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MARIA TAMM

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Supervisors: Kairi Kreegipuu, *PhD*, Senior Researcher
University of Tartu, Estonia

Jüri Allik, *PhD*, Professor
University of Tartu, Estonia

Opponent: John H. Wearden, *PhD*, Professor
Keele University, UK

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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IV Havik, M., Jakobson, A., **Tamm, M.**, Paaver, M., Konstabel, K.; Uusberg, A., Allik, J., Ööpik, V., & Kreegipuu, K. (2012). Links between self-reported and laboratory behavioral impulsivity. *Scandinavian Journal of Psychology, 23(3)*, 216–223.

For studies I and II, the author set the aims, conducted all analyses and wrote the papers as the first author. For study III, the author was responsible for the aims, the analysis of behavioural data and the writing. For study IV, the author was responsible for the aims, and collaborative writing. For studies I, II, and IV, the author participated in designing and conducting the experiments.

1 INTRODUCTION

Time perception is inherently a subjective experience based on the determination of order and duration between different events. In 1860, Karl Ernst von Baer, one of the most celebrated graduates of the University of Tartu, introduced the notion of perceptual moment – the unit of time – suggesting that different species have different durations of moments and consequently different flow of subjective time (von Baer, 1860). William James devoted a whole chapter (XV) of his classical *The Principles of Psychology* (1890) to the perception of time. Unexpectedly, this chapter created an illusion that the most important problems concerning time perception have already been solved. Extensive reasearh on timing in animals followed and the application of animal timing models to humans revived interest in the topic of time perception (for review, see Wearden, 2005). The era of neuroscience has further surged an interest in the brain mechanisms of time perception (Buhusi & Meck, 2005; Harrington, Haaland, & Knight, 1998; Meck, 1996).

It was a long and obstructed journey towards the fundamental unit of time – second – which resulted in the acceptance of the *International Atomic Time* only in 1967. Historically, longer time intervals were measured by the movement of the Sun as it is seen from the Earth; shorter intervals were measured by periodic physiological processes such as breathing or the pulse. However, it was soon discovered that humans can accurately estimate intervals shorter than one second (James, 1890). This indicated that a more rapid periodic physiological or psychological process is used as a unit for time measurement. Although researchers put in a considerable effort to establish the shortest time-interval between two perceptual events that can be discriminated (Dunlap, 1915), the absolute limit was never found.

From the very beginning it was clear that whatever the process used as a subjective time unit, this process is not as stable as atomic clocks based on the oscillations of a Cesium-133 atom. If an atomic clock deviates only 1 second in about 20 million years then the human internal clock is much less precise and vulnerable to many disturbances. In addition to the pace-holder rate itself, the cognitive access to the internal clock is not as easy as is the access to physical devices. The sense of time presupposes an additional process, which retrieves information from an internal clock. As any other psychological process, the retrieval of information from an internal clock is subjected to errors and biases (Woodrow, 1951). Much of human behaviour is shaped by this subjective temporal experience, which in turn is sensitive to both external and internal context. For example, temporal experience is important in sports, whether estimating the time-to-contact or initiating a coordinated response requiring perceptual-motor skills. Emotions, an example of an internal context, have a strong effect on the perceived passage of time, as time seems to fly when a person is having a good time (Gable & Poole, 2012). Additionally, time estimating abilities are important in carrying out daily activities and perceiving the succession of external events. The perception of time is essential for information processing, decision making and action planning in general. Therefore, time perception shares properties similar to visual and auditory perception, and should be considered in relation to other cognitive functions like language and memory processes (Allman, Teki, Griffiths, & Meck, 2014).

Regarding the notable history of time perception, questions about the underlying mechanisms of temporal processes and factors affecting duration percepts still remain essential topics of research. Empirical studies of time perception often originate from the discipline of psychophysics, seeking to quantify psychological time relative to real time and applying Weber's law to timing. Therefore, research in psychological time has been focused on whether perceived duration corresponds to physical time and explores the reasons why psychological and physical time sometimes fail to coincide. The questions raised involve the relative variability of temporal estimations, the role of stimulus modality, reasons for the indifference interval (i.e., the highest point of accuracy as the time judgments are veridical with physical durations, Lejeune & Wearden, 2009) among other aspects of time perception (Wearden, 2005). In that view, time perception is considered to possess psychophysical properties similar to other senses, although no particular sensory organ is responsible for the sense of time. Similar to visual and auditory perception, psychological time increases with physical time and as a result, a linear relationship between the intensity of temporal sensation and the magnitude of external stimulation is observed. Although the clock-based approach in time perception research often shows linear relationship between subjective and real time (Wearden & Jones, 2007), pacemaker-free approach yielding to nonlinear scale for encoding time has been proposed (e.g., multiple time scales related to memory functions; Staddon & Higa, 1999; Staddon & Higa, 2006).

Humans are generally accurate in estimating time even without external timekeepers and therefore the existence of an internal clock-like mechanism (Church, 1984; Treisman, 1963) with neurobiological origins has been proposed (Coull, Cheng, & Meck, 2011). Current theoretical models of internal clock take into account the properties of timing behaviour as revealed by psychophysical methods. The challenge is to identify the mechanism by which the internal clock operates. Insights about how the internal timekeeper works come from observed distortions in timing behaviour caused by a variety of psychological and physiological factors (e.g., arousal or pharmacological manipulations; Matell & Meck, 2000; Mella, Conty, & Pouthas, 2011; Meck, 1996). Manipulation of these factors promotes identification of the mechanisms by which the internal clock operates.

The concept of an internal clock continues to be the most popular theoretical model to explain the properties of psychological time. Michel Treisman (1963) was the first to provide a consistent framework for describing the principles underlying the clock-like mechanism and time perception. His work was based on earlier works by François (1927) and Hoagland (1933), who explored temperature effects on duration production by systematically observing the relationship between changes in temperature and timing performance. Hoagland (1933) proposed the concept of a chemical clock, based on the observations of his wife counting seconds while being ill with a fever, and data from François' (1927) study with two subjects producing intervals on a metronome while receiving diathermic treatment. Thus, the manipulation of temperature offered an early insight into the working of the internal clock in producing time judgments. The conclusion from these studies implied a temperature sensitive mechanism, which is affected by the arousal level of the organism (Wearden & Penton-Voak, 1995). Increased body temperature together with a higher heart rate is proposed to be the indicators of increased arousal, which speeds up the rate of the pacemaker according to the internal clock model. The pacemaker produces a series of impulses ("ticks"), which are accumulated and form a basis for the length of psychological time (Treisman, 1963).

The concept of arousal within the internal clock model has generated interest in exploring how emotions change time perception (Schirmer, 2011). The two primary dimensions of emotional assessment are affective valence, ranging from pleasant to unpleasant, and intensity, ranging from calm to excited (Lang, Bradley, & Cuthbert, 2008). From the time perception perspective, the level of arousal is determined by the magnitude of the excitement induced by an emotion, which is supposed to explain the effects of emotion on behaviour (Gil & Droit-Volet, 2012). Hence, the intensity of emotional experience tends to be the most relevant factor for the arousal-based explanations of time perception. Even though François (1927) was interested in the effect of temperature on subjective duration, he nevertheless preferred to describe psychological time as a "complex psycho-physiological phenomenon", implying a role of internal context in time perception. Indeed, when observing temporal distortions in relation to emotional stimuli, the role of discrete emotions should be accounted for in addition to systematic manipulations of arousal level. Although emotion theorists emphasise the overlapping properties of different emotional systems in the brain and especially the nonspecific arousal systems guided by the norepinephrine and serotonin activity, these emotional systems display distinct subcortical substrates (Panksepp, 2007). Thus, if the emergent emotions contribute to psychologically distinguishable affective states, a simple arousal-based mechanism might not be sufficient to explain temporal distortions.

The internal clock model clearly does not assume that the perception of time results from mere sensory input directly affecting the speed of the pacemaker. In addition to the arousal account, additional mechanisms are important in describing the variability of time perception within the internal clock model. More precisely, the contribution of attentional processes is distinguished from arousal effects (Zakay & Block, 1997). In this view, an adjustment has been made to the internal clock model by adding a switch, which is guided by attention and controls the accumulation of temporal pulses. Applying emotional stimuli provides a means to explore the involvement of the attention mechanism in time perception, assuming that the processing efficiency of emotional stimuli is enhanced relative to neutral ones through attentional systems (Pourtois, Schettino, & Vuilleumier, 2013). Thus, if we consider that there are specific attention biases guiding the processing of emotional stimuli, then the emotional modulation of attention helps to achieve a better understanding of the internal clock mechanisms underlying time perception.

Much of the contemporary research on time perception involves the experience of duration in passing, where the length of the interval is often used as a behaviourally observable variable. Currently, a clear distinction is made between retrospective and prospective paradigms in timing research, partly due to introducing the concept of attention to the internal clock model (Block & Zakay, 1997; Ornstein, 1969; Zakay & Block, 2004). Indeed, there is a difference whether a subject knows in advance that he or she is going to be asked to estimate temporal intervals (i.e., prospective timing) or whether he or she is unexpectedly asked to judge the duration that has already passed (i.e., retrospective timing). The differences between the two types of tasks are assumed to reflect the amount of attention directed towards temporal properties and explained in the context of attention and memory processes (Block & Gruber, 2014).

Methodological considerations in time perception research involve the ways of linking overt timing behaviour with the temporal processing in the brain. Here, advanced psychophysiological techniques together with neuroimaging have created opportunities to observe the passage of time in the brain by studying the internal clock components in more detail. Neuroscience research has resulted in a bulk of evidence implicating specific structures in the brain as being responsible for temporal processing (Buhusi & Meck, 2005; Coull et al., 2011). Pharmacological manipulations have implicated the dopaminergic system in regulating the speed of the internal clock (Rammsayer, 1993) and electroencephalographical studies describe the Contingent Negative Variation (CNV) as an indicator of the temporal accumulation process (Macar & Vidal, 2004; Mella & Pouthas, 2011). Additionally, pathophysiological findings elucidate the neurobiological mechanisms of time perception and suggest that the timing ability is fundamental to cognitive and behavioural processes, referring to the importance of individual differences (Allman & Meck, 2012). Fraisse (1984), reasoning about the conditions under which time is perceived, also stressed the importance of the properties of the perceiver, using the term “subject’s own resources”. The role of individual differences in subjective time has created interest in exploring the trait-dependent effects in time perception. For example, altered temporal processing has been systematically linked with impulsive behaviour and impaired prefrontal cortex functioning, providing support either for the increased cognitive processing speed or dysfunctional allocation of attentional resources between time and task-relevant information in implusive individuals (Wittmann & Paulus, 2008).

The current thesis explores time perception by varying environmental conditions (**Study I** and **Study II**), but also the characteristics of stimuli (**Study III**). Also, individual differences related to time perception are investigated (**Study IV**). **Studies I** and **II** are particularly concerned with temperature sensitive aspects of time perception and the involvement of arousal mechanisms, whereas **Study III** sets out to clarify the attentional mechanism and its role in producing the duration of affective stimuli. Finally, **Study IV** describes the relationship between time perception and impulsive behaviour. The aim of the research presented here is to specify the factors that modulate the perception of time and identify the mechanisms involved (i.e., arousal or attention) within the theoretical framework of the internal clock.

2 THE INTERNAL CLOCK MODEL

Theoretically, it is possible to approach the concept of processing temporal information with assuming either the existence of a central clock mechanism or explaining it in terms of cognitive processes without the reference to the internal clock. The latter theoretical models explain time perception with attention and memory mechanisms (Staddon & Higa, 1999; Zeiler, 1999) or with the modality-specific processing of time (Grondin, 2003). A prevailing approach in the time perception literature assumes the existence of a central timing mechanism, a biological clock, which is responsible for generating the subjective representation of time. John Wearden (2005) has provided an in depth overview on the origins of internal clock theories. A preliminary theoretical model of internal clock was introduced by Michel Treisman (1963) and it was based on the experiments from early studies with temperature manipulations and the "chemical clock" hypothesis (François, 1927; Hoagland, 1933). The main assumption of the model was the existence of an arousal-sensitive pacemaker, which sends pulses to a counter, thus providing the raw material for time judgments. This basic clock mechanism is in the centre of the scalar expectancy theory (*SET*, Church & Meck, 2003; Gibbon, Church, & Meck, 1984; Wearden, 1991; 2003), which is based on the animal conditioning studies and is currently the most prominent theoretical approach in explaining the operating principles of the internal clock. The SET proposes a more complex cognitive system for time perception, as the pacemaker-counter mechanism is not sufficient to explain all the aspects of timing behaviour. More specifically, it introduces the role of memory processes as well as comparison and decision making mechanisms. Figure 1 shows the schematic model of the SET system in terms of a clock, memory and decision making stages as different information processing levels responsible for time perception.

The first level of the SET model is the clock stage, which consists of a pacemaker-accumulator clock. The pacemaker periodically generates a series of pulses ("ticks"), which are recorded in the accumulator and provide the "raw" representation of experienced duration. It is even suggested that the length of the perceived duration is determined directly by the number of time units, or pulses, accumulated (Hemmes, Brown, & Kladopoulos, 2004; Wearden, 2005). These two clock components are connected by a switch that determines the accumulation of pulses in the counter. For example, when a stimulus is being timed, the switch closes at the onset of the timing process and stays closed during the temporal processing, allowing the streaming of the pulses to the accumulator. The switch opens again when the timing of the interval is terminated and cuts off the connection between the pacemaker and the accumulator. At the end of the timing process, the accumulator is expected to contain the amount of pulses that correspond to the duration being timed. Operation of the pacemaker-accumulator has been explored by manipulating pacemaker speed (Droit-Volet & Wearden, 2002; Penton-Voak, Edwards, Percival, & Wearden, 1996) or the functioning of the switch (Brown, 1997; Droit-Volet, 2003). Experimental manipulations on a clock stage generally comprise of investigating arousal and attention mechanisms, which are further described later in this chapter.

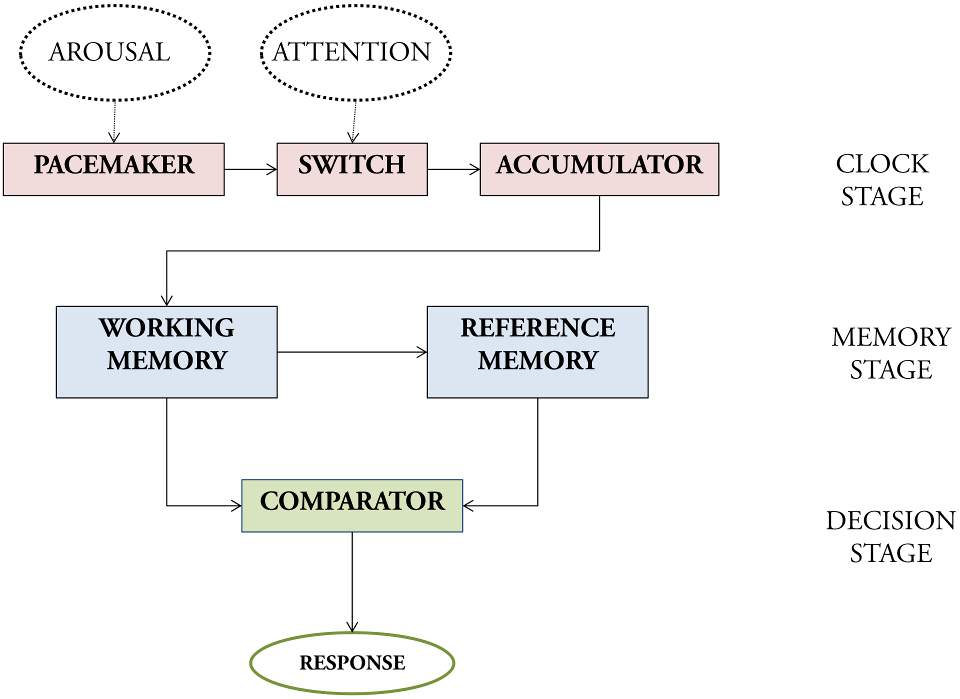

Figure 1. Schematic model of the scalar expectancy theory (SET) system. Adapted from Gibbon, Church, & Meck, 1984.

The next level of the SET is the memory stage, which consists of the reference memory and working memory processes. After stimulus presentation, the representation of timed duration is transferred from the accumulator to the working memory and is assumed to stay there for further processing. The reference memory is considered to contain the criterion duration(s), or a "common reference", which is the memory of the standard or target durations relevant for the timing task. The reference memory is also implicated in generating the scalar property of timing and is partly responsible for the scalar variability in addition to the clock stage processes (Wearden, 2003). Research on the development of temporal representation suggests an active transformation process in forming the relevant standard duration in the reference memory (Jones & Wearden, 2003; 2004). Evidence from animal studies with changing reinforcement times further suggest that the content of reference memory is rather rapidly over-written (Lejeune, Ferrara, Simons, & Wearden, 1997).

At the decision level of the SET, the contents of the working memory are compared to the standard duration that resides in the reference memory and is relevant to the task. The comparison process results in a decision about duration and followed by a behavioural response. The crucial role of decision processes is supported by studies, which applied payoff manipulations when identifying comparisons to standards in the timing tasks (Wearden, 2004; Wearden & Culpin, 1998; Wearden & Grindrod, 2003). For example, in the temporal generalisation task Wearden and Grindrod (2003) assigned more points either for hits (encourage condition) or correct rejections (discourage condition) while keeping the stimulus to be timed similar. The difference in either encouraging or discouraging subject in giving the "yes" response resulted in systematic changes of the response threshold.

One of the assumptions of the SET is the aspect of proportional timing, meaning that instead of absolute values, the behaviour is adjusted to the proportions of temporal intervals (Wearden, 2005). This introduces the concept of scalar timing mechanism, which exhibits two scalar properties: the first being the mean accuracy (i.e., the mean of estimated time increases linearly with physical time) and the second is the scalar property of variance, which dictates that the timing sensitivity remains constant across the range of durations to be timed (Wearden & Lejeune, 2008). For the analysis of scalar variance, a coefficient of variation (CV) is used, where a standard deviation of temporal judgments is divided by the mean. Wearden and Jones (2007) provided evidence that subjective time grows as a linear function of real time in both verbal estimation and temporal generalization tasks. Moreover, in the latter task, subjects were extremely efficient in averaging durations to be used as a standard, providing further support for the existence of a linear time scale. These results are actually in agreement with the SET, which assumes the existence of a central clock mechanism registering durations in a stopwatch-like way. Indeed, if the pacemaker generates pulses in a regular manner, linear timing is achieved. Of course, the observed behaviour may not always exhibit scalar properties due to additional processes (e.g., very short durations and task difficulty effects, Wearden & Lejeune, 2008).

Within the internal clock framework, errors in time perception may originate from all aforementioned processing stages and clock components – the pacemaker may be ticking too quickly or too slowly, the accumulator may occasionally miss pulses, the reference interval may be distorted in a long-term memory, the working-memory capacity may be disturbed and the decision processes disrupted. Thus, all levels of the SET could be responsible for generating the variance in temporal judgments, but so far, the functioning of the pacemaker has been particularly accounted for the variability of subjective time. The accuracy of time perception at the clock stage is modulated through attention and arousal mechanisms (Burle & Casini, 2001; Grondin, 2010; Block & Zakay, 1996). Work presented in the current thesis is involved with the clock stage of the SET framework and assumes the variability of timing behaviour resulting from the pacemaker-accumulator functioning.

2.1 Methodological considerations for studying time perception

Time perception research clearly makes a distinction between retrospective and prospective time judgments (Block & Zakay, 1997; Hicks, 1992). In a prospective paradigm, the subject knows in advance that he or she needs to make a temporal estimation, whereas in the retrospective paradigm, the subject is unexpectedly required to judge time after the duration in question has ended. These operationally different paradigms are considered to involve distinct psychological mechanisms. Prospective timing refers to the use of a clock mechanism, which emits and accumulates pulses during an intentional timing process, whereas retrospective estimations are assumed to involve more cognitive processing of information. Memory processes have been implicated in retrospective experience of time – more information stored in the memory during the time passed increases the respective estimations (Zakay & Block, 2004), as does the remembered amount of contextual change in cognitive activity for the estimated duration (Block, 1985; Block & Reed, 1978; Sahakyan & Smith, 2013). A subject would report a longer interval because it contains more information, which refers to the past experience and serves as an example of the memory processes involved in retrospective time estimation. In the time perception literature, the two processes are therefore often referred to as timing with or without a timer (Block, 2003), or as experienced and remembered time, respectively (Block & Gruber, 2014). SET provides a framework for the prospective time estimation exploring activation and attention effects on temporal processes (Wearden, 2005), which require a specific time-dependent clock-like mechanism. Here, estimation of future durations is performed in several ways, either by producing and reproducing intervals, or verbally estimating them, or making comparisons between durations (Grondin, 2010). In addition, the stimulus timed in different tasks may exhibit various properties (e.g., auditory signal is estimated longer compared to visual stimuli, Wearden, Edwards, Fakhri, & Percival, 1998).

Another distinction in the time perception research is based on the range of durations investigated. Early research showed that overestimation is observed for shorter durations whereas longer durations tend to be underestimated, a result described as Vierordt's law (Lejeune & Wearden, 2009). The processing of sub-second durations is assumed to rely on different processing mechanisms than that of the supra-second range (Buonomano & Karmakar, 2002; Lewis & Miall, 2003a; Lewis & Miall, 2003b; Lewis & Miall, 2009). The timing of durations in the range of hundreds of milliseconds is assumed to be more of a perceptual nature and often related to the engagement of automatic motor reactions, probably of a subcortical origin (Rammsayer & Lima, 1991). Timing in this range is, for example, reflected in the coordination of athletes applying motor skills or musicians playing musical instruments. On the other hand, estimation of durations lasting several seconds is assumed to be cognitively mediated and to dependend on executive functions (Lewis & Miall, 2003a). For example, Rammsayer & Lima (1991) showed that in an interval discrimination task, the performance in processing a second-long interval was considerably affected by the increase in cognitive load, whereas no decrements in performance were observed for the shorter intervals. Neuropharmacological evidence (Rammsayer, 1999) and data from neuroimaging (Penney & Vaitlingam, 2008) support the existence of somewhat separate mechanisms for processing durations in different ranges. Different patterns of brain activity have been reported during the measurement of durations either in the millisecond or in the multi-second range, showing the involvement of the motor system in the former case and the prefrontal cortex in the latter time scale (Lewis & Miall, 2003b). Of course, there is a great deal of overlap in the neural systems when processing time in both duration ranges (Macar, Lejeune, Bonnet, Ferrara et al., 2002). Conceptually, this is in concordance with the fact that most time judgement tasks require some sort of a motor response in addition to duration timing, either vocalizing a response when providing verbal estimations, or terminating the timing of an interval with a button press. Of course, it is possible to distinguish perceptual and motor properties of timing brief intervals, depending on the temporal task applied. More precisely, the difference resides in whether the motor response itself is timed (e.g., rhythmic motor tasks like synchronisation or interval production) or is used to indicate the judgement or decision about time (e.g., discrete-perceptual tasks like temporal generalisation) (Macar et al., 2002).

Another concern with measuring time perception in human subjects is the ability to use explicit counting, a language-based strategy. Chronometric counting is used to ensure the accuracy of time judgment irrespective of the duration length and has been reported to happen spontaneously in 97% of the subjects engaged in a temporal task (Fraisse, 1963). When the task requires processing of intervals longer than 1 second, the use of chronometric counting by the subjects is evident (Hinton, Harrington, Binder, Durgerian et al., 2004; Hinton & Rao, 2004; Penney & Vaitilingam, 2008). Moreover, this occurs in children, when instructed accordingly (Clément, & Droit-Volet, 2006). Grondin, Meilleur-Wells and Lachance (1999) determined the interval length of 1.18 seconds at which the explicit counting becomes a helpful strategy in a temporal discrimination task. Indeed, when the subjects use self-paced chronometric counting, temporal accuracy tends to be higher (Kladopoulos, Hemmes, & Brown, 2004; Rakitin, Gibbon, Penney, Malapani et al., 1998; Wearden, 1991). Of course, explicit counting in timing tasks is prevented with a suppression task, for example, the use of nonsense speech during timing (Droit-Volet, Clément, & Fayol, 2003), which is a commonly applied strategy in verbal working memory studies to restrict sub-vocal rehearsal (Baddeley, Gathercole, & Papagno, 1998).

In relation to the SET model, the aforementioned methodological aspects should be taken into consideration. SET has been previously found to fit the data in prospective timing studies, with intervals in a range of seconds and restrictions on the use of counting (Wearden, 1991). However, the “classical” timing tasks (i.e., interval production, reproduction, verbal estimation) used in human time perception research often violate the scalar properties (Wearden, 2003; Wearden & Lejeune, 2008). In addition, the use of chronometric counting has been shown to produce transgressions from scalar properties (Wearden, 1991). The latter violation of scalar properties might reside in different neural systems used in timing and counting (Hinton et al., 2004).

Finally, the interpretation of results reporting overestimation and underestimation or changes in the clock speed should consider differences in the methodologies of time perception studies. The pacemaker measures a duration of an event in pulses and as a result, a behavioural output is observed (i.e., a response of reporting the perceived time). The latter varies as a function of the pacemaker rate (Pande & Pati, 2010). Hence, when the internal clock is fast and emits more pulses for each “unit” of real time, duration is perceived to be longer. This occurs due to the perception of real time passing more slowly compared to the faster ticking of the internal clock. Of course, in an interval production task, this effect would result in underproduction (i.e., “ticks” are accumulated faster and the production of an interval is terminated earlier), whereas in a verbal estimation task, overestimation is observed (i.e., more “ticks” are accumulated during the time to be judged and the interval is estimated to last longer).

Work presented in the current thesis focuses on interval timing in the range of seconds and assumes a cognitively controlled timing mechanism. Performance in both prospective (i.e., interval production task, **Study I**, **Study II**, **Study III**) and retrospective (**Study II**, **Study IV**) time estimation is observed. In addition, **Study II** further examines the relationship between the two types of time estimation tasks, showing that a shorter retrospective time judgment is related to higher accuracy in the interval production task.

2.2 The role of arousal in time perception

For some time, arousal effects on temporal processing were explored by manipulating body temperature and linking changes in temperature to changes in psychological time (for a review, see Wearden & Penton-Voak, 1995). Hoagland’s (1933) early proposition of a relationship between a chemical reaction and temperature, which refers to the existence of a biological basis for the subjective time scale, was later termed as arousal-sensitivity by Michel Treisman (1963). The evidence refers to the existence of a temperature sensitive time mechanism mediated by the level of arousal – a higher body temperature indicates an increase in the arousal level and this in turn has an effect on the processing of temporal information by speeding up the clock (Aschoff, 1998; Hancock, 1993). However, body temperature is not the only means to manipulate the speed of the clock in terms of arousal changes. For example, Treisman, Faulkner, Naish and Brogan (1990) elegantly demonstrated an increase in clock speed by applying trains of repetitive stimulation (i.e., rhythmic flashes or clicks) and concluded that there are possible oscillatory processes affected by the rhythm imposed, and the frequency of such a temporal oscillator produces the respective temporal estimates. Penton-Voak and colleagues (1996) demonstrated in a series of experiments that preceding stimuli by clicks increased clock speed by 10%. Additionally, as more pulses are generated by the pacemaker due to higher arousal level, counting at the rate of subjective second may become faster as well (Hoagland, 1933; Zakay & Block, 1997). This effect is explained by the alteration of the basic count unit as a result of changes in the speed of an internal clock (Wearden & Penton-Voak, 1995). Wearden, Philpott and Win (1999) used click-trains to produce a relative slowing down of the internal clock in the bisection task, either by applying clicks before standards or comparisons. Moreover, absolute slowing of the internal clock together with a decrease in self-rated arousal has been achieved with the subjectively slow trial pace in the timing task (Wearden, 2008). The results in these studies are interpreted in the framework of the arousal-sensitive pacemaker (Figure 1).

Altogether, physiological arousal seems to distort subjective time by changing the speed of the internal clock. Using this theoretical context, **Studies I** and **II** further elaborate on the traditional approach of temperature manipulation in time perception by including extensive measures of physiological and psychological states. Core temperature, heart rate, hormone response and subjective feelings of fatigue and effort are assumed to reflect different aspects of arousal. Changes in these state-dependent variables are obtained by exercise-heat stress – heat production in the body is increased by strenuous exercise and when combined with increased environmental temperature, cardiovascular, neuromuscular and thermoregulatory processes are altered (Hargreaves, 2008). As core temperature increases, exercise performance shows signs of decline. Increase in body temperature appears to be the important factor inducing changes in the hormone response to moderate exercise in the heat. The rise in core temperature has been linked to a rise in plasma prolactin levels (Burk, Timpmann, Kreegipuu, Tamm et al., 2012; Low, Cable, & Purvis, 2005; Pitsiladis, Strachan, Davidson, & Maughan, 2002), growth hormone response (Bridge, Weller, Rayson, & Jones, 2003; Christensen, Jorgensen, Moller & Orskov, 1984), and to a modulation of cortisol response (Brenner, Zamecnik, Shek, & Shephard, 1997; Bridge et al., 2003). Of course, cortisol response is also affected by psychological stress, which possibly emerges due to feelings of distress and discomfort during exercise in the heat (Follenius, Brandenberger, Oyono, & Candas, 1982).

Although changes in core temperature are the main predictor of the exercise capacity and the development of fatigue at extremely high ambient temperature, increase in energy metabolism (Parkin, Carey, Zhao, & Febbraio, 1999), cardiovascular strain accompanied by dehydration (González-Alonso, Mora-Rodriguez, Below, & Coyle, 1997) and reduction of motor drive in the central nervous system (CNS) are also significant in determining exercise performance (Nybo & Nielsen, 2001b). Previously described alterations in peripheral mechanisms are insufficient to explain the decline in performance (Noakes, 2000). Exercise increases the metabolic rate in various organs of the body (e.g., heart, respiratory system) and especially in active muscle tissue, which is used as an afferent input in addition to the input from the active brain regions. Information from these signals is integrated in the CNS and modulates the motor command in the motor cortex, which is perceived as effort (Kayser, 2003). The CNS serves as an integration centre of both external and internal sensory information and provides feedback for subsequent behaviour regulation. Therefore, changes in CNS functioning might be relevant in explaining the effects of exercise in the heat, where the rise in core temperature becomes the crucial peripheral factor (Nybo & Nielsen, 2001a). Even before the critical level of temperature is obtained and the subjects terminate their exercise at the level of exhaustion, decrements in exercise performance are often observed, resulting from a complex interplay between peripheral and central mechanisms (Galloway & Maughan, 1997).

Taken together, there are several physiological changes in addition to a rise in core temperature that are related to the prolonged exercise in hot environment. **Study I** makes a distinction between physiological and psychological state-dependent effects on time perception and **Study II** further probes these differences with the heat acclimation effects and hormone response to exercise-heat stress.

2.3 The role of attention in time perception

In addition to body temperature, experiments show that the subjective experience of time can be affected by various other physiological and psychological states like emotions and mood (Angrilli, Cherubini, Pavese, & Manfredini, 1997; Droit-Volet & Meck, 2007), boredom (Danckert & Allman, 2005; Watt, 1991), physical exercise (Lambourne, 2012; Vercruyssen, Hancock, & Mihaly, 1989), walking rhythm (Kiefer, Riley, Shockley, Villard et al., 2009), cognitive task load (Block, Hancock, & Zackay, 2010), and sleep deprivation (Esposito, Natale, Martoni, Occhionero et al., 2007; Miró, Cano, Espinosa-Fernandez, & Buela-Casal, 2003). For interpreting the obtained effects with various stimuli within the SET framework, the arousal-pacemaker link previously described has often been found to be inconclusive. Therefore, current time perception research presents a remarkable increase in exploring the role of attention to explain these effects.

Incorporating attention into the SET model is one of the challenges in time perception research (Wearden & Lejeune, 2008). This is difficult for several reasons. First, it should be considered that the origins of the SET model are in animal learning and in that context, the timing process is approached in a more “bottom-up” manner, assuming a direct link between stimulus and response production. However, the premise of attention exhibiting a role in time perception suggests the involvement of more “top-down” processes. Ample research has already provided support for the crucial role of attention in time perception (Brown, 2008; 2010; Brown & Boltz, 2002; Buhusi & Meck, 2009), which has proved to be effective in explaining timing behaviour where the accounts using the arousal-pacemaker link fail.

When describing the role of attention in time perception, the “watched pot never boils” phenomenon might be a useful example. According to the attentional models of time perception, experiencing and processing time depends on a subject dividing attention between temporal and non-temporal information (Block & Zakay, 1997; Zakay & Block, 1996). More specifically, when a subject attends to time, it is perceived to pass slowly, whereas when engaged in some other activity, time feels like it is “flying by”. Of course, there are exceptions in that matter but these aspects are discussed later in the text regarding time estimation in emotional context. The differences in the judgment of time in relation to attention occur as a result of resource allocation between temporal and non-temporal information processing. Within the SET framework, attention effects could be explained by the functioning of the switch between a pacemaker and the accumulator (Figure 1). When attention is directed to time, the switch is closed and the pulses flow to the accumulator. However, when something else catches our attention and we get distracted from the temporal properties of the task, the switch is opened and the flow of pulses to the accumulator is terminated. Block and Zakay (1996) have specified the approach on how attention influences the internal clock by introducing the attentional gate model. It bears great similarity to the attention effects on the switch (as explained by the SET) but allows a more “flexible” account of the mechanism. Here, a gate is placed between the pacemaker and the accumulator. More attention to time results in a wider gate, allowing more pulses to be accumulated and thus, the perceived time is lengthened. The pulses in the clock system may get lost, which would be an indicator of a “flickering” switch as a result of disturbed attentional processing (Meck & Benson, 2002). Directing attention to time is one of the sources of variability in time perception, most likely controlling the switch (or the gate) and directly affecting the pulse count in the accumulator (Coull, Vidal, Nazarian, & Macar, 2004; Lejeune, 1998; Macar, Grondin, & Casini, 1994).

The role of attention in time perception is especially obvious in prospective judgments, where a person knows in advance about the temporal requirements of the task. For successful timing performance, the subject would direct attention towards temporal cues and, if permitted, use chronometric counting. Higher temporal awareness is generally accompanied by more accurate timing behaviour. In a retrospective paradigm, due to being unaware of the timing requirements, attention is more captured by non-temporal information (Brown, 2010). When considering the two paradigms, Brown and Stubbs (1992) proposed to observe the differences (or similarities) by assigning the degree of attentiveness to the time in a task. Thus, the two types of timing are really situated on the same continuum and the differences are explained by the level of attention to temporal properties in the task.

Additional evidence for the involvement of attention processes in time perception comes from the research applying the dual-task paradigm. When less attention is allocated to time, for example, by engaging in a concurrent task and distracting the temporal aspect with other task demands, a reduction in subjective duration occurs. Also, temporal accuracy is reduced as judgments become more variable. As already mentioned, if more attention is allocated to time and processing of temporal cues, the perceived duration is more accurate (Brown, 2008; Brown & Merchant, 2007; Buhusi & Meck, 2009). These effects are explained by the two simultaneous tasks competing for the limited pool of attentional resources, and time perception depends on how much attention the temporal aspects of the task receive. Dual-task studies have revealed that temporal behaviour is remarkably sensitive to interference and processing demands, as even the smallest demands might impair temporal performance (Brown, 2010). In addition, the nature of interference and the conformity between the distractor and the stimuli to be timed has proved to be inconclusive. Rather, the general aspect of disrupting attention is responsible for deteriorated temporal performance (Brown, 2008). Research showing bidirectional effects of interference has proposed a question about the availability of multiple resources (Brown, 2010). Indeed, several studies have provided evidence that the tasks related to executive functioning might share resources used by temporal processes, demonstrating a reciprocal trade-off between the tasks (Brown, 1997; Brown, Collier, & Night, 2013). However, it should be noted that processing and timing of more complex stimuli (e.g., emotional pictures) could introduce specific attention effects (Lui, Penney, & Schirmer, 2011; Schirmer, 2011), which will be discussed in later chapters.

In relation to attention mechanisms, a distinction between automatic and controlled processes becomes important; hence the concept of “top-down” processing should be introduced. The common notion is that automatic tasks require less attention and cause less interference with other concurrent activities, whereas controlled or executive processes require intentional approach (for a review, see Lustig, 2003). Of course, under complex and adverse conditions, dividing attention between different tasks becomes even more difficult – automatic processes might require more processing resources and the cognitively controlled processing is therefore significantly impaired (Cian, Barraud, Melin, & Raphel, 2001; Cian, Koulmann, Barraud, Jimenez et al., 2000; Dietrich & Audiffren, 2011; Tomporowski, 2003). Thus, in the case of an overwhelming fatigue or exertion, or due to concurrent task demands, less accurate temporal performance with relatively longer productions and shorter estimations is expected. Furthermore, intervals in a multi-second range require the use of the cognitively mediated temporal system as the subject is able to use a certain segmenting strategy to divide temporal intervals into smaller units (Hellström & Rammsayer, 2004; Rammsayer, 2008).

Because of the possible role of attention in time perception, **Study III** takes advantage of the affective attention paradigm, assuming the preferential processing of emotional information in the brain. As the perceptual capacity to process information is somewhat limited, attention selects the relevant information that is subjected to further processing and priority is given to emotionally salient or goal-relevant stimuli (Pourtois et al., 2013). Information selected by attention involves both stimulus driven (bottom-up, exogenous) and goal-driven (top-down, endogenous) factors. A task-irrelevant stimulus with distinctive physical features that can be novel or unexpected might gain preferential processing among other stimuli and conversely an otherwise unobtrusive stimulus might be preferred because of its importance within the current goals and expectations (Posner, 1980; Theeuwes, 1994). These attentional processes are not exclusive and do not operate independently and, although stimulus-driven attention is mostly reflexive, top-down factors related to task-relevant goals might influence the former processes. These two attention mechanisms are involved with different brain circuits in the frontal and parietal cortex but also show functional and structural overlap (Corbetta & Schulman, 2002).

The main function of attention mechanisms is to amplify sensory processing of stimuli, which, when presented simultaneously, compete for the processing resources in order to access awareness through higher cognitive processing (Pourtois et al., 2013; Vuilleumier, 2005). Emotional stimuli have the ability to engage neural systems relative to neutral stimuli and through attentional processes the former gains additional weight for further processing (Corbetta & Schulman, 2002). Enhanced sensory processing for emotional stimuli is observed on various occasions. The neural response to emotional stimuli is enhanced relative to neutral stimuli with additional specific dynamics in temporal processing. The emotional information elicits earlier responses in certain frontoparietal areas, which affect the following sensory and cognitive processing (Pourtois, Spinelli, Seeck, & Vuilleumier, 2010). It is possible that the gain control mechanisms of affective attention might explain how emotions modulate time perception. If emotional and temporal information compete for the capture of attention, attention is diverted faster and more strongly towards an emotional stimulus whereas fewer resources are available for the timer. Of course, the effects of emotional attention might be dependent on current emotional context and the emotional state of the subject (e.g., enhanced sensory response by anxiety, Cornwell, Alvarez, Lissek, Kaplan et al., 2011).

Taken together, emotional stimuli have the ability to influence the ongoing sensory processing through stimulus-driven as well as task-relevant mechanisms more efficiently than neutral stimuli. Perception and attention processes are not just dependent on the modulation of top-down resources but emerge from the competitive processes among different factors to attain selection of relevant information (Pourtois et al., 2013). Of course, different emotional stimuli might elicit distinct patterns of activation and attentional capture, which might explain the differences in estimating time and further unravel the attention mechanism in the SET framework.

2.4 Time perception in the brain

Although as noted by Gibbon and Malapani (2001) that "current understanding of the psychophysics of temporal processing far exceeds our understanding of the neural substrates of timing", recent advances to specify brain systems involved in time perception have been noteworthy. To identify whether humans actually possess a biological clock-like mechanism and how a duration is represented in the brain, recent developments have linked the SET framework and behavioural data to psychophysiological processes (Buhusi & Meck, 2005; Coull et al., 2011; Grondin, 2010; Livesey, Wall, & Smith, 2007; Wittmann, 2009). Recent evidence suggests that there is a specialized brain system involved in temporal behaviour. When the neural origins of timing mechanisms are considered, it is important to differentiate between perceptual and motor timing processes and also explicit and implicit timing (Coull et al., 2011; Coull & Nobre, 2008). In the explicit timing tasks, subjects generally provide an overt estimate of certain durations, whereas implicit timing tasks require making temporal predictions based on the regularity of the temporal pattern (Coull & Nobre, 2008). Temporal predictability is achieved through temporal sensory cues and also through subjective sense of temporal expectations, which have been shown to improve performance related to non-temporal task goals (Barnes & Jones, 2000; Coull & Nobre, 1998).

Specific brain structures often implicated in temporal processing are the cerebellum and the basal ganglia (Allan, 1998; Coull et al., 2004). The cerebellum is proposed to be involved in both time perception and in the timing of movement (Ivry & Hazeltine, 1995; Ivry & Keele, 1989). There is still a debate whether the cerebellum is involved in the timing of brief intervals (i.e., milliseconds range, Bueti, Walsh, Frith, & Rees, 2008; Lewis & Miall, 2003b) or is rather related to the processing of intervals in the seconds range (Harrington, Lee, Boyd, Rapcsak et al., 2004; Nichelli, Alway, & Grafman, 1996). Evidence from recent studies using transcranial magnetic stimulation

(TMS) showed that repetitive TMS to the cerebellum impairs timing of sub-second durations (Koch, Oliveri, Torriero, Salerno et al., 2007). The basal ganglia have been found to be relevant for the encoding of temporal stimuli and determine the speed of the pacemaker (Harrington & Haaland, 1999; Malapani, Deweer, & Gibbon, 2002). More recent evidence from functional neuroimaging has shown the basal ganglia activity to be independent of duration range (Jahanshahi, Jones, Dirnberger, & Frith, 2006) and sensory modality (Shih, Kuo, Yeh, Tseng et al., 2009) during timing. These results implicate the basal ganglia as a possible centralised timer with context-independent properties, although they are often related to the activity of various cortical regions (Coull et al., 2011). With respect to co-activation patterns in the brain, the basal ganglia and the supplementary motor area (SMA), which are responsible for the control of motor processes in general, are suggested to have a central role in motor timing processes (Jantzen, Oullier, Marshall, Steinberg et al., 2007). However, the basal ganglia are activated alone when the duration is produced based on the internally specified representation (Garraux, McKinney, Wu, Kansaku et al., 2005). The role of the SMA in timing tasks have been described for shorter (Ferrandez, Hugueville, Lehericy, Poline et al., 2003) and longer intervals (Rao, Mayer, & Harrington, 2001) as well as for chronometric counting (Hinton et al., 2004). Therefore, when considering a typical time estimation task, both external (e.g., providing a motor response) and internal representations (i.e., perceptual processing) are required for successful performance and thus, the SMA and the basal ganglia are both activated.

In addition, several cortical regions like frontal and parietal cortices have been implicated in the processing of temporal information (Coull, Frackowiak, & Frith, 1998; Lewis & Miall, 2006; Macar & Vidal, 2009). In particular, TMS (Koch et al., 2007) and neuropsychological evidence (Danckert, Ferber, Pun, Broderick et al., 2007) show the role of the right prefrontal cortex in the temporal processing of longer supra-second durations. The same region has been shown to be involved in making temporal predictions due to its monitoring role and using sensory input for updating temporal expectations (Vallesi, Shallice, & Walsh, 2007). Updating temporal information is also involved in explicit timing, especially during the passing of the temporal interval. A constant comparison process of the currently lapsing time and reference memory representation is assumed to involve prefrontal cortical activity and reflect the accumulation of temporal pulses (Coull et al., 2011).

Pharmacological manipulations in animals indicate that the speed of the pacemaker is presumably modulated by the dopamine (DA) system (Matell, King, & Meck, 2004; Meck, 1983; 1986; Rammsayer, 1993; Rammsayer & Vogel, 1992). Dopaminergic drugs selectively affect the speed of an internal clock – DA antagonists (e.g., haloperidol) produce a deceleration in the rate of the pacemaker whereas administration of DA agonists methamphetamine and cocaine elicit a contrary effect, indicative of an increased rate of the pacemaker (Maricq & Church, 1983; Matell, Bateson, & Meck, 2006; Matell et al., 2004).

Timing of brief intervals in the millisecond range is controlled by the dopamine activity in the basal ganglia and the behavioural effects are not dependent on the increased availability of DA in the brain but more related to the DA receptor activity (Rammsayer, 1993; 2009). The D_2 receptor has been suggested to be the mediator of the pharmacological effects described (MacDonald & Meck, 2006). These proportional effects were explained by the proposal that dopaminergic agonists increase the speed of the pacemaker in a way that the perceived time (i.e. the output of the clock stage) grows more rapidly than the real time (Meck, 1983; 1986). For example, if the speed of the internal clock actually doubled, subjects would provide a temporal response 50% earlier, irrespective of the duration being timed.

Nonetheless, several neuropharmacological studies on temporal processing in humans indicate a somewhat complex picture and this is possibly related to the cognitive mediation of time perception. Lewis and Miall (2006) strongly advocate for the important role of DA projections into the dorsolateral prefrontal cortex (DLPFC), an area involved in both working memory and timing process. Pharmacological manipulations targeting working memory processes are responsible for impaired timing of intervals in the range of seconds (Rammsayer, 1999). While dopaminergic drugs selectively affect the speed of the internal clock, the cholinergic system has been proposed to affect the memory processes involved in timing (Meck, 1983; 1996). Rammsayer (2009) concluded that any pharmacological intervention that affects working memory and attention, irrespective of the neurotransmitter system, modulates the estimation of longer intervals.

Taken together, there is still a lively debate as to whether there is a neural timer in the brain that is central to all timing-related performance or, rather, the timing behaviour is a distributed pattern of neural activity in functionally specific areas in the brain. Indeed, there are modality differences in timing (Bueti, Bahrami, & Walsh, 2008) and duration-specific patterns of activity (Matell & Meck, 2004), but these generally involve timing of durations in a millisecond range. The distinction between perceptual timing and motor timing should be considered when various tasks are applied to explore the temporal processing in the brain. Several components of the internal clock model are involved in estimating longer durations (e.g., attention, working-memory, decision making), which includes extensive perceptual discrimination but also, depending on the task, providing a motor response (e.g., a button press to produce temporal intervals). Thus, neuroscientific evidence supports the idea of two distinct timing circuits in the brain (Buhusi & Meck, 2002) – an automatic timing system for the millisecond range, involving the cerebellum and a cognitively controlled timing circuit, which requires attention and working memory, and involves cortical regions together with the basal ganglia.

The experimental design applied in **Study I** and **Study II** provides an opportunity to suggest possible brain mechanisms involved in time production. More specifically, described changes in core temperature, heart rate and peripheral hormone response provide indirect evidence about the brain mechanisms and neurotransmitter activity related to experiencing exercise-heat stress. Recent studies implicate the role of the DA and noradrenaline (NA) systems in regulating core temperature in the brain during prolonged exercise in the heat (Roelands & Meeusen, 2010). Administration of a dual DA reuptake inhibitor improved exercise performance in high ambient temperature conditions and the subjects were able to maintain the level of arousal after attaining critical core temperature (Roelands, Hasegawa, Watson, Piacentini et al., 2008). Although core temperature and heart rate had risen significantly compared to the placebo condition, the subjects did not report higher perceived thermal stress or effort, indicating the role of DA in dampening the conscious response to heat stress. The prolactin response during prolonged exercise in the heat is often considered to be an indicator of the CNS functioning as it is stimulated by serotonergic (5-HT) activity and inhibited by DA (Bridge et al., 2003; Wright, Selkirk, Rhind, & McLellan, 2012) along with a strong link to changes in core temperature (Pitsiladis et al., 2002). Although increased levels of 5-HT are related to the feelings of fatigue and decreases in arousal, its exact role in thermoregulation and exercise performance is yet to be determined (Roelands & Meeusen, 2010). In addition to linking 5-HT and DA activity with the development of central fatigue (Davies & Bailey, 1997; Roelands & Meeusen, 2010) and control of thermoregulation (Hasegawa, Yazawa, Yasumatsu, Otokawa et al., 2000; Lee, Mora, & Myers, 1985), the involvement of DA neurotransmission in regulating motor drive and motivational processes support its role in changes in mood and affective behaviour (Ashby, Isen, & Turken, 1999; Rubinsztein, Rogers, Riedel, Mehta et al., 2001).

The previously described peripheral and central changes during exercise-heat stress might result from the various stages of the pathway between the CNS and the musculoskeletal system (Nybo & Nielsen, 2001b). For example, perceived exertion is related to an altered EEG response in the frontal cortex during prolonged exercise in the heat, rather than to muscle activity (Nybo & Nielsen, 2001a). The dynamics in the frontal EEG high frequency β band have been shown to initially increase with transition from the resting state to exercise and then follow a progressive decline – a process accompanied by a gradual increase in core temperature (Nielsen, Hyldig, Bidstrup, González-Alonso et al., 2001). These alterations in frontal cortical activity presumably reflect changes in the general arousal level of the CNS and in the metabolic activity in focal brain regions. For example, Cheung and Sleivert (2004) suggest an important role of competition between the thermoregulatory and metabolic demands. Indeed, cerebral blood flow shows a gradual decrease during prolonged exercise in the heat but this does not indicate a similar decrease in cerebral metabolism (Nybo, Moller, Volianitis, Nielsen et al., 2002). For example, the rise in core temperature increased cerebral metabolic rate in the hypothalamus, the thalamus, the (lateral) cerebellum, the cingulate gyrus and the corpus callosum whereas a decrease in metabolic activity was observed in the basal ganglia, the insula and the posterior cingulum (Nunneley, Martin, Slauson, Hearon et al., 2002). Note that the cerebellum and the basal ganglia have been previously implicated in temporal processing (Coull et al., 2011). Hence, the feelings of fatigue, arousal and central drive, and also time perception might share common neural mechanisms that become important during temperature manipulation.

2.5 Aims and hypotheses

The aim of this thesis is to explain the mechanisms responsible for changes in perceived time. Arousal and attention processes are further probed with temperature manipulations and processing of emotional stimuli to gain a better understanding of time perception. Taking into consideration the amount of research on these mechanisms in different contexts of temporal processing, there is still little knowledge about the way how these mechanisms together contribute to interval production. Changes in arousal elicit changes in the speed of the internal clock by modulating the rate at which the pacemaker emits pulses (Gibbon et al., 1984; Treisman, 1963). Body temperature (Wearden & Penton-Voak, 1995) and timing of emotional stimuli (Droit-Volet & Gil, 2009; Schirmer, 2011) are proposed to be responsible for these changes. Although both factors are assumed to act through the arousal-pacemaker mechanism, the complex pattern of results in different time perception tasks introduces additional interpretations, with the plausible involvment of the attention-switch mechanism and the interaction between the two proposed mechanisms.

The temperature sensitive changes in the speed of the pacemaker have been traditionally explained by physiological changes. More specifically, a rise in body temperature increases the speed of the pacemaker resulting in subjective lengthening of time and conversely, decreasing the body temperature decelerates the internal clock (Wearden & Penton-Voak, 1995). **Study I** and **Study II** support the dissociation of different facets of arousal, as the absence of direct temperature effect suggests the significant role of psychological factors (i.e., perceived fatigue, **Studies I** and **II**) and hormone response (**Study II**) to exercise-heat stress. In addition, **Study II** implicates the role of attention in time perception as retrospective and prospective timing performance is closely related. Subjects who were able to concentrate on a non-temporal task demands (i.e., underestimating time retrospectively) were also more accurate in producing temporal intervals in stressful conditions. Thus, they were more effectively directing attention to task-relevant goals in both time perception tasks – towards temporal information in the interval production task and non-temporal information in the retrospective time estimation task. The role of attention in time perception is further explored in **Study III** with emotional stimuli. Here, a rather novel approach to study emotional time perception by adopting widely recognised event-related potentials (ERPs) of the affective attention processes (see also Uusberg, 2014). More precisely, a two-stage paradigm of affective attention is applied to study time perception with ERP correlates, which differentiate the emotion-induced early attentional processing and subsequent arousal processes. In the SET model, emotion effects on time perception are assumed to operate through the arousal mechanism and modulate the rate of the pacemaker (Droit-Volet & Gil, 2009). The results in **Study III** revealed the valence-specificity of producing durations filled by affective stimuli, referring to the involvement of an attentional mechanism in emotional time perception. Although time perception is state-dependent and altered by changes in physiological and psychological factors as demonstrated by **Studies I–III**, individual differences in certain predispositions determine the way temporal information is processed. For example, impulsive individuals overestimate time, which in turn affects their decision making behaviour, particularly in behavioural impulsivity tasks (Wittmann & Paulus, 2008). **Study IV** assessed the impulsivity of the subjects with self-reported measures and performance in a stop-signal task (SST), reflecting response inhibition. Individuals with higher Thoughtlessness score and behavioural response in SST referring to higher levels of impulsivity, made longer retrospective time judgements. These results can be interpreted from several perspectives. First, impulsive individuals might possess a faster cognitive tempo (i.e., higher speed of the internal clock) and therefore exhibit altered sense of time. On the other hand, the findings suggest the involvement of attention mechanisms as impulsive individuals might have trouble allocating attention to relevant non-temporal information. The affective response of impulsive individuals is considered in relation to the attention mechanism to explain the overestimation of time.

The general aim of the current thesis is to specify the factors that modulate the perception of time and clarify the role of arousal and attention processes within the theoretical framework of the internal clock. The results from the presented four studies clearly show that the arousal-pacemaker link and attention mechanism independently do not provide sufficient interpretation for the current findings. Rather, if interval timing is a cognitively mediated process, the arousal-related and attention-related mechanisms are not necessarily operating exclusively, but might contribute to alterations in subjective time in an additive or interactive way. That said, Schirmer (2011) has proposed a hybrid model for affective time perception, which integrates the concepts of arousal and attention from the SET model within the interoceptive framework (Craig, 2002; 2008; 2009b) to explain temporal behaviour. More specifically, assuming emotional modulation of time perception, the stimulus-specific sentient representations (i.e., being aware of one’s self) explain various changes in subjective time, which often do not follow a classical arousal-pacemaker or attention-switch approach. Current findings suggest that the temperature sensitive internal clock should be explained with a more elaborated temperature-emotion-timing relationship.

3 TIME PERCEPTION UNDER EXERCISE-HEAT STRESS

Raising or lowering body temperature alters the perception of time, indicating the existence of a temperature-sensitive internal clock (Wearden & Penton-Voak, 1995). The rate of subjective time tends to increase with a respective increase in body temperature (François, 1927; Hoagland, 1933) and decreases when body temperature is reduced (Baddeley, 1966; Bell, 1975). Generally, the former effect is found and with higher temperature shorter subjective durations are produced. These effects are explained by temperature-increased arousal as physiological processes in the body affecting the speed of the internal pacemaker. However, contrary effects have also been found with cold stress increasing the rate of subjective time (Fox, Bradbury, & Hampton, 1967; Lockhart, 1967). These equivocal results speak against a simple relationship between temperature and time perception within the SET framework. Hancock (1993) sensibly comments that previous research has not distinguished temperature effects from the experienced distress resulting from being exposed to extreme conditions. Of course, changes in core temperature are crucial in eliciting physiological alterations, in both direct and indirect manner. However, the question remains how these effects are related to a psychological response and whether the effects of exercise-heat stress on cognitive functioning could be explained similarly to exercise performance. If we consider time perception to be a cognitively mediated process, both physiological changes and psychological factors might have a role in the timing performance. **Studies I** and **II** dissect the arousal mechanism of the internal clock and elaborate how temperature manipulations change time perception.

3.1 Affective response and cognitive performance during prolonged exercise at high ambient temperature

The overview in the previous chapter introduced a general understanding concerning the physiological effects of prolonged exercise in warm environments. Indeed, the changes in cardiovascular, neuromuscular, thermoregulatory and hormone response have been extensively studied (Hargreaves, 2008) with some of the process dynamics better understood than others. However, heat stress exhibits adverse effects on cognitive functioning with prolonged or high intensity exercise being an additional stress-inducing factor (Hancock & Vasmatzidis, 2003). From exercise studies, perceived exertion is the most often reported psychological factor affected but the mental performance extends beyond the sense of effort. To further complicate matters, there is a variety of cognitive tasks applied in exercise-heat stress studies and different classifications of cognitive processes make the interpretation of effects difficult. As various aspects of cognitive processes exhibit differences in the sensitivity to thermal conditions, the exact underlying mechanisms involved are still in need of much clarification.

Task complexity has been identified as a primary factor in explaining the effects of heat stress on cognitive functioning (Hancock & Vasmatzidis, 2003). Simple tasks of more automatic nature are less sensitive to heat stress compared to more demanding tasks, which require sustained attention and working-memory (Gaoua, Grantham, El Massioui, Girard et al., 2011; Gaoua, Racinais, Grantham, & El Massioui, 2011). Core temperature is suggested to be the main factor contributing to impairments in cognitive functioning, specifically, the rate of change in the respective variable is important (Hancock & Vasmatzidis, 2003; Razmjou & Kjellberg, 1992). However, these changes in cognitive processes cannot be exclusively explained by the core temperature changes, as the decrements in performance have been observed already within half an hour of heat exposure without a significant rise in core temperature (Gaoua, Grantham, Racinais, & El Massioui, 2012; Ramsey & Kwon, 1992). An increase in skin temperature has been shown to be a reliable predictor of a decrease in cognitive performance and the sensitivity of these processes has been related to the environmental temperature per se rather than to the physiological response (Hancock & Vasmatzidis, 2003). Changes in skin temperature are proposed to reflect sensory displeasure in the hot environment with subjects reporting more negative feelings, which in addition are related to disturbances in cognitive functioning (Gaoua et al., 2012).

In regards to both exercise performance and cognitive functioning, affective response in extreme environments should be considered as an important mediating factor. Exercise in extreme environments, whether it is cold, heat or altitude, imposes psychological stress in addition to physiological alterations (Acevedo & Ekkekakis, 2001; Lane, Terry, Stevens, Barney et al., 2004). Affective response has been suggested to be more sensitive to environmental change (Bahrke & Shukitt-Hale, 1993; Lane et al., 2004) and the psychological processes are thus influenced earlier by the respective changes compared to physiological functioning (Kobrick & Johnson, 1991). Performance in the hot environment is related to various mood states (Ekkekakis, Parfitt, & Petruzzello, 2011) and psychological state might be involved in mediating the negative physiological effects (e.g., reappraisal of higher levels of heart rate, Cheung, 2010). Both exercise and cognitive performance in warm environments are affected by the interplay between physiological changes to thermal stimuli and psychological input related to conscious perception of the environment and bodily changes. Acevedo and Ekkekakis (2001) have proposed a psycho-biological model to explain the significance of cognitive appraisal during exercise in extreme conditions. According to this model, the perceived capability to handle the demands imposed by exercise-heat stress influences the subsequent physiological activation. For example, the rating of perceived effort

(RPE, Borg, 1998) has proven to be a useful measure to observe psychological response to physiological variables. The RPE is proposed to receive both central (sensations from the cardiorespiratory system) and local (e.g., exercising muscles) input (Pandolf, 1978; Robertson, Gillespie, McCarthy, & Rose, 1979). Moreover, psychological factors are suggested to explain about 30% of the variance in the RPE (Morgan, 1973) and personality factors with previous experience and emotional predispositions contributing as well (Rejeski, 1985). The relative contribution of these factors is dependent on exercise intensity (Acevedo, Rinehardt, & Kraemer, 1994; Noble & Robertson, 1996) and duration (Acevedo, Gill, Goldfarb, & Boyer, 1996) – in case of exercise at high intensity and for a long duration more attention is directed towards physiological sensation. In reference to the physiological factors related to heat stress, sensory cues of ventilation and heart rate have shown to make a higher contribution to the RPE than thermal sensations (Maw, Boutcher, & Taylor, 1993). Thus, the appraisal of effort is an important observable variable and provides information about the dynamic and possibly reciprocal relationship between physiological and psychological responses to exercising in environmentally stressful conditions. To sum up, several theoretical models clearly differentiate central and peripheral factors contributing to both exercise performance and cognitive functioning. Physiological changes that occur during prolonged exercise in the heat are not sufficient to explain the subsequent changes in cognitive functioning, hence the role of psychological factors and affective response to stressful experimental conditions is emphasised.

A conceptual framework for explaining how both psychological (central) and physiological (peripheral) changes during exercise contribute to observed performance is provided by the model of interoception (Craig, 2002). The proposed model postulates a cortically based subjective awareness, where a number of affective representations at each instantaneous moment extend across a certain period of time. The changes in these consecutive emotional moments in time provide a perspective of a “sentient self”. Hence, there is an internal temporal representation, which is subjective and emotionally laden and therefore possesses certain flexibility (Craig, 2009a). According to this paradigm, the perceived temperature, the level of hydration and muscular pain generate a sense of physical self (i.e., physiological condition of the body), which is processed in the CNS. More specifically, the sense of homeostatic awareness stems from the anterior insular cortex, where the activity is related to subjective feelings (e.g., perceived thermal intensity) rather than physiological changes observed (Craig, Chen, Bandy, & Reiman, 2000). This cortical integration of the physiological state provides a subjective sense of homeostasis, which in turn is responsible for the affective response and conscious regulation of behaviour. The series of neural representations of homeostatic feelings from the body integrates the salience of all moments to generate a “global emotional moment” (Craig 2009a), which describes the sentient self at the very instant. Of course, for experiencing oneself in the “now”, a comparison of representations of the past moments and anticipation of future feelings with the present occurs. In other words, to obtain a global emotional moment of the present, in addition to registering the feelings, the environment and the context in real time, previous experience is also important, especially when future expectations about global emotional moment are generated (Craig, 2009b). The anterior insular cortex is closely connected to the amygdala and the hypothalamus but its co-activation with the anterior cingulate cortex is responsible for providing the substrate for emotions, motivations, cognitive and behavioural control (Craig, 2008; Thielscher & Pessoa, 2007). There is some evidence of psychological interventions enhancing physiological tolerance to heat, possibly modulating the motivational processes (Barwood, Thelwell, & Tipton, 2008). Therefore, the psychological state is as important as the physiological changes related to exercise-heat stress.

Marc Wittmann (2013) suggests that the specific climbing neural activity in the insular cortex is behind the cortical representation of time, which is dependent on emotions and the perceived state of the body. If the temporal context of sentient processing is considered, it would be reasonable to assume that these processes are linked to the processing of temporal intervals and that their neural basis are similar. Indeed, neuroimaging studies have provided evidence that the anterior insular cortex is also activated during time estimation tasks (Lewis & Miall, 2006). Recently, Kosillo and Smith (2010) showed that the the anterior insula is activated during various timing tasks irrespective of stimulus modality, suggesting a more general role in the timing process. The role of interoception regarding time perception has been investigated by Pollatos, Laubrock and Wittmann (2014), who showed that fearful movie clips accompanied by interoceptive focus were significantly dilated while feelings of amusement made the passage of time quicker. They concluded that a higher awareness of bodily sensations results in a more pronounced emotional modulation of subjective time. The mechanism behind these effects is proposed to be the autonomic reactivity and more precisely, sympathetic salience, which is lowered by the positive valence and activated by negative valence (Pollatos et al., 2014). More specifically, the subjective passage of time depends on the emotional and physiological states processed in the brain and the neural representation of time and interoception appear to be closely related.

Within the internal clock model, the arousal mechanism is commonly applied to interpret the relationship between mental performance (e.g., interval production) and changes in body temperature (Wearden & Penton-Voak, 1995). A unitary arousal theory postulates an inverted-U relationship between the performance and the arousal level of the performer (Hebb, 1955; Kahneman, 1973). According to this, as core temperature rises as a result of prolonged exercise in the heat, the arousal level of the subject increases as well, accompanied by improved performance. However, at some point performance starts to decrease as the temperature further increases (Provins, 1966; Vasmatzidis, Schlegel, & Hancock, 2002). The theory has received a great deal of criticism, mostly due to the flexible approach to locating the arousal level where performance efficiency is observed (Hancock, 1989). Risto Näätänen (1973) emphasised the qualitative aspects of arousal, which affect performance. According to this, performance efficiency is determined by the optimal level of activation required for a specific task – if this optimal level of arousal is altered, performance decrements occur. Thus, in the current experimental context, exercise-heat stress would disrupt the optimal level of activation required for adequate performance in the time production task that would occur in otherwise normal conditions.

Considering the issues with defining arousal in the time-sharing context in extreme conditions (Vasmatzidis et al., 2002) and the structural model of interoception (Craig, 2009b), the possible involvement of attention processes in time perception becomes relevant. It should also be considered that constant sentient processing might require additional processing resources. Exercising in the heat requires allocation of attentional processes, probably between the interval production task and walking on a treadmill. If the affective response is considered, additional resources might be needed for regulating the emotional experience. When the exercise becomes more resource-demanding as time progresses, the remaining resources are directed towards relevant activities like exercise performance and maintaining motor control (Dietrich & Audiffren, 2011). Consequently, as the stress increases, attention towards temporal cues is decreased or resources for temporal processing are sparse. This leads to erroneous performance in a concurrent cognitive task (e.g., temporal discrimination) and greater variability of responses.

Taken together, exercising in extreme environmental conditions is accompanied by consequent experience of stress, which is observed in various physiological and psychological changes. The aim of **Study I** is to disentangle the different aspects of response to exercise-heat stress in relation to time perception. The concept of a temperature-sensitive internal clock is further elaborated and the significant role of psychological factors is considered. In **Study II**, acclimation to heat evokes physiological and psychological adaptations, which in turn, are related to performance in the interval production task. In addition, hormone response as an indicator of the experienced heat stress serves as a possible predictor of temporal processing in extreme environmental conditions.

3.2 Study I "The compression of perceived time in a hot environment depends on physiological and psychological factors"

When considering the physiological and psychological implications of heat stress and heat acclimation previously described, the concept of arousal needs to be specified. Arousal is assumed to affect time perception through the pacemaker-accumulator mechanism within the SET framework. This effect is assumed to be similar regardless of experimental manipulation to change the level of activation. However, it is unreasonable to expect that temperature manipulations (Wearden & Penton-Voak, 1995), emotions (Droit-Volet & Gil, 2009) and stimulation with repetitive sounds (Penton-Voak et al., 1996) or flashes (Treisman et al., 1990) influence time perception through a similarly "arousing" process. The differences of these experimental manipulations for exploring the internal clock mechanisms have been less acknowledged in relation to the pacemaker activity. Hoagland's (1933) view of a chemical clock to interpret the temperature effects on temporal judgments needs further elaboration.

The objective of **Study I** was to detail and refine the concept of arousal and its role in influencing the subjective time. The assumption behind the applied experimental design was the multidimensionality of arousal, registered by various physiological and psychological state-dependent variables. By recognising the number of processes affected by exercise-heat stress, different facets of arousal were identified. In addition to body temperature and heart rate as physiological and somewhat peripheral indicators of arousal, it is possible to investigate the activation level of the CNS with the critical flicker frequency, indexing the ability to separate very short temporal samples from a continuous visual input (CFF, Simonson & Brozek, 1952). Extensive research has demonstrated that physiological signs of prolonged exercise in warm environments are generally accompanied by psychological changes, more precisely, feelings of fatigue and effort (measured by CR-10 and RPE, respectively; Borg, 1998), emanating from the subjective experience of physical performance and physiological sensations (Acevedo & Ekkekakis, 2001). During prolonged exercise in hot environment, the perceived exertion (RPE) exhibits a linear increase in relation to the rise in core temperature and heart rate (González-Alonso, Teller, Andersen, Jensen et al., 1999). Therefore, it is possible to differentiate various state-dependent processes in relation to exercise-heat stress and elaborate the concept of arousal relevant to interval production. It is somewhat surprising that in previous research concerning temperature effects on temporal processing (Wearden & Penton-Voak, 1995), psychological factors are rarely if ever considered. Rather, the mechanism behind all those changes in temporal processing is assumed to be the arousal level of the subject, induced by the changes in metabolic activity, which correspond to changes in body temperature or heart rate (i.e., physiological arousal). At the same time, there is extensive research showing that the processing of emotional stimuli influences performance in similar tasks requiring time judgments (e.g., concept of emotional arousal, Droit-Volet & Gil, 2009; Schirmer, 2011). Therefore, **Study I** contributes to time perception research by integrating the historical concept of temperature effects and the knowledge from recent studies applying the affective stimuli to investigate the contribution of psychological state-dependent variables, presumably reflecting emotional arousal, on temporal judgments.

The previous evidence shows that both exercise (Lambourne, 2012; Vercruyssen et al., 1989) and passive heating (Hancock, 1984; 1993), similar to natural fever (Hoagland, 1933), elicit changes in perceived time. Hence, **Study I** employed an experimental paradigm where these variables were separated. This was done in order to observe the distinct effects of temperature as well as exercise, and interaction between these variables. A sample of 24 healthy fit young men repeatedly produced short intervals in four experimental trials, either in a temperate (22°C, relative humidity 35%) or hot (42 °C, relative humidity 18%) environment, without exercise (passive) or walking on a treadmill with moderate intensity at 60% VO_2max (active). The CFF was measured before and after the exercise test, whereas core temperature (T_C), heart rate (HR), perceived fatigue (CR-10) and effort (RPE) were registered after every 15 minutes during the exercise test. According to the concept of the central fatigue (Nybo, 2008; Nybo & Nielsen, 2001a; 2001b), the dependent measures in **Study I** indicate the possible contribution of both peripheral and central processes involved in exercise-heat stress. Therefore, within the arousal-pacemaker paradigm, it is possible to distinguish the contribution of either peripheral markers (T_C, HR) or psychological and more central factors (CFF, subjective feelings) of arousal to timing behaviour. In addition to the RPE, which is assumed to reflect both the physiological and psychological effects of exercise-heat stress in the current study (Morgan, 1973), CR-10 was included to measure the intensity of fatigue. Fatigue is considered to be a complex emotion affected by motivation, drive, other emotions (e.g., anger, fear) and previous experience (St.Clair-Gibson, Baden, Lambert, Lambert et al., 2003).

Study I employed a temporal production task, where the subjects were required to produce short intervals (0.5, 0.75., 1, 2, 3, 5, 10 seconds) with the instruction to use chronometric counting. The instruction to count was applied for several reasons. As exercise-heat stress was expected to exhibit considerable strain on the subjects, the attempt was to have their focus on the time production task and increase their temporal accuracy by the counting strategy (Grondin et al., 1999; Wearden, 1991) but at the same time assuming temperature to alter the basic count unit and thus the produced durations (Wearden & Penton-Voak, 1995). A linear function was applied to the produced intervals to reduce the numbert of data points and to describe the temporal performance in terms of linear function estimates a_1 and a_0, the slope and the intercept of the function, respectively. The goodness of fit for each participant in all experimental conditions was high (r^2>.97) with no significant differences between experimental trials and individual testing sessions, implying a linear relationship between psychological and the real time. **Study I** interprets the results of the time production task mainly by a_1, which is suggested to indicate the proportionality of the psychological and the real time. The interpretation of a_0 is more complicated but the respective estimate might be viewed as a shortest time residual, presumably reflecting the motor properties of the time production task. For example, if the regression coefficients are a_1=1 and a_0=0, then the produced durations could be interpreted to be close to the target intervals (i.e., veridical to real time). Therefore, the compression of produced intervals is described by a_1<1, indicating a relative underproduction of durations, whereas a_1>1 would refer to a relative overproduction.

The main results from **Study I** demonstrate that produced intervals, mostly in the range of seconds, are compressed after an hour of moderate exercise in the hot environment. The findings are in concordance with the previous studies, where a relative underproduction of intervals has been found (François, 1927; Hoagland, 1933). The results are interpreted within the internal clock model indicating a temperature-induced increase of arousal, which increases the rate of subjective time. As a result, the pacemaker sends out impulses at a higher rate, those impulses are accumulated faster and in turn, shorter intervals are produced due to terminating the durations earlier. With regards to the state-dependent variables (T_C, HR, CR-10, RPE), there was a clear distinction between the active and passive trials. Passive-temperate trial (N_{NE}) served as an exceptional control condition, as no changes in subjective states were observed. The active-hot trial (H_{EX}) induced a significant exercise-heat stress, which was reflected in all dependent measures, including the time production task. In the current context T_C and HR are observed as physiological arousal indicators whereas CR-10 and RPE, suggested to reflect affective response to exercise-heat stress, are considered to be the indicators of psychological arousal. The CFF as an indicator of cortical arousal (Davranche & Pichon, 2005) exhibited a higher threshold after the exercise test in H_{EX} trial and although indicating a rise in arousal level, is less informative as it was measured post-exercise. However, other state-dependent measures showed a continuous rise throughout the exercise test in H_{EX} trial, in parallel to changes in a_1, which indicated relative underproduction of time already after 10 minutes of exercise. Thus, the temporal processing exhibited a faster rate as the state-dependent measures indicated a rise in the level of arousal.

In terms of the SET framework, these findings indicate that the combination of exercise and thermal stimuli increases the speed of the pacemaker component of the clock stage (Figure 1). The coefficient of variation (CV) was similar for all durations with the exception of the shortest (0.5 second) interval, overall indicating scalar properties (Gibbon et al., 1984; Wearden, 1991; 2003). After an hour of exercise in the heat, the relative compression of produced durations was already 23%, which would indicate that a 3-second interval was perceived to be over after 2.6 seconds. According to the internal clock model, the pacemaker was emitting pulses at the higher rate and the relevant pulses required for the target interval were accumulated in a shorter time, resulting in the shorter produced durations.

At first sight, the results support the concept of the “chemical clock” (Hoagland, 1933) – with the higher metabolic rate, the increased speed of the internal clock is observed at the behavioural level. However, the changes in temporal production in **Study I** are not reduced exclusively to the changes in temperature. In addition to core temperature, also heart rate, perceived fatigue and effort increased and might contribute to changes in timing behaviour. Thus, both peripheral and central factors were influenced by exercise-heat stress, a concept elaborated by Nybo and Nielsen (2001a; 2001b). When the relationship between the dependent measures was further observed, perceived fatigue (CR-10) was significant in influencing the relationship between core temperature and a_1. Evidently, this indicates the role of psychological arousal and more central factors mediating the temperature effects on temporal processing. Prolonged exercise in a hot environment elicits an affective response (in this case, higher ratings of perceived fatigue), which explains the changes in temporal performance. These findings are in agreement with the psychobiological model of cognitive appraisal during exercise in extreme environments (Acevedo & Ekkekakis, 2001).

The interpretation of aforementioned findings benefits most from the application of the interoceptive model (Craig, 2002), which on closer inspection incorporates both the psychobiological model (Acevedo & Ekkekakis, 2001) and further elaboration of peripheral and central factors involved in the development of the CNS fatigue in extreme environments (Nybo, 2008). According to the interoceptive model, feedback from the thermoregulatory centres, thermal sensations from the skin, heart rate, exercising muscles and joints is processed in the CNS and as a result, a conscious emotional representation (e.g., the feeling of fatigue and effort) is generated. Representation of the homeostatic afferent activity through sympathetic and parasympathetic pathways of the autonomic nervous system is directed via the thalamo-cortical extension to the anterior insular cortex, where all the information is integrated into bodily feelings and self-awareness. Thus, the afferent sensory representation received is related to the homeostatic condition of the body and forms the basis of the conscious subjective image of the sentient self (Craig, 2002; 2003). Therefore, in the light of the current findings, the subjective feelings and the psychological state (i.e., perceived fatigue) involve a bodily (physiological) representation of exercise-heat stress based on the thermal sensations and heart rate elicited by exercise-heat stress. Interestingly, Critchley and colleagues (2004) propose that the intensity of emotional awareness reflects the variation in sensitivity to bodily reactions and there are frontal-cortex regions involved in the interoceptive attention and affective response. In addition, Pollatos, Gramann and Schandry (2007) demonstrated that subjects with high interoceptive awareness showed enhanced ERP response to processing both pleasant and unpleasant stimuli. Therefore, the level of perceived fatigue in the current study might reflect interoceptive awareness, which in turn is related to time perception. The model of forebrain asymmetry of emotion provides additional support for interpreting the properties of the perceived fatigue in the current experimental context (Craig, 2005). According to this model, the right forebrain is associated with negative emotion, feelings of arousal and avoidance, whereas the left forebrain involves positive affect and approach behaviours. These differences are possibly reflected in the anterior insular cortex as well. If the assumption of asymmetry in homeostatic emotion is considered (Craig, 2005; 2009b), the current findings suggest that high ambient temperature is related to higher sympathetic arousing activity and concomitant activity in the right anterior insular cortex related to negative feelings. In turn, the faster accumulation of emotional moments is related to the higher speed of the internal clock and therefore, relatively shorter intervals are produced.

Although a more detailed arousal-pacemaker link provides a possible framework for interpreting the results obtained in **Study I**, the role of attention processes in relation to time-sharing hypothesis remains important. More precisely, if we assume, according to the interoceptive model, that the psychological and physiological state is constantly being monitored and processed in the CNS, then attention would be allocated away from the time production task and directed towards non-temporal properties (e.g., feelings of fatigue, bodily sensations, maintaining motor control during exercise). In relation to this assumption, more attentional resources should be located away from time (i.e., the interval production task), which generally results in overproduction of intervals as it takes a longer time for the temporal pulses to be accumulated to match the objective duration (Brown, 1997). Nonetheless, a relative underproduction of intervals was observed after an hour of exercise-heat stress in the current study, which is at first sight contradictory to the time-sharing hypothesis of time perception (Buhusi & Meck, 2009).

Although prolonged exercise in the heat leads to a quicker development of critical core temperature, cardiovascular strain, fatigue and exhaustion more quickly compared to exercising in thermoneutral environment (Nybo & Nielsen, 2001a; 2001b), **Study I** indicates that the subjects had not yet reached the critical stage of allocating resources after an hour of exercise in the hot environment. Rather, we witnessed an increase in activation that contributed to the timing performance. Nevertheless, the issues concerning the role of the attention mechanism in the current experimental context within the framework of the interoceptive model persist, as the monitoring and appraisal of one's bodily sensations inevitably suggest the involvement of attention.

3.3 Study II "Effects of heat acclimation on time perception"

Exercise performance and cognitive functioning are impaired during prolonged exercise in hot environments (Cian et al., 2000; 2001; Gonzalez-Alonso et al., 1999). In addition to the thermoregulatory and cardiovascular decrements (Hargreaves, 2008), peripheral hormone response is also altered (Bridge et al., 2003; Low et al., 2005), which provides information about the involvement of possible brain mechanisms in exercise-heat stress. However, chronic exposure to exercise-heat stress evokes physiological adaptations, which encompass improvement in exercise capacity, thermoregulation and metabolic functioning (Sawka, Wenger, & Pandolf, 2011). Concerning the endocrine markers, slower increase in blood growth hormone (Nielsen, Hales, Strange, Christensen et al., 1993; Ööpik, Timpmann, Kreegipuu, Unt et al., 2014) and prolactin concentration (Bridge et al., 2003; Burk et al., 2012) is observed in alignment with the slower rate of increase in core temperature. Lower levels of cortisol are assumed to indicate successful heat acclimation and tolerance (Davies, Harrison, Cochrane, Edwards et al., 1981; Follenius et al., 1982). The effects of heat acclimation on cognitive functioning have rarely been reported. In the military context, Radakovic and colleagues (2007) reported improvements in complex tasks after heat acclimation whereas more automatic tasks requiring simple motor performance were not affected. Interestingly, one study has observed the dynamics of time estimation during the heat acclimation program, showing a significant decrease in temporal estimations on the first day of heat exposure but estimations became actually longer by the 10th day of heat exposure (Curley & Hawkins, 1983). Therefore, the physiological adaptations observed as a result of heat acclimation might provide further information about the underlying mechanisms of time perception.

In **Study II**, the effects of exercise-heat stress on temporal interval production were further elaborated to investigate the role of physiological and psychological factors. In addition to perceived fatigue and exertion measures (CR-10 and RPE, respectively), core temperature (T_C) and heart rate (HR), hormone markers were also included. 20 subjects, who participated in **Study I**, followed a 10-day heat acclimation (HA) program and performed an exercise test to exhaustion after acclimation. Similar interval production data was included from the exercise test after HA. The exercise test from **Study I** (H_{EX}) is here referred to as H1 (pre-acclimation) and the post-acclimation exercise test as H2, with pre-test, 60-minute and post-test measures being compared between different experimental trials H1, H2 and N (representing exercise in the thermoneutral conditions, N_{EX} in **Study I**). In addition to the similarly analysed time production task in **Study I** (a_1, slope of a linear function), retrospective temporal judgements from the first pre-test session were included in the analysis. In the latter task, subjects performed a visuospatial short-term memory task and were required to estimate the duration of one of the slides (3 seconds) presenting the stimuli.

The main findings from **Study II** indicate that the performance in the interval production task is more accurate during the exercise in the heat following HA – a_1 did not exhibit a similar decrease after 60 minutes of exercise in H2 as was observed in H1. Physiological and psychological variables demonstrated the effect of HA exhibiting a slower rate of increase in H2. The prospective timing task, considered here as an indicator of cognitive functioning, shows a similar dynamic to other state-dependent variables. Thus, the exercise capacity together with cognitive performance during exercise-heat stress benefits from active heat acclimation. When **Study I** showed the significant role of core temperature and perceived fatigue in time perception, hormone response was identified as one of the variables related to temporal performance in **Study II**. More precisely, blood prolactin (PRL) concentration predicts a_1 in both H1 and H2. The changes in PRL concentration are generally related to changes in core temperature (Low et al., 2005; Pitsiladis et al., 2002). Moreover, Burk and colleagues (2012) demonstrated that the PRL response during exercise-heat stress explains around 28% of the inter-individual variance in exercise capacity in heat-acclimated subjects. According to **Study II**, PRL levels predict cognitive functioning and in heat-acclimated subjects, perceived fatigue and growth hormone (GH) levels were additionally significant predictors of the interval production performance. Hence, less stressful experimental conditions in H2 are accompanied by a larger a_1, indicative of the relative overproduction of intervals compared to H1. Again, the dynamics of perceived fatigue provides information about the heat tolerance in the psychological domain. Based on the results in **Study II**, perceived fatigue seems to benefit most from the active heat acclimation. The heat-acclimated subjects rated only their fatigue level to be similar when exercising in temperate conditions while the 60-minute measures of H2 for all other variables were significantly higher compared to N.

Interestingly, the retrospective temporal judgments predicted the performance in prospective temporal processing, especially in heat-acclimated subjects ($\beta = -.35, p<.01$). The interpretation of these results would indicate that smaller retrospective judgments were accompanied by a larger a_1, reflecting a more accurate temporal performance. The relationship between prospective and retrospective time judgments is not surprising if a central timing mechanism with a biological basis is considered. There is previous evidence indicating that a performance in one temporal task is generally related to the performance in another type of timing task (Merchant, Harrington, & Meck, 2013). In other words, good performers in one behavioural context appear to be good performers in another as well, suggesting the existence of a common timing mechanism. The current findings also show that the retrospective timing performance is a predictor of prospective performance after heat acclimation, which suggest the possible involvement of attentional processes in the timing of stimuli in stressful conditions. In the retrospective task, the subjects who were more engaged in the non-temporal task and underestimated the duration retrospectively, were more accurate in the prospective task after active heat acclimation. This implies that those subjects, who were probably more efficient in directing their attention towards task-relevant information in the retrospective timing (i.e., non-temporal visuospatial requirements) were also able to direct attention towards task-relevant information in the prospective timing task (i.e., estimate temporal properties) under stressful conditions. Hence, the role of individual differences in cognitive functioning and timing behaviour might be important in stressful conditions.

Additional references based on **Study II** are made regarding the brain mechanisms involved in exercise-heat stress and time perception. When considering the peripheral markers of heat stress in relation to brain mechanisms, PRL secretion is stimulated by serotonin (Weicker & Strüder, 2001; Van der Kar, Rittenhouse, Li, & Levy, 1996) and inhibited by dopamine (Ben-Jonathan & Hnasko, 2001). Blood PRL concentrations are sensitive to temperature effects as the rise in hormone response corresponds to the rise in core temperature during prolonged exercise (Bridge et al., 2003; Low et al., 2005), participating in the onset of central fatigue (Roelands & Meeusen, 2010). As a result, the involvement of central serotonin activity in the development of central fatigue and decline in exercise performance has been implicated (Pitsiladis et al., 2002). With regard to the respective brain mechanisms, the current findings concerning the PRL response suggest a possible involvement of both serotonergic and dopaminergic activity in time perception during exercise-heat stress. Indeed, changes in cerebral metabolism reported in the CNS fatigue research (Nielsen & Nybo, 2003) implicate brain areas involved in both thermoregulation, exercise and time perception. For example, a rise in core temperature has been shown to increase the cerebral metabolic rate in the hypothalamus, thalamus thalamus, the cerebellum, the cingulate gyrus, whereas a decrease in the metabolic activity was observed in the basal ganglia and the insular cortex among other regions in the brain (Nunneley et al., 2002). The cerebellum and the basal ganglia have been previously implicated in temporal processing (Coull et al., 2011) and the current experimental manipulations with temperature presumably induced changes in the activity of these brain regions. In addition, the insular cortex and the cingulate gyrus have been suggested by Craig (2009a; 2009b) to be involved in interoceptive awareness and behavioural control – processes relevant for timing behaviour. Of course, this conclusion is purely inferential as the exact behaviour of these neural systems was not directly observed. However, the underlying brain mechanisms related to timing behaviour could be further explored in a similar experimental setting applying exercise-heat stress.

3.4 Conclusions

The findings from **Study I** and **Study II** suggest that the traditional arousal-pacemaker hypothesis is not sufficient to explain the temperature effects on time perception. Although the concept of arousal is supported, the effect cannot be reduced to the rise in core temperature. The contribution of psychological state-dependent factors, more precisely, perceived fatigue, should be considered as a possible mediator of temperature effects. The interoceptive model (Craig, 2003; 2009a; 2009b) provides a structural framework for interpretation of these results.

The concept of interoception, or sentience, as referred to in affective time perception research (Schirmer, 2011), has become widely prominent when explaining the interaction between the physiological and psychological processes and their contribution to timing behaviour. Interoceptive processing involves integrating series of feelings across time, which is related to the central temporal processing in general (Craig, 2004; 2009b). Sensory displeasure is responsible for the negative affective response during exhaustive exercise and extreme environmental stress (Gaoua et al., 2012), accompanied by increased sympathetic activity (Craig, 2009a). The findings from **Study I** suggested that higher perceived fatigue and also perceived effort might reflect higher sentient processing of bodily state and thus, mediate temporal judgments under exercise-heat stress. **Study II** provided further evidence about the physiological changes in relation to active heat acclimation and the role of hormone response in predicting cognitive functioning measured with interval production. The brain mechanisms, which are important for both time perception and interoceptive awareness, provide a possible explanation for the temperature induced changes in interval production. Increase in both physiological and psychological arousal is accompanied by a higher pacemaker rate and hence, faster internal clock. However, it is important to consider the internal clock model within the interoceptive framework and the role of subjective fatigue, attentional processes and resource allocation.

4 EMOTIONAL FACTORS MODULATING TIME PERCEPTION

Emotions change time perception by speeding up or slowing down the internal clock. Time perception has been shown to be dependent on emotional content irrespective of its modality and overestimation of emotional stimuli compared to neutral ones is generally observed. For example, Lambrechts and colleagues (2011) showed a greater precision for reproducing non-emotional stimuli compared to emotional stimuli (pleasant or unpleasant). The duration of emotional faces was perceived to be longer than of neutral expressions (Droit-Volet, Brunot, & Niedenthal, 2004), especially angry faces (Gil & Droit-Volet, 2011; Tipples, 2008). Similar results were obtained with emotional sounds, which were perceived to last longer and the effect was greater for negative stimuli (Noulhiane, Mella, Samson, Ragot et al., 2007), which relies upon the assumption that the latter generates a stronger response (i.e., more arousing) than positive stimuli (Cacciopo & Gardner, 1999). Thus, the research suggests that emotionally charged events are perceived to last longer relative to neutral ones, indicating subjective lengthening of time. Emotional experience is accompanied by physiological changes, which are assumed to be responsible for the variations in subjective time by affecting the pacemaker rate in emitting pulses into the accumulator (Burle & Casini, 2001). Therefore, emotion effects on timing behaviour are often explained by the arousal-pacemaker link (Droit-Volet and Meck, 2007; Droit-Volet and Gil, 2009).

However, emotional time perception research suffers from the poorly defined concept of arousal, which is considered equal to sympathetic activation. In addition, the concept of emotional arousal and how it is associated with the internal clock is an open question, because the weak relationship between the actual arousal measures and the timing performance suggests alternative interpretations (Schirmer, 2011). These concerns are further supported by the evidence from **Study I** and **Study II**, where physiological state-variables were insufficient to explain timing behaviour, and instead, the role of psychological state and possible contribution of attentional processes were suggested. In **Study III**, the arousal and attentional processes involved in the timing of emotional stimuli are approached within the affective attention paradigm.

4.1 The integration of attention and arousal in the affective modulation of time

Interpretation of emotion effects on time perception through the arousal mechanism becomes even more difficult when considering the time course of physiological changes and timing behaviour. Subjective lengthening of time in relation to emotional stimuli is generally evident in brief durations (i.e., less than 1 second) and rarely observed for durations longer than 2–3 seconds

(Droit-Volet et al., 2004; Mella et al., 2011; Noulhiane et al., 2007). Rather paradoxically, physiological changes indicating the level of arousal are relatively slow, with skin conductance and heart rate taking several seconds to peak (Kreibig, 2010). Moreover, it is suggested that different emotions elicit distinct activation patterns in the autonomic nervous system (Ekman, Levenson, & Friesen, 1983; for a review, see Levenson, 2014). In time perception research, there is evidence of emotions affecting temporal judgments without the increase in concomitant physiological markers, as shown by overestimation of sad faces (Lee, Seelam, & O'Brien, 2011) and in the case of boredom (Danckert & Allman, 2005).

Taking into consideration the sporadic plausibility of the arousal-pacemaker link in explaining how emotions influence time perception, the contribution of attention processes should be investigated. According to this, temporal estimations are dependent on the cognitive resources allocated to the processing of stimuli, more precisely, how much attention is devoted to time. In terms of the SET model, the attention mechanism involves the functioning of the switch at the clock stage (Zakay & Block, 1997), which operates differently for emotional than for neutral stimuli, depending on the allocation of attention. If attention is directed towards temporal properties, fewer pulses are lost and time estimation tends to be rather accurate. However, processing of emotional stimuli is assumed to deflect attention away from the temporal properties of the stimulus towards the emotional properties and relative underestimation of emotional stimuli occurs (Gil, Rousset, & Droit-Volet, 2009; Lui et al., 2011). Of course, if the attention mechanism is indeed involved, the emotional stimuli should always distract attention away from the temporal properties, resulting in relative underestimations compared to the processing of neutral stimuli. However, overestimation of emotional stimuli is often observed, which is inconsistent with the classical interpretation of the attention mechanism (Schirmer, 2011). Nevertheless, a clarification in terms of the attention mechanism is required in relation to estimating temporal properties of emotional stimuli and specifically, the way in which temporal and non-temporal properties require attentional processing. Moreover, the interpretation of emotion effects on timing might benefit from integrating the concepts of arousal and attention in the SET framework. In addition, emotional modulation of time could benefit from the concept of interoceptive awareness (Craig, 2009b, Schirmer, 2011) with elaborating the influence of emotion-induced physiological changes on sentient processing. Indeed, the embodiment of emotion seems to be crucial when emotional stimuli are timed (Effron, Niedenthal, Gil, & Droit-Volet, 2006). Therefore, when considering the mechanisms of affective time perception within the internal clock model, it seems difficult to differentiate activation and attention processes and the direction of temporal distortions. Rather, it should be interesting to explore the complex interplay between the arousal and attention processes.

4.2 Study III “Emotional modulation of attention affects time perception: Evidence from event-related potentials”

Emotions elicit alterations in the internal clock mechanism in two ways. Firstly, emotional stimuli increase bodily arousal and as a result, the pacemaker emits more pulses within the same unit of real time to be gathered in the accumulator. Hence, overestimation (or underproduction) of durations is observed, corresponding to subjective lengthening of time. Secondly, the attention mechanism might affect the functioning of the switch, as described before. If attention is directed away from time towards the emotional dimension of a stimulus, the durations are judged shorter due to the accumulation of fewer pulses, implicating a fluctuation of the switch between opened and closed states (Droit-Volet & Meck, 2007).

Study III applied the affective attention paradigm to investigate emotional influences on time perception. More precisely, event-related potential (ERP) correlates of different stages of affective attention were employed to differentiate arousal and attention processes in timing the emotional stimuli. To further explore the time-course of the attention process and emotional guidance of selective attention and their role in time perception, event related potentials (ERPs) grant a possibility of observing both early and late modulations of neural responses with high temporal sensitivity. These modulations are considered to reflect distinct stages of stimulus processing (Schupp, Flaisch, Stockburger, & Junghöfer, 2006). Although early ERPs P1 and N1 reflect processing of stimulus-specific properties at the pre-attentive level (Hillyard, Vogel, & Luck, 1998), they are also influenced by emotion (Pourtois, Dan, Grandjean, Sander et al., 2005). However, ERP components EPN (Early Posterior Negativity, 150–300 ms from stimulus onset) and LPP (Late Positive Potential, from 300 ms and onwards from stimulus onset) have been shown to exhibit longer and more sustained processing of emotional stimuli (Schupp et al., 2006). These two ERP components suggest a two-stage account of affective attention (Schupp et al., 2006; Uusberg, Uibo, Kreegipuu, Tamm et al., 2013), reflecting more automatic processing of the stimuli in early stages (EPN) compared to later stages, where top-down effects are more evident (LPP). EPN presumably involves the attentional selection of the motivationally significant stimuli for further processing and is considered as a measure of automatic attentional capture. On the contrary, LPP should reflect attentional control and affective experience, which is related to the meaning rather than the physical properties of the stimuli. In addition, LPP is particularly informative about the overall emotional arousal induced by emotional stimuli (Schupp et al., 2006). These two ERP components elicit different patterns for emotional compared to neutral stimuli, indicating two distinct stages of affective attention and possibly reflecting the differences in the engagement of top-down control over stimulus-driven signals (Pessoa, 2010). Therefore, the dissociation between different attentional systems together with specific ERP components provides an opportunity to differentiate the contribution of attention and arousal mechanisms in time perception, with EPN reflecting attentional involvement and LPP affective arousal.

Study III applied the previously described ERP correlates of affective attention in distinguishing different sources behind temporal distortions. 62 students (42 females) produced brief temporal intervals (0.9, 1.5, 2.7 and 3.3 seconds) while observing images with highly arousing content (erotic and aversive) in addition to neutral images from the International Affective Picture System (Lang et al, 2008). P1, EPN and LPP components were analysed in relation to affective attention stages (Schupp et al., 2006). Additionally, the Contingent Negative Variation (CNV) was analysed as the respective ERP component, which has been suggested to reflect the accumulation of pulses encompassing the perceived duration (Macar & Vidal, 2004; Mella & Pouthas, 2011), although some recent work casts doubt on this (van Rijn, Kononowicz, Meck, Ng et al., 2011).

The main findings from **Study III** indicate that emotional effects on time perception varied with the duration to be timed. At the behavioural level, affective alterations were present for 0.9, 1.5 and 2.7 s intervals. The differences between unpleasant and pleasant stimuli were observed for 0.9 and 1.5 s intervals. The durations produced during unpleasant images where relatively shorter compared to neutral and pleasant trials for the 0.9 s interval. However, pleasant stimuli significantly lengthened produced durations for 1.5 s and shortened them for 2.7 s intervals. For the 3.3 s interval, all stimuli were relatively underproduced. Thus, the complex pattern observed for the behavioural results cannot be explained by any single underlying mechanism. In addition, Coefficient of Variation (CV) was affected by both, affective category and duration, indicating a larger CV for unpleasant stimuli and a progressive decrease of CV with the larger durations. Specifically, the 0.9 s interval exhibited differences between the affective categories in the respective manner. Concurrently, the ERPs demonstrated enhanced amplitudes equally in P1 and LPP components for both unpleasant and pleasant stimuli. With regard to EPN, the respective ERP component showed enhanced response to pleasant than to unpleasant stimuli (see Figure 3 in **Study III**). For CNV analysis, all trials were distributed to short, accurate and long responses for the two longer durations (2.7 and 3.3 s). However, CNV showed no differences regarding production performance as well as affective modulation, which is in line with the proposal by van Rijn et al., (2011) that CNV might reflect peripheral aspects of time perception (e.g., the processes related to motor preparation and decision making).

These findings lead to several conclusions. First, although a complex pattern of behavioural response was observed, the overall tendency for the affective stimuli was to increase the rate of subjective time rather than decrease it. These results are in line with previous research suggesting an increased speed of the internal clock in emotional states (Angrilli et al, 1997; Droit-Volet et al., 2004; Gil & Droit-Volet, 2011; Noulhiane et al., 2007). Second, a duration-dependent valence-specificity occurred, whereby the shortest durations were affected by unpleasant stimuli and the longer intervals by pleasant stimuli. Third, the results also replicated the common finding that emotions tend to elicit changes in time perception for relatively brief durations (Mella et al., 2011; Noulhiane et al., 2007), in **Study III** up to 2.7 s.

The behavioural results observed in **Study III** are difficult to explain through the arousal-pacemaker link, proposed by the SET model. More precisely, the effects of emotional arousal speeding up or slowing down the internal clock cannot exclusively account for the affective distortions in timing performance. Therefore, a possible role of the attention mechanism should be considered. Furthermore, CV did not remain constant across durations, contrary to the assumption of scalar properties (Wearden, 1999; 2003). Significant differences in variation between pleasant and unpleasant stimuli for 0.9 s and a substantial underproduction of unpleasant stimuli indicate valence effects on the internal clock. However, this valence-specificity was observed to be duration dependent, as a relative underproduction of unpleasant intervals for shorter durations (0.9 and 1.5 s) was reversed at the 2.7 s duration, where the pleasant stimuli were relatively more underproduced. The observed decrease in CV values with the increase of duration to be timed might suggest that the subjects were engaged in chronometric counting, generally shown to yield a decrease in temporal variation (Wearden, 1999). Although, in the current study, counting strategy was not directly instructed in addition to the use of integers as target durations, it was neither prohibited. Thus, the involvement of chronometric counting, responsible for the observed CV values, cannot be ruled out. However, respective changes in behavioural results might provide additional information about the underlying mechanism, presumably implicating the role of attention. A rather similar finding was obtained by Noulhiane et al. (2007), who interpreted it with possible interference between the attention and arousal mechanisms, which reduced the difference between affective and neutral stimuli, especially for longer durations and highly arousing stimuli. The absence of an emotional effect on longer durations might indicate increased activation by the emotional stimuli accompanied by a progressive increase of attention allocation between emotional and temporal properties. Attentional sharing would elicit a loss of pulses and thereby differences are not present for the affective and neutral stimuli, especially for longer durations. Nevertheless, the detection of the exact source of variance in behavioural response is problematic, as the various clock components and their respective contributions are difficult to disentangle.

The present findings in ERPs provide additional information about the possible role of the attention mechanisms. In respect to behavioural data, both unpleasant and pleasant stimuli evoked significant modulations relative to neutral stimuli in all ERP components in the expected direction. Pleasant images evoked stronger affective modulation in EPN compared to unpleasant images, which suggests that the former were more captivating of early attention resources. Differences were absent in P1 and LPP, indicating a somewhat similar arousal level for various stimuli. Thus, the results suggest that the valence-sensitivity of timing behaviour might be related to the valence differences reflected in automatic selective attention. According to this, high-arousal pleasant stimuli were more efficient in capturing attention.

However, taking into account the duration-dependent behaviour, the interplay between arousal and attention mechanisms should be considered. The involvement of the arousal mechanism in timing is more prevalent at shorter durations whereas the attention processes become relevant at longer durations. Indeed, previous evidence shows the overestimation of negative stimuli for durations less than 1 s (Gil & Droit-Volet, 2012; Tipples, 2008), which is characteristic of the negativity bias reflecting fear-induced arousal effects (Caccioppo & Gardner, 1999). Therefore in **Study III**, the relative under-production of 0.9 s unpleasant images with more variability implicates the arousal mechanism, which is in line with the assumption that the processing of negative stimuli, reflecting withdrawal and avoidance behaviour (Gable & Poole, 2012; Pourtois et al., 2013) evokes greater activation. Hence, the shorter intervals involve perceptual responses to emotional stimuli, especially rapid detection of threat, whereas longer durations reflect a more elaborate cognitive processing of emotional information, presumably related to subjective experience and the appraisal of emotions.

Emotional and physiological states both contribute to the timing behaviour and thus, the awareness of emotions might be crucial to subjective passage of time. For example, self-regulation of emotions has been found to affect time perception, based on the assumption that regulatory behaviour directs attention to time (Vohs & Schmeichel, 2003). Of course, in the current experimental context, self-regulation was not monitored. Moreover, emotional attention might be dependent on current emotional context but also on the emotional state of the subject (Cornwell et al., 2011), implicating both stimulus-driven and top-down attention processes. Thus, at longer durations, where attention processes are predominant, they might be directed towards time, physical features or goal-relevant properties of emotional stimuli but also to emotional awareness and appraisal. Although EPN indeed suggests that early attention mechanisms might be involved in timing the pleasant stimuli, the way attention affects the internal clock is still an open question.

In the former context, the model of interoceptive awareness might again prove to be useful for explaining the emotional distortion of time (Craig, 2009b; Wittmann, 2009) by integrating the concepts of arousal and attention by adding the aspect of sentient processing. All these mechanisms might have different weights in contributing to the experience of time under emotional modulation, depending on the stimulus properties, current situation and even individual differences. For example, fear-inducing stimulus might increase attentional focus to gain prioritized processing in the perceptual system (Pourtois et al., 2013), thereby increasing physiological arousal and increasing sentient processing. As a result, the internal clock runs faster and temporal intervals are overestimated (or underproduced). Furthermore, stimulus-specific sentient processing would explain the differences in temporal processing of emotional stimuli, thus the variation in subjective time depends on the specific experience of oneself in relation to stimulus properties and different events (Schirmer, 2011). This would also explain temporal variations for emotional stimuli with a similar arousal level. For example, Gil and Droit-Volet (2012) recently showed that disgust-eliciting images were overestimated compared to fear-inducing images. Although they concluded that arousal is the main mediator behind these effects, the influence of pictorial content has a significant role. Pollatos and colleagues (2014) demonstrated that interoceptive focus changes subjective time depending on the emotional valence, supposedly reflecting differences in autonomic reactivity. Thus, the arousal and attention mechanisms are presumably inherently linked regarding time perception.

Associating emotional awareness and stimulus-specific sentient processing with time perception would not require explaining attentional effects in regards to allocating resources between temporal and non-temporal information. Instead, the sentient processing theory assumes that a close link between emotional and temporal processing results in increased or decreased allocation of attention to both emotions and time (Craig, 2009b; Schirmer, 2011). Indeed, prioritised processing of emotional stimuli might actually convey evolutionary benefits. For example, it is reasonable to assume that detecting a threat should involve temporal information in addition to processing stimulus-specific features and thereby, sustained attention to stimulus processing might enhance temporal processing as well. Taken together, emotional stimuli might indeed capture more attention, which also facilitates the perception of temporal properties of the stimuli.

4.3 Conclusions

Arousal as well as attention processes are implicated by the emotional modulation of time perception. Duration-dependent valence-specificity of behavioural response suggests that the arousal-pacemaker link alone is insufficient to explain emotional distortions of subjective time. The absence of clear distinction in the produced durations between affective and neutral stimuli restricts interpretation of behavioural results in terms of arousal mechanisms. Instead, ERPs suggest the involvement of attention processes in timing the affective stimuli. More specifically, the valence differences in EPN refer to more pronounced attentional capture of pleasant stimuli and the affective modulation of time perception. However, the traditional interpretation of attention within the SET model including the switch component is not applicable as the attentional capture of non-temporal information would yield to relative overproduction of the emotional stimuli. Rather, the results suggest the possible facilitation of temporal processing with the increased attention to affective stimuli. Valence effects observed are duration-dependent, suggesting that the estimation of shorter intervals involves perceptual responses to emotional stimuli and physiological activation, whereas longer durations involve top-down modulation of emotional information. These findings suggest that a complex interplay between arousal and attention mechanisms are involved in affective modulation of time perception. In addition, the sentient processing might reflect the specific valence-dependent effects on subjective time, incorporated in the integrated model by Schirmer (2011). Emotional modulation of subjective time evokes bodily changes, which modify the experience of self across time and affect the way stimulus duration is perceived. Different affective states might involve specific activation patterns, which explain the differences in temporal processing of various emotional stimuli. Therefore, the intrinsic relationship between the attention and arousal mechanisms with the contingent role of sentient processing should be considered.

More importantly, **Study III** demonstrated the benefits of applying a two-stage paradigm of affective attention in time perception, especially the use of ERP correlates differentiating the early attentional capture and subsequent arousal processes induced by emotional stimuli. The processing stages of affective stimuli could be further applied to disentangle the arousal and attention mechanisms of the internal clock.

5 THE ROLE OF INDIVIDUAL DIFFERENCES IN TIME PERCEPTION

Temperature manipulations and emotional stimuli affect temporal processing, which is often explained by the alterations in the physiological state. As a result, the level of arousal changes, inducing alterations in the internal clock and time perception. However, the possible involvement of psychological state in explaining the effects of temperature (**Study I** and **Study II**) and the valence of emotional stimuli resulting in temporal processing differences (**Study III**) suggest the possible role of attention in the variability of timing behaviour. Thus, in addition to bottom-up processes involved with sensory information, top-down processes related to attention and behaviour regulation should be considered. The role of individual differences in both trait and state becomes evident with the assumption that time perception is a cognitively mediated process, which requires integration of information at different information processing levels (Hancock, Szalma, & Oron-Gilad, 2005). For example, the valence of emotion would provide information about the stimulus beyond the sensory processing level (e.g., flight-response), affecting memory processes at the higher levels of cognitive processing (Bower, 1981; Martin & Clore, 2001). Assuming that time perception depends on how an individual is directing attention towards temporal or non-temporal information (i.e., in prospective tasks) or how a duration already passed is remembered (i.e., in retrospective tasks), cognitive abilities including working memory capacity, are important for time estimation (Fink & Neubauer, 2005). Processing of temporal information has also been associated to music-related abilities, as musicians are more accurate with auditory fusion, rhythm perception and temporal discrimination (Rammsayer & Altenmüller, 2006), they tend to have better rhythmical precision and therefore, better timing control (Wagner, 1971), and they are better in detecting small temporal changes in auditory sequences (Jones & Yee, 1997), reflecting mainly the automatic and perceptual processing of time. Regarding personality, inconsistent results have been found with introverted neurotics overproducing intervals compared to extraverted neurotics (Eysenck, 1959), whereas a linear relationship was not observed between neuroticism and time estimation (Rammsayer, 1997). Interestingly, participants with higher psychoticism have been found to be more accurate with lower tendency to overestimate time in the range of seconds, presumably indicating better allocation of attention to temporal information (Rammsayer, 2002). Although gender-related differences are often found with female participants over-estimating time (Glicksohn & Hadad, 2012), personality traits should be considered (Rammsayer, 2002). Age-related differences in time perception are often reported as small children exhibit a primitive sense of time with scalar properties (Droit-Volet, 2011), which develops throughout childhood and displays distinct patterns for implicit and explicit time judgments. This developmental evidence supports the role of maturation of the fronto-striatal systems, which are related to attention and working-memory processes (Droit-Volet, 2013a).

Alterations in time perception are present in individuals suffering from affective disorders. Spider-fearful individuals tend to overestimate images with spiders (Buetti & Lleras, 2012; Watts & Sharrock, 1984). Individual differences in fearfulness (Tipples, 2011) and trait anxiety (Bar-Haim, Kerem, Lamy, & Zakay, 2009) predict overestimation. In a less clinical setting, boredom-prone individuals perceive time passing more slowly, presumably due to depressed affect (Watt, 1991). Moreover, boredom-prone individuals tend to be more impulsive (Watt & Vodanovich, 1992). Suffering from depression alters subjective time (Droit-Volet, 2013b; Gil & Droit-Volet, 2009) with depressed individuals feeling time passing more slowly. Interestingly, time perception is altered in the suprasecond range rather than in the processing of brief intervals (Sévigny, Everett, & Grondin, 2013), implicating different brain mechanisms (Lewis & Miall, 2006). In the case of mood disorders, processing longer durations requires sustained attention, which is probably impaired in depressive individuals and therefore, negative thoughts might disrupt temporal processing (Droit-Volet, 2013b). Of course, these behaviourally manifested impairments in various neurological and psychiatric populations are often presented with concurrent disruptions in the brain mechanisms related to time perception (Meck, 2005).

Therefore, individual differences in time perception suggest that there might be certain differences in the functioning of an internal clock (Glicksohn & Hadad, 2012), assuming a common clock mechanism in a variety of contexts does exist (Merchant et al., 2013). However, time perception and temporal processing of information are among the fundamental properties of human behaviour. If taking into consideration how different cognitive processes are involved in estimating shorter and longer durations, perceiving temporal properties in stressful conditions or in relation to emotional stimuli, complex behaviour could be reduced to the underlying mechanisms. More precisely, time perception might reveal attention or activation mechanisms inherent to the temporal aspects of cognitive or emotional information processing and decision making in general.

5.1 Relationship between impulsivity and time perception

Impulsivity is a multidimensional concept and is generally assessed as a trait measure (Barratt, 1993) or a personality dimension (Whiteside & Lynam, 2001). According to Evenden (1999), impulsivity is a disposition to react to both internal and external stimuli with insufficient forethought and insensitivity towards consequences, resulting in a disinhibited behaviour. Impulsivity has been consistently related to substance abuse (Colder & Chassin, 1997; de Wit, 2009), risky driving (Paaver, Eensoo, Pulver, & Harro, 2006; Pearson, Murphy, & Doane, 2013), pathological gambling (Kräplin, Bühringer, Oosterlaan, van den Brink, et al., 2014) and psychopathological disorders (ADHD; Sonuga-Barke, 2002). In self-reported measures, impulsivity is considered to reflect limited deliberation (Dickman, 1990), whereas behavioural measures of impulsivity often focus on impaired response inhibition (Logan, Schachar & Tannock, 1997). Self-reported and behavioural task measures of impulsive behaviour are often found to be unrelated, presumably measuring different forms of impulsivity. Assessment of the component structure of self-reported measures of impulsivity revealed three factors: *Non-planning Dysfunctional, Functional Venturesomeness* and *Drive/Rewards Responsiveness* (Miller, Jospeh, & Tudway, 2004). Regarding behavioural tasks, a similar analysis by Reynolds, Ortengren, Richards and de Wit (2006) resulted in two distinct components of behavioural impulsivity: *Impulsive Disinhibition* (Stop Signal and Go/No-Go tasks) and *Impulsive Decision Making* (Delay Discounting).

In behavioural impulsivity tasks, impulsive decision making assessed by delay discounting paradigm involves deliberately making choices about rewards, which requires conscious evaluation of potential outcome of delayed versus immediate gains and losses (Reynolds et al., 2006). Hence, this refers to more comprehensive cognitive processing, self-control and attention (Wittmann & Paulus, 2008). On the other hand, the stop signal paradigm tends to measure response inhibition, which is related to more automatic processes and motor control. Behavioural excitatory and inhibitory processes are explained in terms of a Horse-Race Model (Logan & Cowan, 1984), where two processes, initiating and stopping a response, compete with each other. The inability to stop a response (i.e., failure to override a reaction already initiated) should be characteristic of impulsive behaviour. Inhibitory control is closely linked to executive functions and coordinated functioning of selective attention and working-memory processes are assumed to be relevant for performance monitoring (Reynolds et al., 2006). According to Bari and Robbins (2013), attention to abrupt changes in the environment is required to identify the stimuli, which signal the inhibition of already planned action or thought. This is followed by a shift to a novel behavioural or a cognitive set of response. In addition, studies concerning selective attention have shown that irrelevant information is not ignored but actually actively suppressed (Posner & Cohen, 1984). The inhibitory loci in the brain should involve prefrontal regions as well as subcortical areas. The areas specifically related to response suppression are the basal ganglia, the cerebellum and the hippocampus among several other regions (for a review, see Bari & Robbins, 2013). In addition, the noradrenergic system in the prefrontal cortex is important for response inhibition and suppression of prepotent reaction, whereas dopaminergic activity in the striatum is involved in both response activation and inhibition in regards of motor preparation process (Bari, Mar, Theobald, Elands et al., 2011).

It has been proposed that impulsivity and time perception are closely linked constructs (Berlin & Rolls, 2004; Berlin, Rolls, & Kischka, 2004) and time estimation is even considered to be a behavioural task directly measuring impulsivity (Glicksohn, Leshem, & Aharoni, 2006). Although time perception predicts impulsivity in general (Baumann & Odum, 2012), the relationship between impulsive behaviour and time perception has been studied most often with a delay-discounting paradigm, focusing on the temporal properties of a decision making process (Wittmann & Paulus, 2008). According to this, temporally delayed rewards have less value for impulsive individuals and this is directly related to their sense of time. More specifically, they choose immediate smaller rewards over delayed bigger rewards because they have a tendency to overestimate the duration between "now" and the moment, when a reward is obtained. Due to alterations in perceived time, the value of a future reward is perceived to be lower (Rubia, Halari, Christakou, & Taylor, 2009). Thus, the subjective value of a reward is a function of time and it tends to vary for different individuals (Wittmann & Paulus, 2008). Stimulant-dependent individuals demonstrate impaired time perception and non-planning impulsiveness on the Barratt Impulsiveness Scale (BIS-11, Barratt, Stanford, Dowdy, Liebmann et al., 1999) tends to be a mediating factor in longer intervals (53 s) but not for 1 s and 2 s intervals (Wittmann, Leleand, Churan, & Paulus, 2007). These results are in accordance with distinct timing systems differentiating between automatic timing of shorter durations and cognitively mediated timing of longer intervals (Lewis & Miall, 2003a). Recently, Wittmann and colleagues (2014) showed that individuals with a higher dispositional mindfulness were more accurate in the duration estimation and also reported themselves being less impulsive. These results were interpreted in regards to stronger awareness of sensory experience and better temporal self-control in more mindful individuals, which includes a better awareness of brief temporal durations as well (Wittmann & Schmidt, 2014). Neuroimaging studies show altered brain mechanisms in individuals with high impulsivity, dysfunctional behaviour and impaired time perception (Christakou, Brammer, & Rubia, 2011; Rubia et al., 2009). Children with ADHD had abnormalities in prefrontal, cingulate, striatal and cerebellar regions, which are all implicated in time perception (Rubia et al., 2009). Moreover, in regards to the dopamine (DA) hypothesis (Allman & Meck, 2012; Meck, 1996), behavioural dysfunctions in ADHD were normalized as a result of administering DA agonists and thus, linking impulsivity, time perception and ADHD with dopaminergic dysregulation in the brain (Rubia et al., 2009). Patients with lesions in the orbitofrontal cortex overestimated time intervals while performing more impulsively on both self-reported and behavioural measures of impulsivity (Berlin et al., 2004). This was suggested to reflect faster cognitive tempo together with higher level of subjective anger and the frustration towards delayed rewards. The underlying cognitive processes of impulsive behaviour are unresolved and the role of affective and cognitive processes, self-control and time perception are yet to be determined.

According to the SET model, the underlying mechanism behind the observed effects might be different. For example, impulsive tendencies may affect timing behaviour in a way that the accumulator processes are terminated much earlier or the pacemaker mechanism may be functioning differently in relation to the personality dispositions (Hancock & Weaver, 2005). On the other hand, the attention mechanism could be operating differently on the switch component. For example, in regards to affective disorders, depressive individuals are more easily distracted from temporal properties (Droit-Volet, 2013b). Exploring the relationship between time perception and various impulsivity measures is a rather challenging aim of **Study IV**, as the impulsive tendencies detected by either self-reports or behavioural tasks are assumed to be different. In addition to the multidimensional nature of impulsivity (Evenden, 1999), impulsive tendencies might be sensitive to various states and stimuli, thereby exhibiting variability depending on the context. The properties of time perception and impulsive behaviour most probably involve the interplay of several cognitive processes and discovering distinct contributions of the underlying mechanisms is therefore difficult.

5.2 Study IV "Links between self-reported and laboratory behavioural impulsivity"

Impulsive behaviour and time perception presumably exhibit a great degree of overlap in functional properties. Although time perception is suggested to involve a central clock mechanism, the distinct processes underlying different time scales have been identified – more automatic perceptual processes related to the motor response and cognitively mediated processes, which require cognitive control and attention (Lewis & Miall, 2003a). A similar differentiation has been suggested for behavioural impulsivity tasks, with response inhibition reflecting a more automatic motor reaction and, impulsive decision making, which requires a more elaborate cognitive processing in order to make a conscious choice (Reynolds et al., 2006). Of course, despite the differentiation between these underlying processes, aspects of mood, affective processing, attention and activation have been associated with impulsive behaviour in general (Wittmann & Paulus, 2008). The relative contribution of these processes underlying different aspects of impulsive and timing behaviour is yet to be resolved.

The aim of **Study IV** was to provide a better understanding between time perception and different aspects of impulsivity. 58 healthy subjects (28 females, average age 21.9 ± 2.7 years) performed the Stop Signal Task (SST) together with self-reported impulsivity on Adaptive and Maladaptive Impulsivity Scale (AMIS, Eensoo, Harro, Pullmann, Allik, & Harro, 2007), which consists of

Functional and Dysfunctional Impulsivity scales (Dickman, 1990) as well as two impulsivity-related scales Impulsivity and Excitement Seeking from the Estonian version of the International Personality Item Pool (Mõttus, Pullmann, & Allik, 2006). SST was used as a measure of behavioural impulsivity to assess excitation and inhibition response, with 25% of Stop-trials among Go-trials and applying the adaptive delay of a stop signal depending on the subject's response. For successful performance in the SST, constant monitoring of performance and adjustment of reaction is required, which means finding an optimal balance between a quick excitatory and inhibitory response production. This is based on the assumption that subjects tend to adjust response strategies proactively when they expect the Stop-trial to appear or, reactively after the Stop-trials (Verbruggen & Logan, 2008). For the assessment of response inhibition, stop signal reaction time (SSRT) was found by subtracting the stop signal delay (SSD) from median reaction time on Go-trials (GoRT). Those task parameters are generally used in studies applying the SST paradigm (Aron & Poldrack, 2006). In addition, the after-effects of preceding trials were analysed, as it might result in switch costs or repetition benefits in the following trials (Monsell, 2003). For example, children suffering from ADHD have been shown to slow their reaction less compared to healthy subjects after failing to stop a response (Schachar, Chen, Logan, Ornstein et al., 2004). Finally, time estimation was measured by retrospective time estimation task, similar to **Study II**. The subjects were performing a visual short-term memory task on a slide presentation program, and after the third slide the subjects were asked to estimate the duration of the slide presenting visual stimuli (actual presentation time 3 s).

The main findings from **Study IV** corroborate some of the previous findings, where a weak or absent relationship between the self-reported and behavioural impulsivity measures was observed (Lane et al., 2003; Reynolds et al., 2006). However, retrospective time judgment was correlated with both types of impulsivity measures. A positive relationship was found for Thoughtlessness subscale in AMIS (AMIS-D) and negative relationship was observed for several SST parameters (see Table 2, **Study IV**). The longer estimated 3 s duration was related to faster reaction in Go-trials and higher probability of erroneous performance on Stop-trials. Furthermore, overestimation of duration was accompanied by a shorter delay of the stop signal (SSD) by the end of the SST. Taken together, overestimation of time was related to both stopping and initiating a response in SST, and to reporting higher rate of dysfunctional decision making. Interestingly, men significantly underestimated time compared to women (2.9 and 3.3 s, respectively). When gender was included as a categorical predictor in the regression model, AMIS-D (i.e., Thoughtlessness) and reaction time on Go-trials explained 32% of the variance in the time estimation task.

These results suggest that the temporal properties underlying impulsive behaviour are also related to time judgment. Thus, impulsive individuals might indeed perceive time to pass differently from less impulsive individuals, which is assumed to reflect differences in the rate of cognitive tempo (Wittmann & Paulus, 2008). However, the underlying mechanism of the cognitive tempo remains unclear. The role of mood and affective state could be additional factors mediating the impulsive behaviour and timing performance. Considering that temporal awareness is related to emotional experience (Craig, 2009a; 2009b), impulsive individuals might present stronger sentient processing and interoceptive awareness. For example, they might get more frustrated (Berlin et al., 2004) when failing to inhibit their response or being unable to adjust their behaviour according to task requirements. Higher erroneous performance in Stop-trials provides support for this assumption. Sentient processing in impulsive individuals could reflect heightened emotional arousal and lowered ability to exercise self-control, including inhibitory control (Wittmann et al., 2014). Thus, the impulsive "presence" in the moment could modulate the timing processes accordingly. In the current study, the relative overestimation of time was related to higher Thoughtlessness in self-reported impulsivity and shorter responses in SST. It is important to note that the retrospective time estimation paradigm was applied. In the prospective time judgment, temporal processes related to the clock stage of the SET model would be more evident and are generally associated with various impulsivity measures (Baumann & Odum, 2012; Reynolds et al., 2006). Retrospective timing is assumed to reflect memory-related and attention processes (Zakay & Block, 2004). In retrospective time judgment, contextual change is related to the processing of non-temporal stimuli, with more information encoded in the memory resulting in the overestimation of duration. In the emotional context, retrospective duration judgments are related to both the valence of affect and interoceptive attentional focus (Pollatos et al., 2014). Hence, the differences in sentient processing might be important in retrospective judgments as stronger levels of emotional activation during the timing task would also affect the attention mechanism, contributing to the processing of temporal and non-temporal information. The overall negative affect experienced by impulsive individuals could explain the relative time dilation whereas past positive experience is perceived to have passed quikly (Danckert & Allman, 2005; Pollatos et al., 2014). The results obtained regarding the relationship between prospective and retrospective timing tasks in **Study II** indicate the involvement of some common timing mechanism, irrespective to the temporal task. Therefore, it is possible that common clock mechanisms are involved in a variety of context, contributing to self-reported and behavioural impulsivity. In addition, common brain circuits underlying both impulsive behaviour and time perception have been implicated. More precisely, Bari and Robbins (2013) have suggested that inhibitory processes in the brain are related to the activity in the basal ganglia and the cerebellum, which have also been suggested to be important regions for time perception (Coull et al., 2011). Moreover, DA activity in the striatum is related to response activation and inhibition regarding the motor preparation process in impulsive behaviour (Bari et al., 2011), which in turn bears similarities with the DA hypothesis in the time perception research (Allman & Meck, 2012; Meck, 1996).

5.3 Conclusions

Self-reported and behavioural impulsivity probably reflect different aspects of impulsive behaviour. The results from **Study IV** suggest that the sense of time, reflecting a clock mechanism fundamental to temporal processing, could account for various forms of impulsive behaviour. However, which exact processes within the SET framework (e.g., pacemaker, attention, accumulator, memory), involved in the passage of subjective time, explain the impulsive behaviour remains unresolved. Presently, activation, attention and memory processes are all implicated. Similarly to **Studies I–III**, the awareness of time and affective experience are implied to have a significant role in linking time perception and impulsive behaviour. The affective state of impulsive individuals might be related to their level of physiological arousal, attentional capture and thereby affecting the further processing of information in the memory. In addition, sentient processing is presumably different for an impulsive individual, contributing to the sense of time. These processes involved in time perception could also contribute to response inhibition in SST and self-attributed dysfunctional behaviour.

6 GENERAL SUMMARY AND CONCLUSIONS

The human brain is generally very accurate in estimating time and therefore, the existence of an internal clock-like mechanism with biological origin has been proposed. Nevertheless, like any other psychological process, the estimation of time is sensitive to disturbances and occasionally subjected to errors. The research presented in this thesis explores time perception by varying the environmental conditions, the affective properties of the stimuli to be timed, and probes the role of time perception in relation to impulsive behaviour. Specifically, the attempt of the thesis is to further describe the mechanisms involved in time perception within the theoretical framework of the internal clock (Gibbon et al., 1984; Treisman, 1963). The obtained results suggest that arousal and attention processes independently are insufficient to explain the temperature effects and emotional modulations of time perception.

The sensitivity of the internal clock to temperature changes is further elaborated in the traditional view of the "chemical clock" hypothesis (Hoagland, 1933), according to which the pacemaker rate is affected by physiological arousal. An increase in core temperature is expected to increase the rate of the pacemaker and the time is perceived to pass slowly, thus resulting in an overestimation of temporal intervals. Studies I and II applied an interval production method in exercise-heat stress condition, which resulted in relative underproductions after an hour of exercise, indicating an increase in the rate of the pacemaker. A closer observation of several state-dependent variables in Study I suggested that physiological changes alone cannot account for the alterations of subjective time. Of course, the rise in core temperature is responsible for the perceived fatigue and exertion, affecting the overall perceived state of the subject. Study II provided further support to explain the temperature effects on time perception with changes in the hormone response and psychological state-dependent variables.

Psychological state, more precisely, perceived fatigue appears to be an important factor explaining the impaired temporal processing in extreme environments. This implies a significant role of the emotional arousal and the emotional experience imposed by prolonged exercise in the hot environment. Physiological changes are accompanied by psychological changes and in terms of peripheral and central factors, the latter are involved in generating the conscious feeling of fatigue (St. Clair Gibson et al., 2003). Explaining the role of environmental factors, physiological changes and emotional processing in time perception benefits most from the interoceptive model (Craig, 2002; 2009b), which provides a theoretical framework for describing how the general homeostatic state contributes to conscious bodily awareness. As a result, emotional experience and awareness of time within the current moment affect the sense of time. However, interoceptive processing does not rely solely on arousal and physiological changes. The conscious perception of self interacting with the ambient environment refers to the involvement of attention in processing emotional and temporal information. Therefore, the arousal-pacemaker link is insufficient for interpreting the findings obtained in Studies I and II.

Timing of emotional stimuli further emphasises the complex interplay between arousal, attention and sentient processing as revealed by Study III. More importantly, the emotional modulation of time strongly suggests applying a two-stage paradigm of affective attention in time perception. Use of the ERP correlates differentiating the early attentional capture and subsequent arousal processes induced by emotional stimuli provide means to disentangle the attention and arousal mechanisms of the internal clock. The behavioural results show no clear distinction in the produced durations between emotional and neutral stimuli, which confines interpretation solely in terms of arousal mechanism. Instead, the valence differences in the Early Posterior Negativity (EPN) indicate a more pronounced attentional capture of pleasant stimuli. In addition, the observed duration-dependent valence-specificity of time perception implies the role of a perceptual response and arousal mechanisms in timing the shorter intervals and the top-down attentional modulation in case of longer durations. Again, the results implicate interoceptive awareness in emotional modulation of time perception, which emphasises the role of context-specific sentient processing (Schirmer, 2011). Therefore, the inherent relationship between activation and attention mechanisms with supplementary sentient processing should be considered.

Finally, Study IV suggests that time perception appears to be the general property of impulsive behaviour, explaining the differences in both self-reported and behavioural impulsivity. More specifically, both the excitatory and inhibitory responses are related to the sense of time, possibly indicating a faster cognitive tempo of impulsive individuals. However, the underlying mechanism of the altered sense of time remains inconclusive. Clearly, the affective properties of impulsive behaviour should be considered, especially when temporal awareness and emotional experience are closely linked (Craig, 2009). The differences in timing performance could be explained by stronger sentient processing in impulsive individuals when unsuccessfully inhibiting their response or exhibiting inability to adjust their performance to task requirements (Wittmann et al., 2014). The affective disposition of impulsive individuals might be related to the level of activation, attentional capture and also to inefficient sentient processing, resulting in self-attributed dysfunctional behaviour, the inability to apply inhibition control and accurately estimate time.

To conclude, there is still considerable uncertainty about the way time is perceived in the brain but the work presented in this thesis provides additional insight into the mechanisms of time perception. More precisely, the investigation of the way time perception mechanisms operate should include the role of psychological state in perceived time. Specifically, the significant contribution of emotional factors reveals that our subjective time is closely related to the conscious experience of the environment and physiological state.

From the methodological aspect, time perception research would immensely benefit from other disciplines of cognitive neuroscience, especially from employing the affective attention paradigm. In conclusion, attention and arousal mechanisms in time perception tend to be inherently linked and should be further explored regarding affective experience and temporal awareness.

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SUMMARY IN ESTONIAN

Ajataju mõjutavad füsioloogilised ja psühholoogilised tegurid

Inimese aju on aja kulgemise hindamisel üldiselt väga täpne ning seetõttu eeldatakse, et meil on olemas bioloogilist päritolu kellalaadne mehhanism. Olenemata sellest on ajataju sarnaselt teistele psühholoogilistele töötlusprotsessidele tundlik erinevate ärritajate suhtes ning seetõttu võib ajahinnangutes ilmneda ka ebatäpsust. Käesolev doktoritöö uurib ajataju ekstreemsetes keskkonnatingimustes, emotsionaalsete ärritajate töötlemisel ning seoses impulsiivse käitumisega. Töö põhiliseks eesmärgiks on kirjeldada ajataju mehhanisme sisemise kella teoreetilisest raamistikust lähtuvalt (Gibbon jt., 1984; Treisman, 1963) ning täpsustada organismi aktivatsioonitaseme ja tähelepanuprotsesside rolli ajahinnangute muutlikkuses.

Uuringud I ja II lähtuvad sisemise kella temperatuuritundlikkusest ning täpsustavad traditsioonilist "keemilise kella" käsitlust (Hoagland, 1993), mille kohaselt muudab kehaline erutusseisund sisemise taktiseadja tööd. Keha süvatemperatuuri tõusuga kaasneb sisemise kella kiirenemine ning sellest tulenevalt tajutakse väliseid sündmusi aeglasemalt ja ajalisi kestusi hinnatakse pikemaks. Uuringud I ja II kasutasid ajataju uurimiseks intervallide produtseerimise ülesannet ning seda kuumastressi tingimuses treenimise jooksul, mille tulemusena muutusid produtseeritud intervallid tunni aja järel oluliselt lühemaks. See osutab sisemise kella kiirenenud tööle. Uuring I näitas, et taoline kiirenemine ei ole tingitud vaid kehatemperatuuri tõusust, kuigi kehatemperatuuri tõusu tulemusena ilmnevad muutused psüühilises seisundis ja enesetunde näitajates, mis on omakorda seotud väsimuse ja pingutuse kohta antavate subjektiivsete hinnangutega. Uuringu II eesmärk oli tuvastada ajataju protsesside muutlikkust kuumaga adapteerumisel. Saadud tulemused toetasid psüühilise seisundi olulisust temperatuuri mõju avaldumisel subjektiivse ajamulje kujunemisele kuumastressi tingimustes.

Psüühiline seisund, mida käesolevas uuringus väljendasid väsimustundele antud hinnangud, on kõrge temperatuuriga keskkonnas subjektiivse ajamulje kujunemisel oluline. Seda saab sisemise kella raamistikus vaadelda ka kui emotsionaalse erutusseisundi näitajat. Lähtudes sellest, et füsioloogiliste muutustega kaasnevad muutused psüühilises seisundis (ja vastupidi), siis peegeldavad tajutud väsimushinnangud pigem kesknärvisüsteemi kõrgemate struktuuride osalust kui otseseid muutusi kehalistes protsessides (St. Clair Gibson jt., 2003). Antud tulemusi on võimalik tõlgendada interotseptiivse teadlikkuse mudeli põhjal (Craig, 2002; 2009b), mille järgi keha üldine homöostaatiline seisund annab sisendi kehalise seisundi teadvustatud tunnetamisele ja hindamisele. Oma kehalise seisundi tunnetamine on omakorda seotud emotsionaalse kogemuse ja olemasolevast ajahetkest teadlik olemisega, mis moonutab ajataju. Interotseptiivsed protsessid ei hõlma aga vaid kehalist erutusseisundit ja füsioloogilisi muutusi. Subjektiivse ajamulje kujunemisel (siin just kuumastressi tingimustes) on oluline ka tähelepanu suunamine oma psüühilisele ja kehalisele seisundile. Seetõttu on uuringutes I ja II saadud ajataju tulemuste seletamine erutusprotsesside ja taktiseadja töö põhjal ebapiisav.

Emotsionaalsete ärritajate kestuse hindamine uuringus III rõhutab veelgi enam tähelepanu osaluse olulisust ajataju muutlikkuses lisaks aktivatsiooni tasemes toimuvatele muutustele. Lisaks julgustab uuring III emotsionaalse ajataju uurimisel lähtuma kahe-faasilisest emotsionaalse tähelepanu käsitlusest ning rakendama ajataju ajukorrelaatide registreerimisel afektiivse ärritaja töötlusega seotud sündmuspotentsiaale (ERP). Viimased eristavad täpsemalt nii tähelepanu varajast ja pigem automaatset töötlusstaadiumit kui ka hilisemat spetsiifilisemat töötlust, mis peegeldab ärritaja poolt esilekutsutud üldist aktivatsiooni. Selline lähenemine võimaldab emotsionaalse ajataju alusmehhanisme paremini tuvastada ning võimalusel eristada aktivatsiooni ja tähelepanu kaasatust. Produtseeritud kestused uuringus III ei eristanud emotsionaalsete ja neutraalsete stiimulite töötlust piisava täpsusega, seetõttu ei ole võimalik ajatajus toimunud muutusi vaid afektiivse erutusseisundi ja sisemise kella kiiruse muutustega seletada. Afektiivse tähelepanu ajukorrelaadid näitasid positiivse valentsiga visuaalse ärritaja ajastamisel tähelepanu varajase töötluse suuremat osalust. Lisaks ilmnesid intervallist sõltuvad erinevused positiivse ja negatiivse ärritaja puhul. Need erinevused viitavad aktivatsioonimehhanismi ja automaatsete töötlusprotsesside osalusele lühemate intervallide korral ning tähelepanu rollile pikemate kestuste hindamisel. Kui negatiivsed ärritajad tingisid subjektiivse aja kiirenemise lühemate kestuste juures, siis positiivsed ärritajad viisid sama tulemuseni pikemate kestuste hindamisel. Uuringus III saadud tulemused rõhutavad nii aktivatsiooni kui tähelepanu osalust emotsionaalsete ajamodulatsioonide ilmnemisel ning lubavad oletada, et emotsionaalse kogemuse hindamine on kontekstispetsiifiline (Schirmer, 2011).

Uuringus IV leiti seos ajahinnangute ning erinevate impulsiivsusemõõdikute vahel, mille põhjal saab järeldada, et ajataju on üks impulsiivset käitumist kirjeldavatest omadustest. Võimalik, et impulsiivsetel indiviididel on kiirem kognitiivne tempo, mis väljendub nii impulsi kontrolli ja reaktsioonide pidurdamise häirumises kui ka enesekohaste impulsiivsete käitumisviiside raporteerimises. Täpne alusmehhanism käesoleva seose puhul on ebaselge, kuid tõenäoliselt saab ka siin luua seoseid afektiivsete töötlusprotsesside ja ajahinnangute vahel. Impulsiivsete indiviidide ajataju erinevusi saab seletada ka intensiivsema emotsionaalse kogemuse ja infotöötlusega, mistõttu reaktsioonide pidurdamine häirub ning ilmneb suutmatus kohandada oma sooritust ülesande nõuetele vastavalt (Wittmann jt., 2014). Impulsiivsete indiviidide kalduvus intensiivsemale afektiivsele kogemusele võib olla seotud eripäradega nii erutusseisundis kui ka tähelepanu töötluses.

Käesolev töö näitab, et ajataju tundlikkus erinevates seisundites ei ole seotud ainult füsioloogilise erutusega vaid hõlmab ka psühholoogilisi tegureid ning eelkõige emotsionaalset seisundit. Lisaks ilmneb, et nii ekstreemsetes keskkonnatingimustes kui ka afektiivsete ärritajate korral on oluline roll ajataju alusmehhanismide – tähelepanu töötlusprotsesside ja aktivatsioonitaseme – koostööl. Sealjuures on vajalik täpsustada emotsionaalsele ja kehalisele seisundile hinnangu andmise rolli subjektiivse ajamulje kujunemisel. Kokkuvõttes saab öelda, et ajataju alusmehhanismide uurimisel tasub rakendada afektiivse tähelepanu lähenemist ning pigem vaadelda organismi aktivatsiooni ja tähelepanu töötlusega seonduvat teineteisest sõltuvalt.

PUBLICATIONS

CURRICULUM VITAE

Name:	Maria Tamm
Date of birth:	27.07.1982
Citizenship:	Estonian
E-mail:	maria.tamm@ut.ee

Education:

University of Tartu, psychology, doctoral studies, 2006–2014
University of Tartu, psychology, MSc, 2006
University of Tartu, psychology, BSc, 2004

Professional career, including current position:

2014 – ...	researcher, Institute of Psychology, University of Tartu
2010 – 2014	HR expert, Estonian Air Navigation Services
2005 – 2013	laboratory assistant, Institute of Psychology, University of Tartu

Scientific publications:

Tamm, M., Uusberg, A., Allik, J., & Kreegipuu, K. (2014). Emotional modulation of attention affects time perception: Evidence from event-related potentials. *Acta Psychologica*, *149*, 148–156. DOI:10.1016/j.actpsy.2014.02.008

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ELULOOKIRJELDUS

Nimi:	Maria Tamm
Sünniaeg:	27.07.1982
Kodakondsus:	Eesti
E-post:	maria.tamm@ut.ee

Hariduskäik:
Tartu Ülikool, psühholoogia, doktoriõpe, 2006–2014
Tartu Ülikool, psühholoogia, magistrikraad (MSc), 2006
Tartu Ülikool, psühholoogia, bakalaureuse kraad, 2004

Teenistuskäik, sh praegune ametikoht:

2014–...	teadur, Tartu Ülikooli psühholoogia instituut
2010–2014	inimressursside ekspert, Eesti Lennuliiklusteeninduse AS
2005–2013	laborant, Tartu Ülikooli psühholoogia instituut

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