body. For a schematic display of the test arrangement see Figure 6. It was ensured by the experimenter that the participants were comfortable, with clear view of the computer monitor, and the computer keys easily controllable.

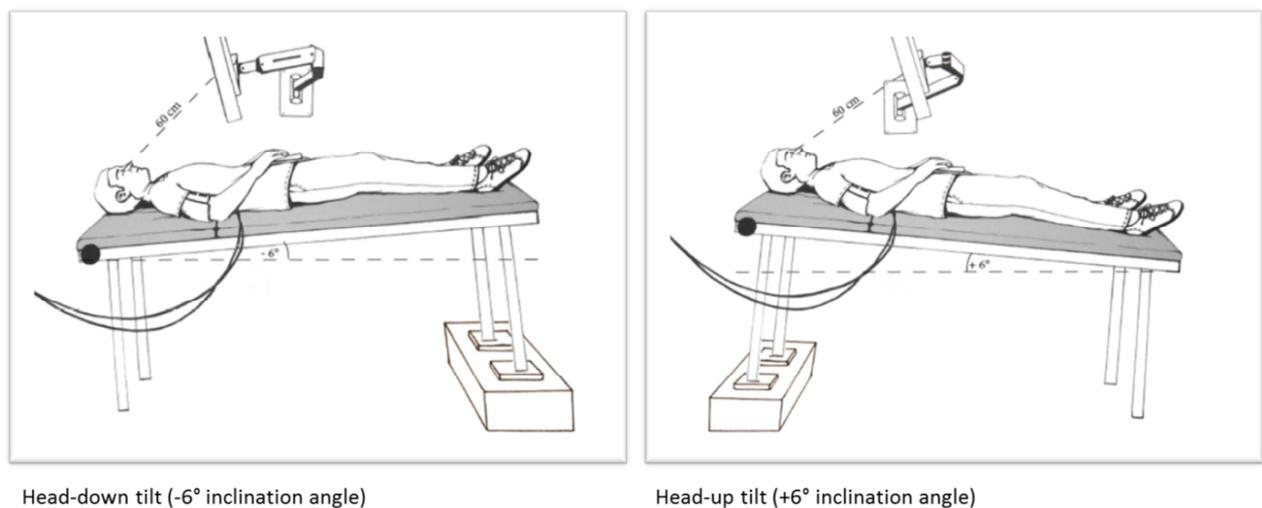


Figure 6. Schematic display of the experimental set-up. Half of the participants performed the experimental task head-down with an inclination angle of -6° , half of the participants head-up with an inclination angle of $+6^\circ$.

4.3.4 Procedure

Each participant was tested individually in a quiet room. The assignment to one of two experimental groups (head-down tilt vs. head-up tilt) was set before each session on a rotating basis. At the beginning of each session, participants were familiarized with the apparatus and

a health questionnaire was completed. A ten minute resting period, a practice block of about five minutes, a four minute adaptation phase, and the experimental task with a duration of approximately ten minutes followed. A session ended with a six minute resting phase. Before the beginning of the adaptation phase the tilt table was either tilted by -6° or $+6^\circ$ inclination angle by the experimenter.³ During resting participants were positioned in a seated, during practice in a horizontal body position. The experimental task consisted of 140 trials divided into two blocks of 70 trials. Previous to the first block 42 practice trials were completed. Between the two experimental blocks there was a one minute break. For the task participants placed their left and right middle and index fingers on the four computer keys attached to the response board. Instructions were given on the computer display. The participant's task was to identify the red target letter by pressing the corresponding response key as fast and accurately as possible. The two distractor letters flanking the target ought to be ignored. Each trial consisted of one prime and one probe display, which could be interrelated to each other in seven different ways. The target letter in prime and probe and therefore the required response could be identical (response repetition) or changed (response change). At the same time the prime and probe distractors could be identical (distractor repetition) or changed (distractor change). Furthermore, the target letter of the probe could be a repetition of the distractors of the prime display (IR). But also could the distractors of the probe be identical to the target of the prime (target-to-distractor), or the target of the probe could be identical to the distractors of the prime with the probe distractors being the same letters as the target of the prime at the same time (switch condition). The trials were presented in random order with the letters randomly assigned to the prime and probe targets and distractors according to the current condition.

³ A control experiment ($N = 10$) indicated that for an experiment of the same duration, same experimental set-up, and a similar task no differences in pleasantness/unpleasantness, positive and negative affect, interest, arousal, and alertness due to the chosen inclination angles are to be expected, all $ps > .05$.

Each condition was run with 20 trials in total during the experimental phase and practiced with 6 trials during the practice block. The exact trial procedure is depicted in Figure 7. Each trial began with the presentation of a fixation cross for 500 ms, then a black screen appeared for another 500 ms, after which the prime display emerged on the screen until a response was made. Subsequently, a black screen was inserted for 500 ms before the probe display was presented; again until a response was made. During the practice block participants received feedback about the correctness of the responses made via a respective display presented for 1000 ms following the response. In the experimental blocks only false responses were followed by an error message. In the course of a session fourteen blood pressure and heart rate measurements were taken per subject, one at the beginning followed by five every two minutes during initial resting baseline, one at the end of the practice block, four during the experimental tilt block, and three (one every two minutes) during the post experimental resting phase. The four measurements during the experimental tilt block included two measurements during the adaptation phase (one every two minutes), one during the one minute break between the two experimental blocks and one immediately after the end of the experimental task. Cardiovascular measures usually habituate over time. This linear trend was removed by individual linear regression analysis. The second measurement point during the experimental tilt block (target heart rate time point) was a priori chosen for statistical comparisons, because at this time point arousal effects from position change and cognitive testing were expected to be minimal.

4.3.5 Design

To test the hypothesis on controlled distractor processing NP effects were computed. The NP effect is indexed by a difference score. Therefore for each participant the mean RT to probe displays within IR trials is subtracted from the mean RT within control trials in which no stimulus is repeated (i.e., distractor and response change). NP effects were compared with

respect to the body position (head-down tilt vs. head-up tilt). To test the hypothesis on automatic distractor processing, DRB effects were computed. The DRB effect is indexed by the interaction of distractor and response relation. That is, the effect of a distractor-to-distractor repetition on response repetition trials is compared to the effect of a distractor-to-distractor repetition on response change trials. It is therefore calculated by subtracting the difference of the mean RTs to probe displays for trials in which both the response and the distractors change versus trials in which only the response but not the distractors change from the difference of the mean RTs to probe displays for trials in which both response and distractors are repeated versus trials in which only the response but not the distractors are repeated. Distractor-response binding effects were then compared with respect to the body position (head-down tilt vs. head-up tilt).

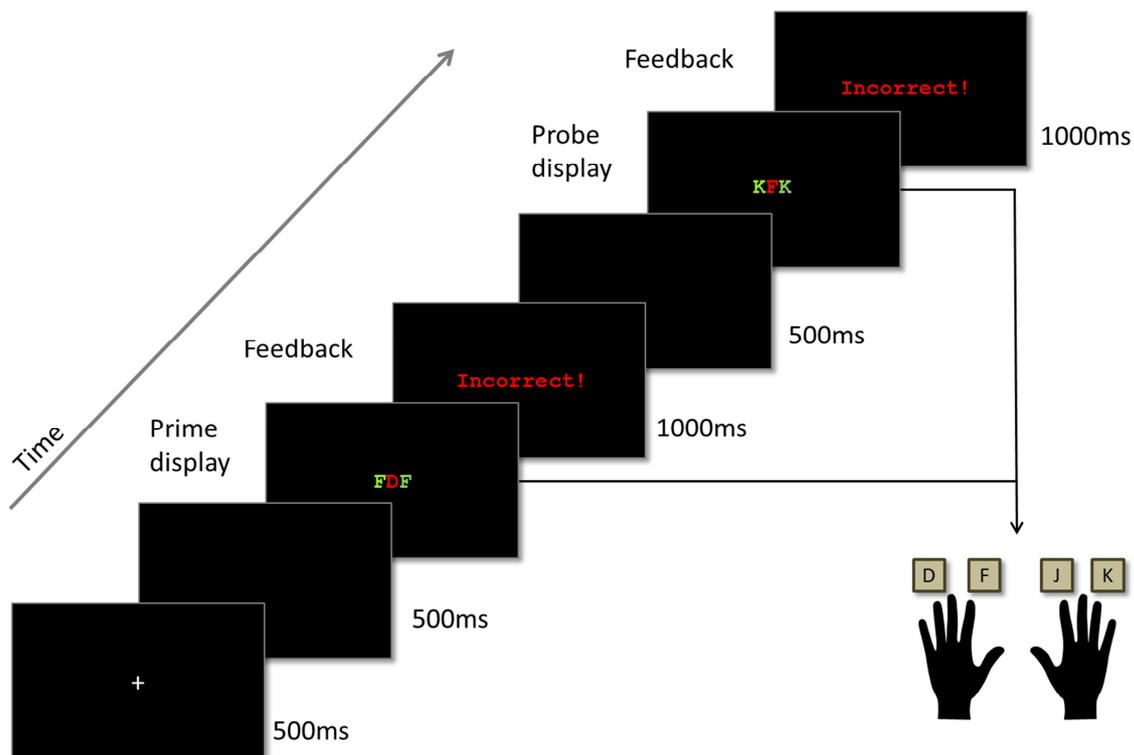


Figure 7. Sequence of events in an experimental trial. Middle letters (targets; always depicted in red) had to be identified via the corresponding key press. Flanking letters (distractors; always depicted in green) were to be ignored. An example of an Ignored Repetition trial is depicted.

4.4 Results

4.4.1 Cardiovascular Measures and Manipulation Check

Since heart rate data during the tilt procedure differed from normal distribution (Kolmogorov-Smirnov test, $Z_{K-S} = .171$, $p < .01$) non-parametric statistical procedures were chosen to test for differences between groups. As expected, initial (baseline) cardio-vascular measures did not differ between groups. There was also no difference between groups for blood pressure during the tilt procedure. However, heart rate during head-down tilt was lower as compared to head-up tilt (two-group Savage Test, $Z = 1.71$, one-sided $p < .04$) (see Table 3).

Table 3. Mean heart rate (HR; in bpm), systolic blood pressure (SBP; in mmHg), and diastolic blood pressure (DBP; in mmHg) (standard deviations in parentheses) for initial (baseline) measurement and the experimental phase (during tilt procedure) as a function of body position.

	Initial (Baseline)			Tilt Procedure		
	HR	SBP	DBP	HR	SBP	DBP
HDT	66.0 (12.3)	112 (9.6)	68.4 (4.6)	62.8 (6.4)	109 (11.0)	59.7 (4.9)
HUT	65.8 (8.9)	111 (11.4)	71.4 (5.5)	66.2 (10.9)	111 (9.5)	59.6 (5.1)

Note. HDT: Head-down tilt (-6° ; $n = 34$); HUT: Head-up tilt ($+6^\circ$; $n = 33$). Initial (baseline) was set in seated body position for both groups.

For RT analysis only sequences with correct responses on prime and probe were considered. Individual RT distributions for each participant were computed. RTs, which exceeded the third quartile of the participants RT distribution by more than three interquartile ranges or were faster than 200 ms were considered outliers and not incorporated in the statistical analysis.

sis. Two participants showing unusually large NP effects (-156 ms and +135 ms) when compared to the sample mean of -13 ms, 95% confidence interval (95% CI) [-26, 0] were dropped for the RT analyses (all RT results remain exactly the same when these participants were included and non-parametric tests were used⁴). Mean RTs and error rates are depicted in Table 4. Note that tilt position revealed no main effects on RTs or error rates, both $ps > 1$.

4.4.2 Controlled Distractor Processing (Negative Priming)

A two-way analysis of variance (ANOVA) on RT with priming condition (control versus ignored repetition) as within and body position (head-down tilt versus head-up tilt) as between subjects variables revealed a Negative Priming effect of -13 ms, 95% CI [-25, -2], $F(1, 63) = 5.93$, $p = .018$, $\eta_p^2 = .09$. This effect was further qualified by body position, $F(1, 63) = 6.49$, $p = .013$, $\eta_p^2 = .09$, indicating a statistically different Negative Priming effect in dependence of the body position with a mean difference between the two body positions of $M_{HDT-HUT} = 28$ ms, 95% CI [6, 50] (see Figure 8). In particular, further analyses showed that participants in the head-up condition showed a Negative Priming effect that was statistically different from zero, $M_{NP-HUT} = -28$ ms, 95% CI [-47, -8], $t(31) = -2.90$, $p = .007$, $d_z = .52^5$, whereas par-

⁴ A Kolmogorov-Smirnov test for two samples on NP effects based on participants' RTs revealed a statistically significant difference in the distribution of the ranked NP effects between the two groups $z_{K-S} = 1.62$, $p = .011$ (Mann-Whitney U $z_U = -1.84$, $p = .065$). Participants in the head-up condition showed an NP effect in a Wilcoxon-signed rank test, $z_W = -2.3$, $p = .022$ ($z_S = -2.09$, $p = .037$, in a sign-test) whereas participants absolving the task with their head down did not show an NP effect in a Wilcoxon-signed rank test $z_W = -.74$, $p = .457$ ($z_S = -.51$, $p = .607$ in a sign-test). A Kolmogorov-Smirnov test for two samples on DRB effects on the other hand revealed no statistical difference in the distribution of the ranked DRB effects between the two groups $z_{K-S} = .704$, $p = .705$ (Mann-Whitney U $z_U = -.64$, $p = .522$). Participants in the head-up tilt condition, $z_W = -3.73$, $p < .001$ ($z_S = -3.83$, $p < .001$, in a sign-test), and in the head-down tilt condition, $z_W = -2.95$, $p = .003$ ($z_S = -2.57$, $p = .010$, in a sign-test), showed a distractor-response binding effect.

⁵ Cohen's d_z based on the formula $d = \frac{t}{\sqrt{df}}$ is reported (Rosenthal, 1984).

Participants absolving the task with their head down did not show a Negative Priming effect,

$M_{NP,HDT} = 1$ ms, 95% CI [-11, 12], $t(32) = .11$, $p = .916$.

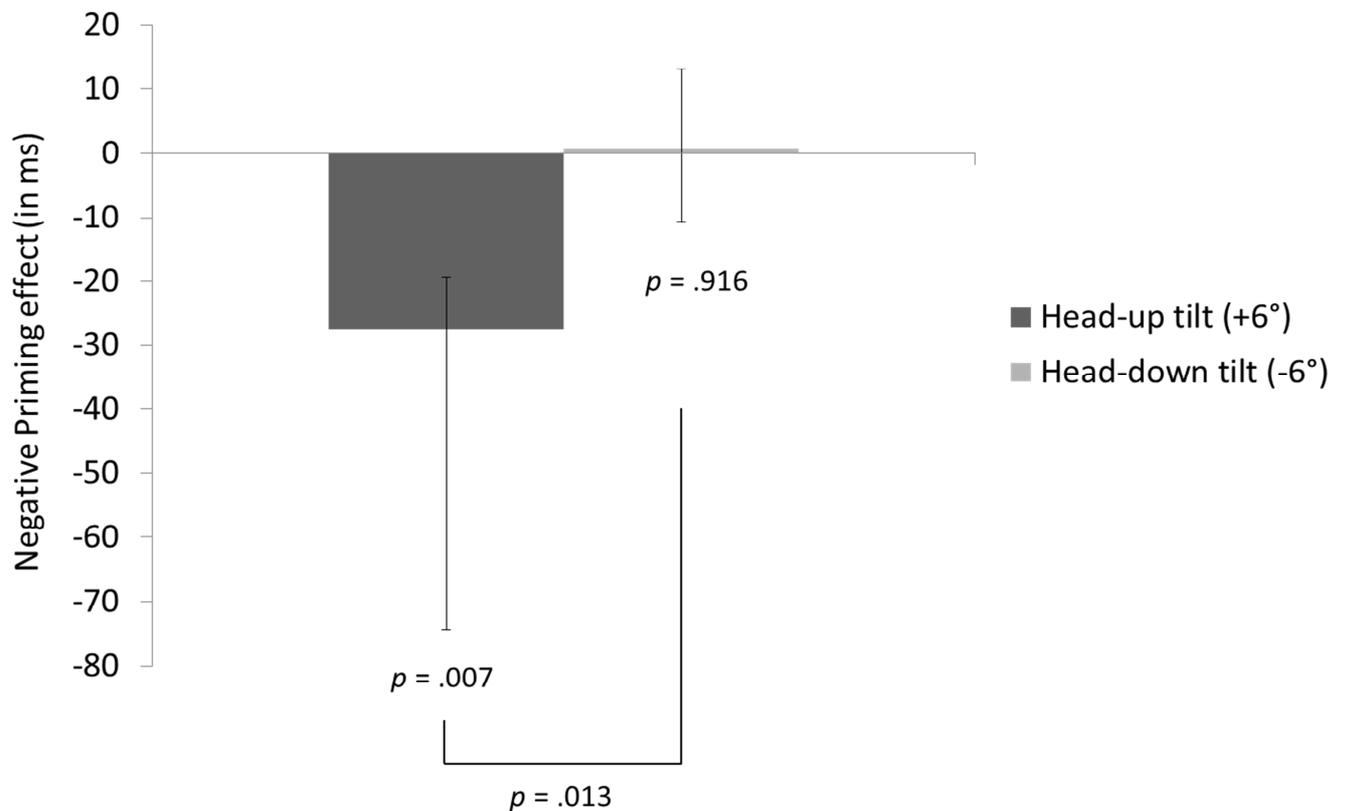


Figure 8. Negative Priming effects (in ms; within-subjects comparison) as a function of body position (between-subjects comparison). Averaged RT differences and 95% confidence intervals of the mean are depicted. The NP effect is calculated by subtracting the ignored repetition from control trials.

Overall RT was not modulated by body position, $F < 1$. A two-way ANOVA on error rates indicated no main effect of priming condition, $M_{NP} = -0.5\%$, 95% CI [-1.8, 0.7], $F < 1$. Negative Priming in error rates was modulated by body position, $M_{HDT-HUT} = -2.6\%$, 95% CI [-5.0, -0.2], $F(1, 63) = 4.62$, $p < .05$, $\eta_p^2 = .068$, with a Negative Priming effect that statistically differed from zero for the head-down condition, $M_{NP,HDT} = -1.8\%$, 95% CI [-3.5, -0.2], $t(32) = -2.248$, $p < .05$, $d_z = .40$, but not for participants absolving the task with their head up,

$M_{NP,HUT} = 0.8\%$, 95% CI [-1.1, 2.6], $t(31) < 1$. Overall error rate was not modulated by body position, $F < 1$.⁶

Table 4. Mean Reaction Times (RTs) for responses to the probe display (in ms; standard deviations in parentheses) and Percentages of Errors (PEs) as a function of body position and the response and distractor relations between prime and probe display.

	RT		PE	
	HDT	HUT	HDT	HUT
Response Change Distractor Change	747 (128)	758 (158)	1.8 (2.4)	2.5 (4.0)
Response Repetition Distractor Repetition	568 (111)	575 (120)	0.5 (1.5)	0.2 (0.9)
Response Repetition Distractor Change	601 (108)	617 (109)	0.5 (1.5)	0.3 (1.2)
Response Change Distractor Repetition	753 (146)	773 (153)	3.9 (3.9)	2.0 (3.3)
Ignored Repetition	746 (123)	786 (156)	3.6 (4.9)	1.7 (3.3)
Overall	705 (120)	721 (132)	2.4 (1.6)	1.8 (2.2)

Note. HDT: Head-down tilt (-6° ; $n = 33$); HUT: Head-up tilt ($+6^\circ$; $n = 32$).

⁶ In contrast to NP effects based on RTs, which showed the same pattern of results regardless of whether parametric as well as non-parametric analyzes were computed, NP effects based on error rates were unreliable as non-parametric analysis did not reveal the IA as well as NP effects. We therefore limit our discussion to the RTs.

4.4.3 Automatic Distractor Processing (Distractor-Response Binding)

A three-way analysis of variance (ANOVA) on RT with response relation (response repetition versus response change) and distractor relation (distractor repetition versus distractor change) as within and body position (head-down tilt versus head-up tilt) as between subjects variables revealed a main effect of response relation, $F(1, 63) = 255.46, p < .001, \eta_p^2 = .80$, indicating faster responses when the prime response had to be repeated as probe response, $M_{RR} = 158$ ms, 95% CI [139, 176]. A main effect of distractor relation was also significant, $F(1, 63) = 6.83, p = .011, \eta_p^2 = .10$, indicating faster responses when the distractor of the prime was the same as the probe distractor, $M_{DR} = 20$ ms, 95% CI [12,28]. Most importantly, the distractor-response binding effect as indicated by an interaction of response and distractor relation was also statistically significant, $F(1, 63) = 13.89, p < .001, \eta_p^2 = .28$, with $M_{DRB} = 23$ ms, 95% CI [14, 33] but the magnitude of the distractor-response binding effect was not modulated by body position, $M_{HDT-HUT} = -9$ ms, 95% CI [-28, 10], $F(1, 63) = .89, p = .348, \eta_p^2 = .01$ (see Figure 9). Distractor-response binding effects were then computed as the difference between distractor-repetition and distractor-change trials with respect to response repetition. Further analyses showed that both participants in the head-up tilt condition, $M_{DRB,HUT} = 28$ ms, 95% CI [12, 43], $t(31) = 3.63, p = .001, d_z = .65$, and in the head-down tilt condition, $M_{DRB,HDT} = 19$ ms, 95% CI [7, 31], $t(32) = 3.28, p = .003, d_z = .57$, showed a statistically significant distractor-response binding effect. Overall RT was not modulated by body position, $F < 1$. The same three-way ANOVA on error rates showed no distractor-response binding effect, $F(1, 63) = 1.81, p = .183$, with $M_{DRB} = 0.1\%$, 95% CI [0.0, 0.2] that was not modulated by body position, $M_{HDT-HUT} = 0.2\%$, 95% CI [-0.0, 0.5], $F(1, 63) = 3.28, p = .075$. Overall error rate was not modulated by body position, $M_{ER} = 0.8\%$, 95% CI [-0.1, 0.2], $F(1, 63) = 1.40, p = .241$.

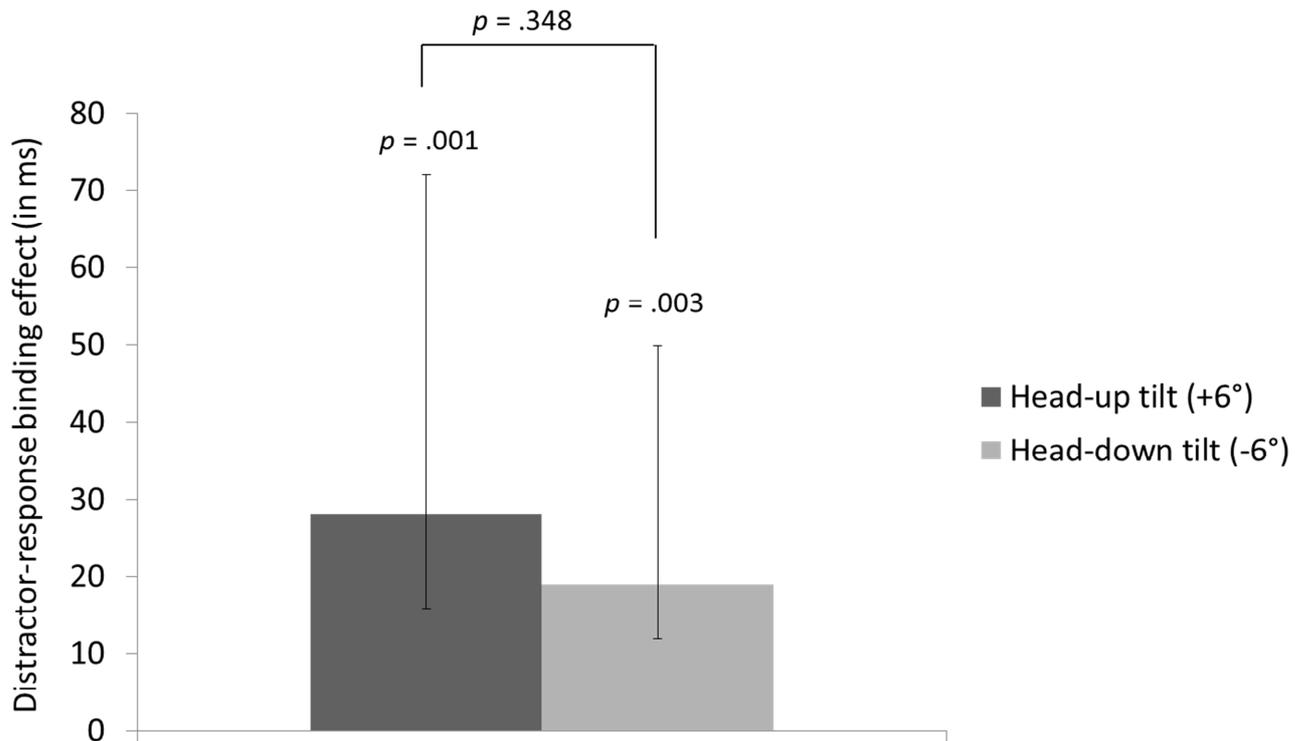


Figure 9. Distractor-response binding effects (in ms; within-subjects comparison) as a function of body position (between-subjects comparison). Averaged RT differences and 95% confidence intervals of the mean are depicted. The DRB effect is calculated by subtracting the mean RT difference of Response Change Distractor Change trials minus Response Change Distractor Repetition trials from the mean RT difference of Response Repetition Distractor Change trials minus Response Repetition Distractor Repetition trials.

4.5 Discussion

In the current study automatic and controlled distractor processing as indexed by distractor-response binding and Negative Priming, respectively, were assessed under decreased and increased baroreceptor loading by slight manipulation of participants' tilt angle during a lying body position. Head-down tilt was accompanied by a statistically significant reduction in heart rate as compared to head-up tilt, indicating that the tilt procedure, indeed, effectively changed baroreceptor activity. Our results show that Negative Priming but not distractor-

response binding was impaired during baroreceptor loading. In particular, both groups showed DRB effects not likely attributable to chance (that were statistically not different) while only the group with decreased baroreceptor loading showed statistically significant NP effects. Our findings indicate an inhibitory heart-brain link for cognitive control processes. However, those detrimental effects are not generalizable to distractor processing as a whole. Whereas cortical inhibition seems to affect controlled processes like inhibition and selection, automatic processes like the retrieval of S-R bindings (e.g., Frings & Wühr, 2007; Hommel, 2005) were not affected. This is in line with the observation that non-cardiovascular influences of baroreceptor activity on the CNS and behavior are not confined to brain stem-based reflexes (e.g., Schulz et al., 2009a; Edwards et al., 2001) or sensory perception (e.g., Requin & Brouchon, 1964; Saxon, 1970), but beyond that apply to cognitive functions based on cortical structures (e.g., Edwards et al., 2007; Elbert et al., 1988; Rau & Elbert, 1991; Schulz et al., 2009b; Vaitl & Gruppe, 1990, 1992; Walker & Sandman, 1982). Further, previous studies demonstrated that baroreceptor activity manipulated by variations in body position is associated with changes in electrocortical activity. Namely, inhibitory effects of increased baroreceptor loading during head-down tilt were indexed by elevated spectral power within the low frequency bands delta and theta (Gruppe, 1993; Vaitl & Gruppe, 1990, 1992); the latter frequency band being associated with states of low alertness (Schacter, 1977), absorbed attention (e.g., Galbraith, London, Leibovitz, Cooper, & Hart, 1970; Graffin, Ray, & Lundy, 1995) as well as the inhibition of neural pathways which are irrelevant for a current task (Nunez & Srinivasan, 2006; Schacter, 1977). The current results are further in line with the notion that baroreceptor related effects tend to be differential in nature (see Edwards et al., 2003; Garfinkel et al., 2014; Martins et al., 2014). On the one hand, controlled processes like the evaluation of stimulus intensities (Garfinkel et al., 2014; Gray et al., 2012; Schulz et al., 2009b) and the encoding and retrieval of information (Garfinkel et al., 2013; Martins et al., 2014) seem to be sus-

ceptible to naturally occurring variations in baroreceptor activation, the discrimination and identification of stimuli presented under low selection capacities on the other hand appear to be robust (Garfinkel et al., 2013, 2014). On a neural basis differential effects of baroreceptor activation on CNS structures distinguishable for NP and DRB might be conceivable as to account for the current results. That is, baroreceptor information exerts influences on brain structures beyond primary cardiovascular centers on the one hand via marked afferent connections to the (hypo-) thalamus, limbic structures and the cortex. On the other hand by inhibitory and excitatory input to the reticular formation and a wide range of other brain stem regions that themselves project to a number of structures within the CNS (Critchley & Harrison, 2013; Dembowsky & Sellar, 1995). In particular, cortical structures influenced by baroreceptor information are defined regions within the prefrontal, frontoparietal, and orbitofrontal cortex as well as the anterior cingulate and insular cortex (Cechetti & Saper, 1987; Henderson et al., 2004; Kimmerly, O'Leary, Menon, Gati, & Shoemaker, 2005). As recent neuropsychological studies hint at, likely candidates for CNS structures distinctive for NP include regions located within the frontal lobe (Metzler & Parkin, 2000; Stuss et al., 1999). Inhibitory influences of baro-afferent signal transmission might therefore impair inhibitory processes involved in NP by affecting corresponding neural substrates. Indeed, neural activity within the right dorsolateral PFC has repeatedly been shown to be increased during IR trials in both spatial and identity NP (Krueger, Fischer, Heinecke, & Hagedorf, 2007; Ungar, Nestor, Niznikiewicz, Wible, & Kubicki, 2010). That is, a structure found both to be involved in cognitive control processes (Cole & Schneider, 2007) and also to display increased activity during baroreceptor unloading (Kimmerly et al., 2005). Furthermore, regions of the parietal lobule and pallidum of the basal ganglia that are likely to be involved in NP (Bauer, Gebhardt, Ruprecht, Gallhofer, & Sammer, 2012; de Zubicaray, McMahon, Eastburn, Pringle, & Lorenz, 2006; Krueger et al., 2007) might be affected. By contrast, different brain areas have been distinguished for automatic

responses based on S-R bindings. That is, studies on repetition suppression, a potential CNS-based correlate of behavioral priming (Grill-Spector, Henson, & Martin, 2006), point to ventrolateral regions of the PFC, namely the left posterior and left inferior PFC, to be involved in the retrieval of previously formed S-R bindings (Dobbins, Schnyer, Verfaellie, & Schacter, 2004; Horner & Henson, 2008). Moreover, the left dorsal premotor cortex (PMd) and right inferior frontal gyrus are assumed to reflect the retrieval of S-R bindings (Horner & Henson, 2012; Race, Shanker, & Wagner, 2008). Interestingly, the left presupplementary motor area, and the PMd, areas involved in the selection, preparation, and control of movement (Kennerly, Sakai, & Rushworth, 2004; van Gaal, Scholte, Lamme, Fahrenfort, & Ridderinkhof, 2011; Yamagata, Nakayama, Tanji, & Hoshi, 2012), are in fact related to S-R learning (Race et al., 2008) but neither to NP nor have they been found to be modulated by baroreceptor loading or unloading (Kimmerly et al., 2005). Neural correlates responsible for movement control are therefore likely candidates to prevent automatic S-R retrieval from being disrupted by baro-afferent inhibition. On these grounds, the impairment of controlled distractor processing during a state of augmented baroreceptor activity, i.e., head-down body position, might be based on the inhibition of cortical structures such as the dorsolateral PFC that are involved in tasks that demand ample cognitive control (e.g., for the suppression of prepotent but inadequate responses in IR trials), but that are not recruited for relative automatic processes such as the retrieval of S-R bindings (cf. Cole & Schneider, 2007) or, in other words, that are bypassed by the automatic retrieval of S-R bindings (Horner & Henson, 2008; Race et al., 2008). In our study, we manipulated baroreceptor activity by means of changes in systemic circulation parameters due to variations in body position; a method originally introduced by Vaitl (1989). As changes in cardiovascular parameters like shifts in blood pressure and heart rate set in nearly immediately but remain constant for at least 30 minutes (Vaitl, 1989) long-term effects of baroreceptor induced inhibition on neural and behavioral parameters can be

well studied. Further, in distinction to the application of pharmacological substances impinging on vasoconstriction and -dilatation but that also bind to receptors located above the blood brain barrier (Rau & Elbert, 2001) no direct effects of different body position on the CNS are to be expected. By implementing relatively small inclination angles of -6° and $+6^\circ$ we further made the manipulation of body position a suitable method for the study of cognitive processes. Previous examinations show that extreme inclination angles provoke more discomfort and aversiveness than those closer to supine body position whereas participants' ratings do not differ for tilt orientation, i.e., between head-up and head-down tilt (Gruppe, 1993; Vaitl & Gruppe, 1992). In order to avoid any psychological side effects we therefore chose the smallest possible angles that have been proven to still evoke changes in baroreceptor activity (Iida et al., 1999). Further, small inclination angles minimize physiological effects other than cardiovascular volume shifts that are to be expected with more extreme inclination angles (e.g., Hayano et al., 1993; Katkov & Chestukhin, 1980; Naylor et al., 2005; Smith & Ebert, 1990). The monitoring of blood pressure and heart rate by measurements at several time points throughout the experimental session served as manipulation check for circulatory changes due to variations in participants' body position. The physiological data obtained validate the intended modulation of systemic circulation, i.e., of baroreceptor activation. That is, heart rate during head-down tilt body position during the experimental block was more reduced compared to the head-up tilt condition; probably reflecting a counter-regulatory mechanism induced by increased baroreceptor activation initiated by risen thoracic blood volume due to the body tilted head-downwards (cf. Iida et al., 1999; Nixon et al., 1982). Establishing this connection is of importance as to pinpoint the inhibitory effects in our study to baro-afferent feedback mechanisms as was shown to be the crucial factor for dampening effects during states of increased arterial pressure (Schulz et al., 2009a). It is to note, however, that the head-down tilted body position might have also gone along with an increase in interoceptive signal

transmission as it is to be expected that cardiac detection performance enhances with tilted compared to perpendicular body positions (e.g., Schandry, Bestler, & Montoya, 1993; but see Ring, Liu, & Brener, 1994). As it was indicated previously that individuals higher in trait sensitivity to heartbeat responses might be able to compensate to a certain degree for deteriorating effects of baroreceptor activation on cognition (Garfinkel et al., 2013), changes in interoception seem to be unlikely to account for the current results, though, as enhanced interoception would counteract the diminished NP-effect observed during head-down compared to head-up tilt. Nevertheless, future studies might be able to disentangle merely baro-afferent from viscerosensitive processing in general by incorporating measures of interoception allowing for comparisons between participants and conditions (see Garfinkel et al., 2013). Furthermore, it is worth noting that the NP and DRB effect differ in reliability and effect size. While both cognitive effects proved to be robust (for NP see for example Fox, 1995; May, Kane & Hasher, 1995; for DRB see for example Frings, Moeller, & Rothermund, 2013; Giesen et al., 2012; Moeller & Frings, 2011), the NP usually displays a small reliability (e.g., Bestgen & Dupont, 2000; Friedman & Miyake, 2004; Park et al., 1996; Titz, Behrendt, Hasselhorn, & Schmuck, 2003). Conforming to this, NP and DRB differed with respect to effect sizes. NP showed an effect size of $\eta_p^2 = .09$ ($M_{NP} = -13$ ms) versus the DRB an effect size of $\eta_p^2 = .28$ ($M_{DRB} = 23$ ms); effect sizes that are consistent with previous observations (cf. Friedman & Miyake, 2004; Frings et al., 2007). With regard to the interpretation of the current results it should be noted that we observed a modulation of the less reliable effect; this hedges against explanations in terms of power issues. Still, future studies might want to use measures of controlled and automatic processing that elicit effects of equal size. It should further be complemented that during head-down tilt increased activation not only of arterial but further of cardiopulmonary baroreceptors is to be expected (Mark & Mancia, 2011; Vaitl & Gruppe, 1991). As stretch sensitive receptors located within the cardiopulmonary system cardiopulmonary

baroreceptors are primarily sensitive to changes in central venous pressure (Smith & Kampine, 1990). Their afferents project to similar CNS structures (Eckberg & Sleight, 1992; Henderson et al., 2004; Kimmerly et al., 2005), and, although psychophysiological less explored, they seem to exert inhibitory effects on non-cardiovascular parameters comparable to those of their arterial counterparts. That is, dampening effects of cardiopulmonary baroreceptor activity were found for startle responses (Richter, Schulz, Port, Blumenthal, & Schächinger, 2009), pain perception (D'Antono, Ditto, Sita, & Miller, 2000; Randich & Maixner, 1984; Sheps et al., 1992; Vaitl, Gruppe, Stark, & Pössel, 1996), and spontaneous cortical activity (Vaitl & Gruppe, 1990). Nevertheless, effects of arterial and cardiopulmonary baroreceptor activation must not be lumped together as there are several studies that indicate differential effects. That is, some studies found reflex elicitation (McIntyre, Kavussanu, & Ring, 2008) and reaction times (McIntyre, Ring, Hamer, & Carroll, 2007; Richter et al., 2009) being subject to arterial but not cardiopulmonary baroreceptor activation. The nature of arterial and cardiopulmonary modes of action therefore remains subject to further examination. Experimental set-ups warranting the differentiation between those two receptor types might be an encouraging way to pursue (cf. McIntyre et al., 2008; Richter et al., 2009). To conclude, our results provide a first indication that cortical inhibition due to increased baroreceptor activation affects cognitive control processes of selective attention while automatic distractor processing is not impaired. Negative Priming but not distractor-response binding was impaired by increased baroreceptor stimulation during head-down body position. The study therefore yields evidence for the modulation of controlled attention by differences in baroreceptor activity.

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Chapter V

Distractor Inhibition: Evidence From Lateralized Readiness Potentials

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5.1 Abstract

The present study investigated distractor inhibition on the level of stimulus representation. In a sequential distractor-to-distractor priming task participants had to respond to target letters flanked by distractor digits. Reaction time and stimulus-locked lateralized readiness potentials (S-LRPs) of probe responses were measured. Distractor-target onset asynchrony was varied. For RTs responses to probe targets were faster in the case of prime-distractor repetition compared to distractor changes indicating distractor inhibition. Benefits in RTs and the latency of S-LRP onsets for distractor repetition were also modulated by distractor-target onset asynchrony. For S-LRPs distractor inhibition was only present with a simultaneous onset of distractors and target. The results confirm previous results indicating inhibitory mechanisms of object-based selective attention on the level of distractor representations.

5.2 Introduction

In every waking moment, an abundance of multisensory stimuli impinges upon our sensory systems, with each stimulus potentially affording a range of different actions. In order to maneuver our way through the complex world around us, our brain has to rely on a limited number of simple and efficient processes and mechanisms. In particular, given the current action goals of an organism it is helpful to roughly divide the information into relevant and irrelevant information. In fact, our cognitive system has several ways as to process currently irrelevant information. One important mechanism is selective attention, that is, the ability to discriminate between relevant and irrelevant information. Attending and responding to only those aspects of our environment that are related to our goals, and not being distracted by stimuli that are irrelevant for or might interfere with the current task, is important for the top-

down control of behavior (Allport, 1987; Tipper, 1992). Selective attention is commonly assumed to entail two components (Frings, Wentura, & Wühr, 2012; Houghton & Tipper, 1994): A preferred processing of relevant information (activation) is accompanied by an active suppression of irrelevant, distracting information (distractor inhibition, DI). That is, once a stimulus is identified as being irrelevant, inhibition dampens the activation of the distractor representation (Houghton & Tipper, 1994; Wühr & Frings, 2008) or blocks its access to the response system to reduce interference (Buckolz, Edgar, Kajaste, Lok, & Khan, 2012; Tipper & Cranston, 1985). Another mechanism entails the integration of (ir-)relevant stimuli and responses into Stimulus-Response (S-R) episodes and their retrieval later on. The retrieval of previous behavioral episodes plays an important role for the automatization of behavior. According to instance-based or binding models the compound of stimulus and response is stored as an “instance” (Logan, 1988) or “event file” (Hommel, 1998, 2004) in episodic memory. Re-encountering the stimulus of such an event file leads to a retrieval of the entire episode from memory, including the associated response (e.g., Denkinger & Koutstaal, 2009; Hommel, 1998, 2004; Logan, 1988; Pösse, Waszak, & Hommel, 2006). This retrieval of previous actions operates fast and automatically, exerting efficient bottom-up control of behavior by establishing stimulus-driven behavioral routines (Henson, Eckstein, Waszak, Frings, & Horner, 2014). The storage and retrieval of event files is not restricted to relevant stimulus features. Even distractors can be integrated with responses, so that subsequent presentations of a distractor stimulus can also lead to a retrieval of the response that was executed during a previous encounter with the distractor (Frings, Rothermund, & Wentura, 2007; Gibbons & Stahl, 2008; Mayr & Buchner, 2006; Mayr, Buchner, & Dentale, 2009; Rothermund, Wentura, & De Houwer, 2005). There is a growing body of evidence suggesting that DI and distractor-based SR retrieval operate independently of each other (e.g., Giesen, Frings, & Rothermund, 2012; Moeller, Hommel, & Frings, 2015). Here we focus on the concept of DI. While response in-

hibition seems to be an accepted phenomenon (e.g., Aron, 2007; Hazeltine, Poldrack, & Gabrieli, 2006; Miyake et al., 2000; Verbruggen & Logan, 2008, 2009), probably based on a network of right lateralized prefrontal and parietal cortical regions (e.g., Aron & Poldrack, 2005; Simmonds, Pekar, & Mostofsky, 2008), inhibition of distractor representation remains a hotly debated topic (for an overview, Gorfein & MacLeod, 2007; Wühr & Frings, 2008). Using a sequential distractor-to-distractor task, it is possible to measure DI as the difference between distractor repetition and distractor change trials (Frings & Wühr, 2007): if two times in a row the same distractor has to be inhibited, responding should be easier the second time because the distractor is still inhibited. Yet, measuring only reaction times, response inhibition and inhibition at the level of stimulus representation cannot be disentangled as both would lead to faster responses to target stimuli in the case of distractor repetitions. Therefore, here we use the lateralized readiness potential (LRP; De Jong, Wierda, Mulder, & Mulder, 1988; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). The LRP is obtained by subtracting activity over the motor cortex ipsilateral to the responding hand from contralateral activity (Coles, 1989; De Jong et al., 1988). By that means, the time course of hand specific motor activation during the interval between stimulus presentation and response execution can be monitored (Kutas & Donchin, 1980). Typically, in a two-choice reaction time task with left and right-hand responses the LRP remains close to zero until about 300-400 ms post-stimulus, then turns into a sharp-rising negativity that peaks shortly before the overt response, and returns to baseline within some 100 ms (e.g., Jentsch & Sommer, 2002; Prime & Ward, 2004, 2006). Intriguingly, the temporal pattern of the LRP can be used to partition the time between the stimulus presentation and the response by locking the LRP to the stimulus (S-LRP) or to the response (R-LRP; for an overview see Eimer, 1998; Smulders & Miller, 2012). The S-LRP reflects stimulus processing prior to the point at which response activation begins while the R-LRP reflects response activation and peripheral motor processes. Processes underlying

overt responses can therefore be localized at early perceptual or later processing stages of motor activation (e.g., Jentzsch, Leuthold, & Ulrich, 2007; Jentzsch & Sommer, 2002; Osman & Moore, 1993). Thus, to evidence inhibition of distractor stimuli at the level of stimulus processing, we used a sequential distractor-to-distractor priming task. Importantly, distractors were not mapped to responses and could hence not interfere with responding to targets at the level of response selection; instead they could only interfere at the level of perceptual selection. Finally, we varied whether probe distractors appeared shortly before the probe targets or simultaneously with them. Distractors presented prior to targets should be easier to inhibit and as a result render persisting inhibition from repeated distractors redundant. DI effects should be less pronounced for distractors preceding the target onset (Frings & Moeller, 2012). Taken together, if distractors were inhibited at the level of stimulus processing, we should observe differences in S-LRP onset latency for distractor repetition vs. distractor change trials with respect to differences in the distractor-target onsets. Effects unambiguously interpreted as DI should be not further specified by response repetitions (indicating distractor-based SR retrieval).

5.3 Method

5.3.1 Participants

Twenty-five undergraduate students (24 female) from the University of Trier took part and were paid 16€ for participation. One participant was excluded due to unusable EEG-data as non-cortical artifacts were found in more than 50% of segments. The average age of the valid sample was 22 years (ranging from 19 to 30 years). All participants were German native speakers, right-handed and declared to have normal or corrected-to-normal vision. All partici-

participants signed written informed consent and were made aware of their right to discontinue participation in the study at any time.

5.3.2 Materials and Apparatus

The experiment was conducted using E-prime software (E-prime 2.0). Stimuli were shown on a LCD monitor (48.3 cm (1900), FlexScan S2031W, Eizo) with a viewing distance of 100 cm. The letters D, F, J, and K were used as targets and the digits 1, 2, 3, and 4 as distractors. Font was Courier New and the background color was black. Each stimulus was about $.4^\circ$ in width and $.52^\circ$ in height and assigned to one of two response keys on a standard QWERTZ-keyboard. Prime and probe displays consisted of a horizontal row of three adjacent stimuli (e.g., 1D1; width of stimulus triplet circa 1.26°), with the two outer digits (distractors) being always identical and depicted in green, while the centered stimulus (target) was depicted in red.

5.3.3 Procedure

Participants were tested individually, comfortably seated in a dimly lit sound-attenuated room. Before the experimental session EEG-electrodes were applied. Instructions were given on the computer screen, instructing the participant to place their left and right index finger on the response keys in front of them and to respond as fast and accurately as possible. The experimental task was to classify the identity of the red target letter by a left key press for the letters D and F and a right key press for the letters J and K (corresponding response keys 'C' and 'M' on a QWERTZ computer keyboard), while ignoring the green distractor digits. Two trials in a row were initiated by participant's press of the space bar (indicated by an asterisk displayed in the middle of the screen). A trial started with a blank screen for a duration randomly set at an interval of 500, 600, 700, 800, 900, or 1000 ms (750 ms on

average). The prime display followed and remained on the screen until the participant's response. The prime display consisted of a red target letter flanked by two green distractor digits. 500 ms after the prime response the probe target appeared. Distractors were either presented simultaneous with the target onset (Distractor-Target SOA of 0 ms), that is, both target and distractors were presented 500 ms after the prime response, or distractor onset preceded the target by 150 ms, that is, the distractors were presented 350 ms after the prime response, while the target was presented 500 ms after the prime response (Distractor-Target SOA of -150 ms). In either case the target always remained on the screen until the participant responded with a key press categorizing the target letter. In case of an incorrect response an error message was presented for 1500 ms. Each trial concluded with a blank screen of 500 ms duration (see Figure 10). The onset asynchrony between the distractors and the target of the probe was varied blockwise.⁷ Furthermore, response relation and distractor relation between prime and probe were varied randomly. That is, in half of the trials the prime-target, and consequently the indicated response, was repeated for the probe (Response Repetition, RR) and changed in the other half of trials (Response Change, RC). Orthogonally to the response relation, in half of the trials the prime-distractors were repeated (Distractor Repetition, DR) and changed in the other half of trials (Distractor Change, DC). The identity of the target letters (D, F, J, K) and distractor digits (1, 2, 3, 4) were randomly drawn; first for the prime display and second for the probe display with the constraint to meet the randomly assigned response and distractor relation. An experimental session consisted of six blocks of 120 trials with a participant-timed pause after three blocks. The sequence of blocks was randomized. Within each block all combinations of response and distractor relations were realized and randomly

⁷ Note that in one half of the blocks with a Distractor-Target SOA of -150 ms distractors remained on the screen until a probe response was executed whereas on the other half distractors were dismissed simultaneous to target onset and only the targets remained on the screen until response execution. As this manipulation did not have an effect of significance on the distractor repetition benefit neither for behavioral nor for neurophysiological parameters ($F_{corr} < 1$ for S-LRP onset; $F = 1.16$, $p = .293$ for RT) these conditions were collapsed.

selected as was the identity of target letters and distractor digits. By implication, the experiment consisted of 720 trials in which 12 different trial types were realized with each type occurring 60 times. Before the experiment blocks participants passed through 20 trials for practice. Within the practice trials Distractor-Target SOA was always 0 ms.

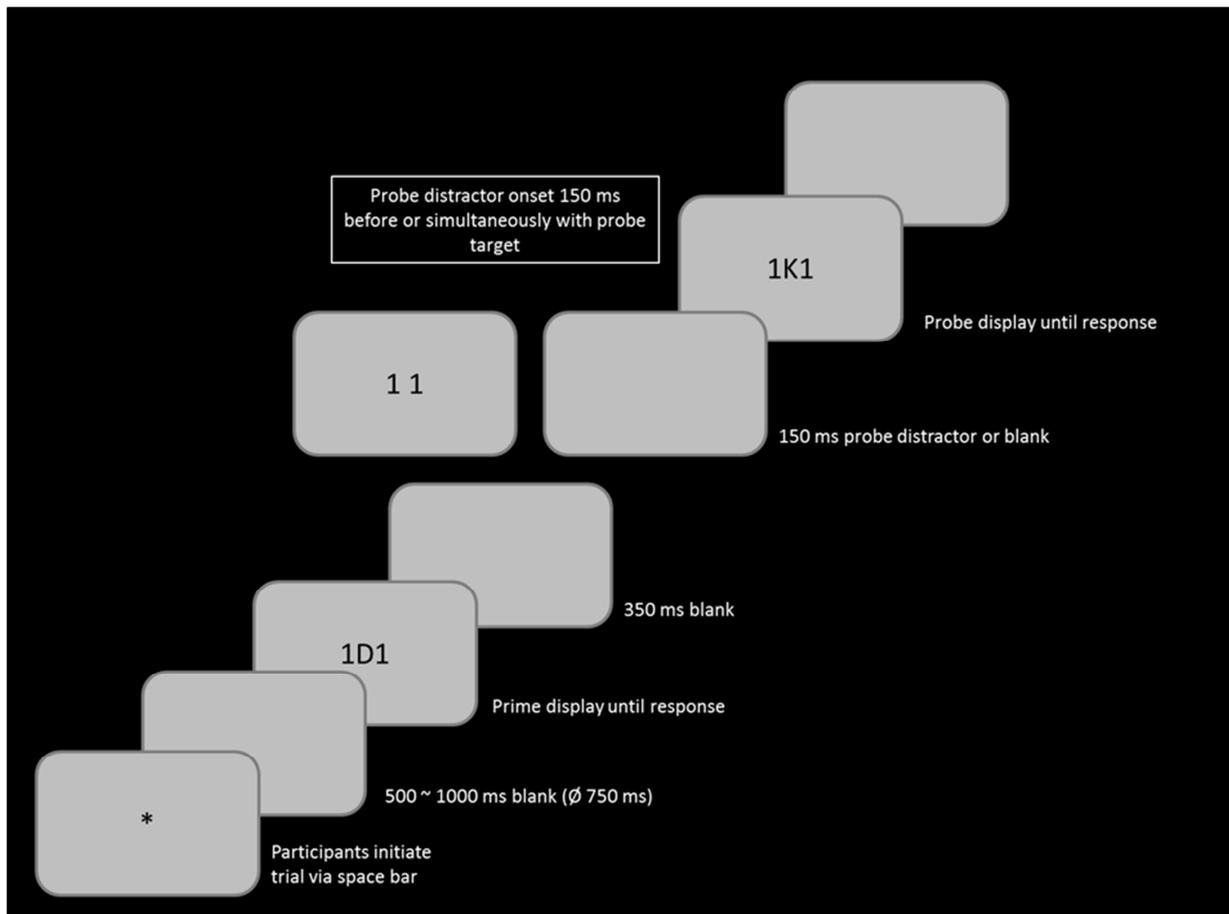


Figure 10. Schematic display of the trial procedure. Stimuli are not drawn to scale.

5.3.4 EEG Recording and Quantification

The EEG was recorded from 32 electrode positions corresponding to the 10-10 electrode reference system (Chatrian, Lettich, & Nelson, 1988) with the Easy-Cap electrode system (Falk Minow Services, Munich). During recording all sites were referenced to FCz. Bipolar horizontal from the epicanthi of both eyes as well as vertical electrooculogram (EOG) from supra- and infraorbital positions of the left eye, were recorded. Furthermore, electromy-

ogram (EMG) was recorded from two electrodes placed over the musculus extensor digitorum communis of the left and right forearm, respectively.⁸ Ag/AgCl electrodes were used for EEG, EMG, and EOG recordings and impedances of the electrodes kept below 10 k Ω . All signals were amplified by means of a 32-channel BrainAmp Model S/N Amp0710716DC amplifier (input impedance: 10 M Ω ; Brain Products, GmbH, Munich) in AC mode. Signals were digitalized at 1000 Hz, using a pass-band set to .016 to 499 Hz (-12 dB/octave roll-off), and filed on hard disk. Brain Vision Analyzer 2.0.4.368 (Brain Products, GmbH, Munich) was used for the editing and quantification of the EEG. For analyses, the EEG was re-referenced to the algebraic average of the left and right mastoid and the sampling rate reduced to 250 Hz. The non-segmented data was low pass filtered using an infinite impulse response (IIR) Butterworth filter with a cut-off frequency (3 dB point) of 4 Hz (24 dB/oct) in order to avoid high frequency noise. Using the algorithm of Gratton, Coles, and Donchin (1983) without raw average subtraction EEG was corrected semi-automatically for blinks and eye movements. EEG and EOG were segmented into intervals of 2350 ms starting 350 ms before and ending 2000 ms after probe target onset. A baseline correction was set with regard to the 200 ms interval ranging from 350 to 150 ms before probe target onset in order to avoid any overlap of the baseline with distractor presentation in the portion of trials with a Distractor-Target SOA of -150 ms. After segmentation and baseline correction segments with non-physiological artifacts were excluded from analysis by means of the semiautomatic artifact rejection. Only the electrodes F3, F4, FC3, FC4, C3, and C4 were considered by the search algorithm and all segments with voltage shifts of more than 20 μ V between adjacent sampling points marked as artifacts. Criteria were based on previous inspection of the whole data set and applied for each participant. Subsequent visual inspection of marked intervals validated the search algorithm in

⁸ Here, EMG data will not further be reported as it is not of interest for the current research question.

consideration of the activation pattern of the respective participant, but was blind to the experimental condition. Average rejection rate was 4.24% ($SD = 2.83$) of all data points. After the rejection of artifacts, trials with response errors or outlier reaction times (see results section) 10.95% of all trials ($SD = 5.02$) were discarded from further analyses.

5.3.5 LRP Analysis

For the analysis of probe S-LRPs, as shown in Figure 11, S-LRPs of trials with correct probe responses for each participant and condition were built from separate ERP averages at C3 and C4 covering -350 to 1000 ms intervals relative to probe display onset. According to the double subtraction technique introduced by Coles (1989), activity ipsilateral to the correct response was subtracted from activity over the contralateral hemisphere for the left and the right hand, respectively, and then averaged. For averaging only segments involving correct probe responses were considered. Separately for the 12 trial types jackknifed S-LRP onsets were determined according to Miller, Patterson, and Ulrich (1998), applying a relative onset criterion of 50% of the LRP-peak amplitude. With jackknifing, separately for each experimental condition each participant i gets assigned an LRP onset equal to the grand-average of the LRP waveform that results when participant i is excluded. By this means, signal-to-noise ratio is increased and unreliable individual onsets from noisy LRP waveforms of single participants are avoided. However, when LRPs are separately jackknifed for each condition, within-condition variability is artificially reduced, relative to variability between conditions. Therefore, corrections have to be applied when comparing mean jackknifed LRP onsets between priming conditions, by dividing t values by $(n-1)$ (Miller et al., 1998) and F values by $(n-1)^2$ (Ulrich & Miller, 2001), where n is the cell size. Reported F and t values were corrected according to Ulrich and Miller (2001) and Miller et al. (1998), respectively.

5.3.6. Design

The design comprised three within-subject factors namely distractor relation (distractor repetition vs. distractor change), response relation (response repetition vs. response change), and Distractor-Target SOA (0 ms vs. -150 ms).

5.4 Results

5.4.1 Behavioral Data

Only reaction times (RTs) from prime-probe sequences with correct probe-responses were considered. Moreover, only RTs above 250 ms and below the individual outlier criterion of three interquartile ranges above the third quartile of the participants RT distribution (Tukey, 1977) were considered for analysis. According to these constraints 6.0% of the trials (error rate on probe displays 4.4%) were dropped from analysis. Mean RTs and error rates are depicted in Table 5.

Probe RTs were subjected to a repeated-measure ANOVA with Distractor Repetition (repeated vs. changed) x Response Repetition (repeated vs. changed) and Distractor-Target SOA (0 ms vs. -150 ms) as factors. A significant effect of Response Repetition emerged, $F(1,23) = 128.11, p < .001, \eta_p^2 = .85$, reflecting faster RTs when the target and response repeated from prime to probe. The main effect of Distractor-Target SOA was also significant, $F(1,23) = 10.03, p = .004, \eta_p^2 = .304$, showing that participants responded faster when the distractor-target SOA was 150 ms. The main effect of Distractor Repetition was also significant, $F(1,23) = 28.56, p < .001, \eta_p^2 = .554$, as participants responded faster if the distractor repeated.

Table 5. Mean reaction times in milliseconds and error rates in percentage (in brackets) as a function of Distractor Repetition (repeated vs. changed) x Response Repetition (repeated vs. changed) and Distractor-Target SOA (0 ms vs. -150 ms).

		SOA 0 ms	SOA -150 ms
Response repeated	<i>Distractor repeated</i>	476 (.1)	478 (.3)
	<i>Distractor changed</i>	493 (.3)	485 (.4)
Response changed	<i>Distractor repeated</i>	594 (10.2)	578 (4.4)
	<i>Distractor changed</i>	600 (9.0)	580 (3.4)

The main effect of distractor repetition was of particular interest as it can be interpreted in terms of DI. Yet, this main effect was further qualified by response repetitions, $F(1,23) = 6.02$, $p = .022$, $\eta_p^2 = .21$, reflecting that benefits due to distractor repetitions were larger in response repetition trials (Frings et al., 2007). Most important was the interaction of Distractor Repetition and Distractor-Target SOA, $F(1,23) = 5.28$, $p = .031$, $\eta_p^2 = .19$, showing that benefits of distractor repetitions were stronger if the distractors were presented simultaneous to the onset of the target (see Figure 11b). That is, while for a simultaneous onset response execution is on average 11 ms ($SD = 12$; $t(23) = 4.60$, $p < .001$) faster for distractor repetition compared to change, this same benefit is reduced to 4 ms ($SD = 8$; $t(23) = 2.58$, $p < .05$) when distractors are presented before the target. Furthermore, the interaction of Response Repetition and Distractor-Target SOA was significant, $F(1,23) = 19.43$, $p < .001$, $\eta_p^2 = .46$, again, showing a larger Response Repetition effect for a simultaneous onset of distractors and target.

Distractor inhibition as evidenced by the LRP

The three-way interaction was not significant, $F < 1$. The same analysis on the error rates revealed a similar pattern, although DI effects were not significantly modulated by SOA variations, $F < 1$.

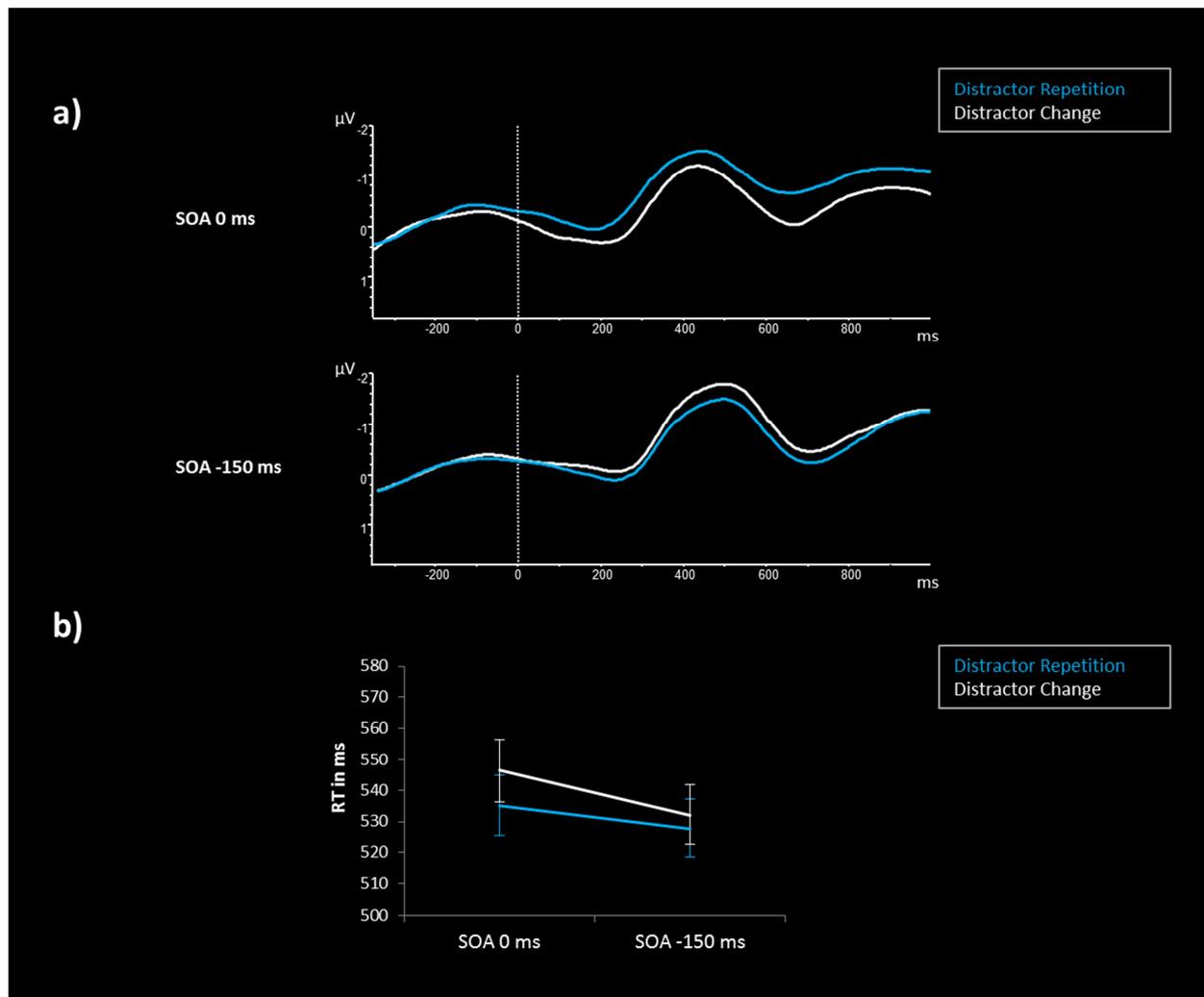


Figure 11. (a) Grand averaged S-LRPs of probe responses as a function of distractor-target SOA (0 ms vs. -150 ms) and distractor repetition (repeated vs. changed). The vertical line at time point 0 ms denotes probe target onset (b) probe reaction times in milliseconds as a function of distractor-target SOA (0 ms vs. -150 ms) and distractor repetition (repeated vs. changed).

5.4.2 LRP Data

As for the RTs, stimulus-locked probe LRP onsets calculated for the C3 and C4 electrodes were subjected to a repeated-measure ANOVA with Distractor Repetition (repeated vs.

changed) x Response Repetition (repeated vs. changed) and Distractor-Target SOA (0 ms vs. -150 ms) as factors. Mean S-LRP onset latencies are depicted in Table 6. A significant effect of Response Repetition emerged, $F_{corr}(1,23) = 18.1, p < .001, \eta_p^2 = .44$, reflecting earlier onsets when the target and response repeated from prime to probe. The main effect of Distractor-Target SOA was also significant, $F_{corr}(1,23) = 25.12, p < .001, \eta_p^2 = .52$, showing earlier onsets when the distractor-target SOA was -150 ms. The main effect of Distractor Repetition was not significant, $F_{corr}(1,23) = 1.22, p = .281$. Yet, most important was the interaction of Distractor Repetition and Distractor-Target SOA, $F_{corr}(1,23) = 6.43, p < .018, \eta_p^2 = .22$, showing in agreement with the RTs that benefits of distractor repetitions were stronger if the distractor was presented simultaneous to the onset of the target (see Figure 11a). The discrepancy in distractor repetition benefit for simultaneous and earlier onset is even more pronounced for S-LRP onsets than RTs. Whereas with a simultaneous onset S-LRP-onset latency is reduced by 24 ms ($SD = 2; t_{corr}(23) = 2.29, p < .05$) for distractor repetition compared to change, no such benefit is present when distractors are presented before the target ($t_{corr}(23) = -.61, p > .05$). All other effects were not significant, all $F_s < 1$.

5.4.3 Control Analyses

We further provide two control analyses with regard to the LRP-data. In a first step, we replicated the results of the S-LRP analysis using a lower onset criterion of 30% of the LRP peak-amplitude. The implementation of an onset criterion of 30% in general adds more noise to the data and represents a less accurate estimate of the difference in S-LRP onset latencies (Miller et al., 1998) but has the advantage of reducing the fraction of response-related activity having commenced before the time of the onset criterion and can therefore be seen as complementary analysis in order to strengthen the claim of the modulation of distractor pro-

cessing on a pre-motor level. All relevant results that were obtained for the 50% onset criterion could be replicated.

Table 6. Mean S-LRP onset latencies of probe responses (standard deviations in brackets) as a function of Distractor Repetition (repeated vs. changed) x Response Repetition (repeated vs. changed) and Distractor-Target SOA (0 ms vs. -150 ms).

		SOA 0 ms	SOA -150 ms
Response repeated	<i>Distractor repeated</i>	279 (2)	277 (3)
	<i>Distractor changed</i>	310 (3)	277 (2)
Response changed	<i>Distractor repeated</i>	347 (2)	325 (3)
	<i>Distractor changed</i>	364 (3)	313 (3)

The main effect of Distractor-Target SOA was again significant, $F_{corr}(1,23) = 43.85$, $p < .01$, with earlier onsets when the Distractor-Target SOA was 150 ms compared to a Distractor-Target SOA of 0 ms. Again no main effect of Distractor Repetition was found, $F_{corr}(1,23) = 1.51$, $p > .05$, but, most important, the interaction of Distractor Repetition and Distractor-Target SOA, $F_{corr}(1,23) = 8.41$, $p < .01$, was replicated, demonstrating in agreement with the results for the 50% onset criterion that benefits of distractor repetitions were stronger if the distractor was presented simultaneous to the onset of the target than if the distractor preceded the probe target by 150 ms. Namely, whereas with a simultaneous onset of the probe target and the distractors the S-LRP-onset latency is reduced by 31 ms ($SD = 2.6$; $t_{corr}(23) = 2.58$, $p < .05$) for distractor repetition compared to distractor change, no such benefit is present when

the distractors are presented prior to the target onset ($t_{corr} < 1$). In a second step, we determined the differences of the onset latencies for the R-LRPs. As the R-LRP waveforms of our data exhibited highly similar waveforms we chose a relative onset criterion of 90% which is, in the case of comparable waveforms, recommended as the most accurate and powerful onset criterion for the detection of R-LRP onsets (Miller et al., 1998). In correspondence to the statistical analyses of reaction times and S-LRPs the R-LRP onsets calculated were subjected to a repeated-measure ANOVA with Distractor Repetition (repeated vs. changed) x Response Repetition (repeated vs. changed) and Distractor-Target SOA (0 ms vs. 150 ms) as factors. No significant effects were found. That is, no effect of Response Repetition, $F_{corr}(1,23) = 1.08$, $p > .05$, or Distractor Repetition, $F_{corr} < 1$, emerged indicating that R-LRP onsets were indifferent towards whether the target and response or the distractors were repeated or changed from prime to probe. Moreover, Distractor-Target SOA did not influence the R-LRP onset latencies, $F_{corr} < 1$. Furthermore, Distractor Repetition and Distractor-Target SOA did not interact, $F_{corr}(1,23) = 1.50$, $p < .05$, reflecting that there was no benefit of distractor repetition in the R-LRPs, neither for a Distractor-Target SOA of 0 ms ($M = 5$ ms, $SD = 1.17$, $t_{corr}(23) < 1$) nor for a Distractor-Target SOA of -150 ms ($M = -2$ ms, $SD = 1.03$, $t_{corr}(23) < 1$). All other effects were also not significant, all $F_{corr} < 1$.

5.5 Discussion

In the current study the inhibition of irrelevant stimuli as important mechanism of selective attention was investigated. To this end, distractor inhibition by means of distractor repetition benefits was measured. In a sequential distractor-to-distractor priming task participants had to respond to a target letter flanked by distractor digits. Furthermore, probe distractor onset was varied. Distractor onset was either 150 ms ahead of probe target onset or oc-

curred simultaneous with the target onset. Our aim was to test the notion that inhibition is effective as early as on a sensory processing stage; that is, at the level of distractor representation (e.g., Frings & Wühr, 2007; Neumann & DeSchepper, 1991). In order to separate stimulus processing from motor preparation, not only RTs but further onset latencies of S-LRPs locked to the onset of the probe target were examined. On the level of RTs, a distinct benefit of distractor repetition when probe distractors and probe target had a simultaneous onset was present, replicating previous findings that demonstrated DI for similar tasks (Frings & Wühr, 2007; Giesen et al., 2012). Yet, giving the distractors a lead over the target, that is presenting the distractor 150 ms prior to the target onset, reduced the distractor repetition benefit by more than 50% (11 ms vs. 4 ms for 0 ms vs. -150 ms Distractor-Target SOA, respectively). Furthermore, we found a main effect of Distractor-Target SOA demonstrating overall faster responses with distractor onset preceding target onset. This overall reduction in RTs indicates a clear processing advantage for the distractors. Having a head start over the target, allows for the processing and inhibition of the distractor representation previous to the target presentation thereby facilitating the selection process at target onset (see also, Frings & Moeller, 2012; Neill, 1997). As the process of distractor inhibition sets off in advance to the target irrespective of prime distractor identity a sustained inhibition in the case of distractor repetition from prime to probe might be rendered redundant, thus leading to a reduction of the distractor repetition benefit for trials with -150 ms Distractor-Target SOA. The pattern found for RTs was even more pronounced for S-LRPs locked to the probe target onset. Whereas, again, we found a marked distractor repetition benefit for a Distractor-Target SOA of 0 ms, reflected by shorter onset latencies of the LRP for distractor repetition compared to distractor change, this benefit was completely absent for a Distractor-Target SOA of -150 ms. Together with overall shorter latencies for 150 ms compared to 0 ms Distractor-Target SOA, this finding indicates in accordance with the RTs that distractor repetition does not bring any advantage over dis-

tractor change when distractors precede the target by 150 ms. This pattern of results was present for a relative onset criterion of 50% of the LRP peak-amplitude which provides the most accurate estimate of differences in S-LRP onset latencies (cf. Miller et al., 1998) and was further replicated by the implementation of an earlier onset criterion of 30% which provides an estimate of differences in S-LRP onset latencies encompassing an even smaller response-related portion of the LRP. Therefore, it can be concluded that sustained inhibition from the prime leads to a reduction in the time needed for probe display processing as the selection of the target becomes easier. But, sustained distractor inhibition does not bring any additional advantage for selection when a lead of the distractor over target presentation allows for a successful distractor inhibition early on. The results of the current experiment are in line with inhibition accounts of selective attention that propose both the facilitation of target processing and the inhibition of distracting information as relevant mechanisms (e.g., Frings et al., 2012; Houghton & Tipper, 1994; Neill, 1997; Tipper, 1985), in that they replicate previous findings displaying benefits of distractor repetition on overt motor responses (e.g., Frings & Wühr, 2007; Giesen et al., 2012; Neumann & DeSchepper, 1991; Tipper & Cranston, 1985). More importantly, though, our results help to solidify the notion that inhibitory mechanisms can be localized on an early perceptual stage, that is, as early as during stimulus processing. A notion that is also supported by event-related lateralizations linked to cognitive control processes that are separable for target and distractor processing like the N_T (Target Negativity) and P_D (Distractor Positivity) (Fortier-Gauthier, Dell'Acqua, & Jolicoeur, 2013; Hickey, Di Lollo, & McDonald, 2009) and the modulation of S-LRP latency as well as early occipital and occipitoparietal ERP-indices of visual processing associated to the inhibition of return phenomenon (Prime & Jolicoeur, 2009; Prime & Ward, 2004, 2006). With S-LRPs reflecting processing sequences prior to central response activation of one of the two effectors (e.g., Osman & Moore, 1993; Smulders & Miller, 2012), it can be concluded that processing advantages due

to distractor repetition in our study set during the perceptual processing of the distractor. That is, inhibitory mechanisms of selective attention are effective not only on the level of response activation and execution as indicated by late-selection theories and models of response inhibition (e.g., Duncan, 1980; Logan & Cowan, 1984; Norman, 1968) but also on the level of perception and the sensory representation of an irrelevant stimulus (e.g., Frings & Wühr, 2007; Lamy, Antebi, Aviani, & Carmel, 2008; Neumann & DeSchepper, 1991). The early locus of inhibition is additionally supported by comparing the influence of Distractor-Target SOA on distractor repetition benefits for RTs and S-LRP onset latencies. Whereas for RTs, we still found a distractor repetition benefit, albeit significantly reduced, this was not the case looking at the S-LRP onset latencies. Assuming that DI reflects the inhibition of distractor representations this pattern is particularly plausible as S-LRPs index the perceptual processing stage only, therefore representing an unequivocal measure of the processing stages prior to response activation. RTs, on the other hand, are affected both by stimulus processing as well as response activation. As a consequence, RTs always display perceptual and response related processes at the same time. The experimental design aimed at disentangling the inhibition of distractor representations from response inhibition. In addition to the recording of S-LRPs this was done by the implementation of neutral distractors, i.e., stimuli not mapped to any of the responses. As a consequence no interference of distractor with target stimuli on a response level was to be expected. The implementation of neutral distractors might explain the absence of a main effect of distractor repetition for S-LRPs as DI has been found to be less pronounced for neutral than for incompatible distractors, i.e., stimuli mapped to a response opposite to that indicated by the target (Giesen et al., 2012; see also Frings & Wentura, 2006; Levithal & Lleras, 2008). For RTs we further found that the repetition of distractors led to a more pronounced benefit when target and responses were also repeated from prime to probe reflecting the storage and retrieval of the target and distractors to an event file (Frings et al.,

2007; Gibbons & Stahl, 2008; Mayr & Buchner, 2006; Mayr et al., 2009; Rothermund et al., 2005). In line with evidence suggesting that DI and distractor-based SR retrieval operate independently of each other (e.g., Giesen et al., 2012; Moeller et al., 2015) the benefit for distractor repetitions on the level of S-LRPs was not modulated by response repetitions and can therefore be unambiguously interpreted as reflecting DI. The slight negative deflection of the LRP baseline activity apparent in Figure 11a, which is equally present in all conditions, most likely stems from a general tendency of the participants to prepare for a repetition of the prime response. This assumption is underpinned by the comparison of response change vs. response repetition trials in which an overall negativity in response repetition trials (correct response preparation is marked as slight negative deflection) and a positivity in response change trials (incorrect response preparation is marked as slight positive deflection) are present. As the negative deflection in response repetition trials is numerically more pronounced than the positivity in response change trials a slight negative deflection prior to probe onset results. Distractor change and distractor repetition trials, respectively, correspond to the average of response repetition and response change trials and should therefore be unswayed by participant's mind set to repeat the prime response. Furthermore, as LRP onsets are determined relative to an average baseline value of zero and the peak-amplitude of the respective LRP waveform, onset latencies should be unaffected. Control analyses showed further that the activation pattern prior to the probe onset for distractor change and distractor repetition trials did not differ systematically and that our results remained unaffected by choosing the time point prior to probe onset at which distractor change and distractor repetition displayed the most pronounced deviation as the lower reference point for the relative S-LRP-onset criterion (the time point of the probe onset).⁹

⁹ For the control computations the relative onset criterion was therefore defined as 50% of the peak-

To conclude, the inhibition of distractor representation seems to constitute an important tool of object-based selective attention in addition to action control based on response inhibition. Whereas for the latter the locus of control is set at later processing stages like response preparation, response activation, and peripheral motor control per se (Aron, 2007; Logan, 1985; Logan & Cowan, 1984) inhibition of perceptual representations allows to reduce the impact of distracting information before (motor) action is prepared or initiated. The inhibition of distractors can therefore be seen as working hand in hand with other mechanisms that help us to effectively control our everyday behavior in the face of irrelevant information.

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amplitude relative to the respective deflection at the time point of the probe onset $[(U_{max} - U(\text{Time}0)) * \text{Onset}(\%) + U(\text{Time}0)]$. As at this point in time the visually apparent discrepancy in the course of distractor change and distractor repetition waveforms previous to the probe onset was already fully developed, a potential bias to the S-LRP-onset detection would be counteracted to the greatest possible extent.

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Chapter VI

General Discussion

The results reported in this dissertation demonstrate the potential of cardiovascular feedback by means of baro-afferent signal transmission as interacting with selection processes in vision. The studies in Chapters II and III illustrate enhanced ability to select relevant from irrelevant visual input during phases of high baroreceptor activity within the course of the cardiac cycle. Specifically, the implementation of a visual masking task in Chapter II displayed reduced mask interference during the ventricular systole in comparison to the diastole, indicating easier temporal selection of mask and target when baroreceptor activity is high. By operationalizing selection efficiency as the comparison of the participants' accuracy in a visual selection task under easy and difficult selection conditions, the first finding was substantiated by the study reported in Chapter III. In the latter study, a letter target flanked by distractors could be identified more accurately when selection was easy. However, the impact a distracting context had on performance was diminished during phases of increased baroreceptor activity. As more extensively discussed in Chapter III, the results currently available suggest that under highly distracting stimulus conditions, the identification of relevant information is facilitated when transient baro-afferent signal transmission is on a high level. This is striking as it indicates that our perceptual performance is not solely determined by the sensitivity of our sensory organs and constrained by dynamic factors such as habituation and physical fatigue (cf. Ansorge & Leder, 2011), but rather that the amount or quality of information that we are able to process may fluctuate within each cardiac cycle.

As discussed in section 3.5, the variation of selection efficiency within the cardiac cycle might be of functional relevance in order to flexibly adjust our perceptual capacity to the rapidly changing behavioral requirements we are facing in each moment. In particular, the cyclic alternation of facilitated focused and divided attention, i.e., serial and parallel processing of the environment, respectively, may strike an important balance between the detailed and thorough processing of the most relevant information at a given point in time and a

less restrained intake of the remainder, which might potentially become relevant in the next moment. Furthermore, the link between autonomous and central nervous functions in general contributes to the effective adaptation of our sensory systems with regard to the organism's physical state imposed by environmental challenges. That is to say, changes in parasympathetic and sympathetic output evoked by physical exercise or mentally demanding tasks may help to shape the excitation level of the CNS in order to reach and maintain an adequate activation level for efficient task performance (compare Duschek et al., 2013).

At first glance, the conjecture of enhanced selection by increased baro-afferent feedback, however, seems at odds with findings on the impairment of sensory and sensorimotor performance in simple detection or simple and choice reaction time tasks (e.g., Edwards et al., 2007b). On second glance, the findings may well be reconciled by considering the different requirements imposed on the sensory system in the respective situation. Similar to the binding of distractors into an event file as well as for the encoding of S-R bindings in general (e.g., Hommel, 2005) the controlled allocation of an attentional focus is not required for simple stimulus detection. However, whereas detection or localization allows for parallel processing of stimulus input, focused target processing by blocking out irrelevant visual input is required when targets have to be identified from among temporally overlapping processing traces of a visual mask, as in Chapter II, or by flanking distractor stimuli as in the studies reported in Chapters III through V (cf. Sagi & Julesz, 1985b, see section 3.5 for a more detailed discussion). Consequently, selection based on the inhibition of irrelevant stimulus input and a simultaneous amplification of relevant processing traces (cf. Desimone & Duncan, 1995) may profit from additional inhibition imposed by baroreceptor activity. In contrast, decreased cortical excitation is of no support for the rapid and unrestrained reception of simple target stimuli, which in general benefits from a state of alertness as well as salient stimulus features that capture attention automatically (Corbetta & Shulman, 2002; Petersen & Posner, 2012).

As relating to the divergent findings of performance decrements in simple sensorimotor tasks and performance benefits in selection tasks, a parallel might further be drawn between the reported results and early studies by Vaitl and Gruppe (1990, 1992), which delineated enhanced theta power at frontal, parietal, and occipital sites of the EEG as a consequence of baroreceptor loading by head-down tilting. Activity within low frequency spectra of the EEG, such as theta, is generally associated with the relative deactivation of brain areas, whereas higher energy expenditure is paralleled by shifts to activity within higher frequency bands (Kilner, Mattout, Henson, & Friston, 2005). For instance, the processing of visual stimuli depicted in high contrast is associated with a shift from lower to higher EEG frequency spectra within the occipital cortex (Niessing et al., 2005). Accordingly, during states of low alertness, medial theta is augmented during sleep onset and states of sleep deprivation concomitant with impaired sensory processing and sensorimotor responses (Cajochen, Foy, & Dijk, 1999; Caldwell, Prazinko, & Caldwell, 2003; Schacter, 1977). These findings are well in accord with decrements in simple sensorimotor performance during phases of higher baroreceptor activity in that they show that theta power is both interrelated to brain activation associated with modest cognitive demands and increased baroreceptor activity.

However, oscillations within the theta frequency band are not only linked to reduced sensorimotor performance during states of low alertness, but also reflect the facilitation of selective and focused processing when cognitive effort is incremented. In this regard, enhanced medial-frontal theta instantiates adaptive top-down control by the entrainment of spatially remote neural populations. For instance, synchronization of medial-frontal theta activity by transcranial direct current stimulation improves adaptive control in a forced-choice target discrimination task (Reinhart, Zhu, Park, & Woodman, 2015) and medial-frontal theta power is enhanced when perceptual or response-related interference in a selective attention task is high (Nigbur, Cohen, Ridderinkhof, & Sturmer, 2012). In particular, analogous to the amplifi-

cation and inhibition of neural pathways that are currently relevant or irrelevant, theta synchronization is conjectured to reflect the alignment of neuronal populations with regard to their functionality for a given task (Cavanagh & Frank, 2014; Ishihara & Yoshii, 1972; Legewie, Simonova, & Creutzfeldt, 1969). Taken together, these findings bolster the role of theta in action selection and the allocation of attention, and although only correlational, a synopsis of results underpins a decisive role of baroreceptor activity for the suppression of irrelevant information. More importantly, this broader view helps to unify the discrepant effects of baroreceptor-mediated inhibition for simple sensorimotor tasks, on the one hand, and controlled selection tasks, on the other hand, by distinguishing between conditions of high and low cognitive demands.

Chapter IV empirically distinguished controlled selective attention from automatic distractor processing. It was demonstrated, that only controlled selection, but not automatic distractor binding is affected by persistently increased baro-afferent feedback induced by head-down tilt. The integration of the results preliminarily confines the impact of baro-afferent signal transmission to relatively controlled selection processes. With regard to the distinction between automatic and controlled processes, the reason for why detection, but not the integration of stimuli into S-R bindings is impaired by increased baro-afferent feedback is yet to be established, in particular as bindings, at least between stimuli, are assumed to be based on links between low-level sensory features (e.g., Colzato et al., 2006). After all, the discrepancy may easily be explained by the use of different measures and the task design implemented. With regard to the former, whereas by the measure of sensory thresholds or simple RTs, values obtained during the systole are directly compared to those originating from the diastole, difference scores are compared when looking at the DRB effect. Consequently, main effects of the cardiac cycle time irrespective of the distractor-response relation between prime and probe are of no consequence for the effect of interest. With regard to the latter, the fact that no

main effect of baroreceptor stimulation was present might further be explained in that responses in the present task were influenced by multiple factors, which might overcast simple effects of impairments on a sensory processing level. To be precise, in contrast to studies that involve the modulation of simple RTs or sensory thresholds, in the present design RTs were not only affected by the perceived stimulus contrast, but, among others also by interference from distractors and episodic retrieval processes. Furthermore, S-R interactions are not confined to stimuli that are clearly visible and also proceed on the level of symbolic stimulus representations (Horner & Henson, 2011; Müsseler & Hommel, 1997). The same is true for the DRB effect as it has been demonstrated that conceptual representations of distractors are bound into event files (Frings et al., 2013). As a consequence, the bindings of stimuli and responses into an event file should not be affected by overall decrements in stimulus perceptibility. This is particularly plausible in view of the fact that in the design reported in Chapter IV baroreceptor-mediated inhibition is assumed to be equally pronounced during the prime and the probe display as well as for different distractor-response relations between the prime and the probe. Together these arguments immediately suggest that DRB unlike the measurement of sensory thresholds and simple RTs is rather unlikely to be affected by potential reductions in the perceptibility of visual stimuli. The results of Chapter IV therefore demonstrate that in contrast to controlled selection processes, automatic distractor processing is not affected by baroreceptor-mediated inhibition.

Another perspective on the results of Chapter IV necessitates considerations on the functional basis of the vanished NP effect during head-down tilt. In this regard, cortical inhibition owing to enhanced stimulation of arterial baroreceptors (see section 4.5 for further discussion), may well limit the cognitive control necessary for selection during the prime and thus reduce aftereffects of prime selection for responses to the probe. The impact of increased inhibitory control might operate analogous to sequential modulations of congruency effects in

various selection tasks (e.g., Gratton, Coles, & Donchin, 1992; Hommel, Proctor, & Vu, 2004) as well as reduced NP with a higher portion of IR trials (Frings & Wentura, 2006). Hence, on the basis of the current results, it might be speculated that inhibitory top-down control to resolve interference may be sustained by CNS structures as those comprised by the central nervous branch of the baroreflex (see section 1.1.2.2). This is exemplified by top-down feedback mechanisms from the anterior cingulate and lateral frontal cortex (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter & Krug, 2011) or the involvement of specialized frontoparietal and cingulo-opercular systems denoted as executive networks of attention (Dosenbach et al., 2007; Petersen & Posner, 2012).

The incorporation of results from the EEG study presented in Chapter V indirectly strengthens this claim. By the partitioning of the information processing stream into stages of stimulus processing and response activation it was demonstrated that the inhibition of distractors affects the former. To be precise, it was shown that sustained inhibition from a prime display leads to a reduction in the time needed for the sensory and central processing stages related to the probe to complete, but brings no advantage for processing stages located after lateralized response activation has taken place. Together with first results that indicate baroreceptor-mediated inhibition to target central, i.e., sensory processing and decision processes, rather than motor stages (Edwards et al., 2007b; Schulz et al., 2009b), these results show that the selective suppression of irrelevant information by both cognitive control and baro-afferent signal transmission presumably act upon central distractor representations. Therefore, besides lending support for the notion that inhibition is effective with respect to sensory distractor processing, preliminary evidence that top-down and baroreceptor-mediated inhibition operate on a comparable processing stage is given.

The modulation of selective attention by afferent signal transmission originating from the NTS is further not implausible as the brain stem has been characterized as center for dif-

ferent mechanisms of attention already several decades ago (Neumann, 1971). For instance, Moruzzi and Magoun (1949) described the ascending brain stem activating system in cats as providing a state of wakefulness or alertness, a function that has been maintained in current models of attention (e.g., Petersen & Posner, 2012). Another example is the early finding that selective inhibition and excitation of afferent sensory signal transmission to the forebrain is exerted by the brain stem (Hernández-Peón, Scherrer, & Jouvet, 1956). Extensive connections of blood pressure sensitive neurons within the brain stem to the forebrain (e.g., Dembowsky & Seller, 1995) as well as the behavioral results discussed so far additionally underline the impact of baro-afferent signal transmission on selection processes in vision.

However, conclusions with regard to the underlying neurobiological mechanisms and a detailed analysis of CNS structures involved are beyond the scope of this dissertation. Future studies therefore might pursue two lines of research. First, it would be beneficial to extend the use of imaging techniques and electrocortical measures in order to delineate the underlying neural mechanisms by implementing experimental designs that permit causal inferences through the combination of selective attention tasks and cardiovascular measures within a single study (decisive examples are given by Critchley & Garfinkel, 2015; Duschek et al., 2013). To exemplify, EEG components that are selectively associated to distractor suppression and target processing, such as the distractor positivity (P_D) and target negativity (N_T), respectively (Hickey, Di Lollo, & McDonald, 2009; Jannati, Gaspar, & McDonald, 2013), might help to specify the mechanisms during selection tasks that are affected by systematic variations in baroreceptor activity. Second, despite the difficulties of experimental baroreceptor activity manipulations under the preclusion of secondary effects on other physiological variables in humans (Rau & Elbert, 2001; see also section 1.4), stringent testing of possible artifacts and alternative explanations to baro-afferent signal transmission, as were already put forward by Velden and Wölk (1995), should be a major focus of further research. Further-

more, it should be noted that the identification of the target stimulus in the study reported in Chapter III combined the need to attend to specific stimulus features and to allocate attention to different spatial locations within the stimulus array. Similarly, with regard to the sequential selection task delineated in Chapter II, temporal and spatial location as well as differences in luminance may have helped to select the target from the mask stimulus. It will therefore be interesting to see in future studies whether selective attention to locations, objects, and features is differentially affected by variations in baroreceptor activity or whether bottom-up inhibitory feedback from the cardiovascular system promotes selective attention processes irrespective of its content.

To conclude, it is suggested on the basis of the currently available results that increased baro-afferent feedback during the ventricular systole or as evoked by changes in body position does not only affect simple task performance based on parallel information processing like stimulus detection or localization, but also complex computations like the selection of visual stimuli from among irrelevant distractors. Taken together, visual selective attention seems to benefit from increased baro-afferent feedback. Baroreceptor-mediated inhibition may therefore facilitate the active suppression of neuronal activity related to sensory input from distractors similar to the reduction of noise within the visual system, and thus promote attention to be focused more effectively.

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Eidesstattliche Erklärung

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbständig verfasst habe und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt sowie die aus fremden Quellen übernommenen Gedanken als solche kenntlich gemacht habe.

Diese Dissertation wurde bisher keinem anderen Prüfer in gleicher oder vergleichbarer Form vorgelegt.

Trier, 12. Januar 2016 _____