

BEHAVIORAL AND ELECTROPHYSIOLOGICAL SIGNATURES OF EXPECTATION,
INTERFERENCE AND DISCRIMINATION IN TIME PERCEPTION

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ABSTRACT

BEHAVIORAL AND ELECTROPHYSIOLOGICAL SIGNATURES OF EXPECTATION, INTERFERENCE AND DISCRIMINATION IN TIME PERCEPTION

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Expectation, interference and temporal discrimination ability are three crucial factors which affect human time perception. In this thesis, expectation is obtained by temporal location manipulation and results indicate that attentional time-sharing between keeping track of time and doing the concurrent task leads to timing disruption which supports the working memory maintenance accounts (Exp-1-2-3). Expectation effect is also studied through electrophysiological markers (Exp-4-5). Results indicate that the change in the CNV (Contingent Negative Variation) course – which is a marker of growing expectation – predicts the subjective timing responses for intervals which are longer than expected. Moreover, the N1 peak shows higher amplitudes when the offset of the interval is not expected in comparison to the threshold.

Evidence for interference between timing and a concurrent task is provided by all behavioral experiments. An independent response inhibition effect on timing occurs during the reproduction stage indicating an overlap between the central response requirements of the timing task and the concurrent task (Exp-3). Moreover, the overlap between the tasks at the end of the interval caused a further disruption in timing in the reproduction stage.

Difficulty in discrimination occurs in situations in which the expectation of a temporal event does not provide a clue for an apparent response. Findings show that the interval

offset P2 peak is sensitive to subjective responses in intervals with no apparent accurate response (Exp-4). A P2 peak modulation in terms of the accuracy in the task performance occurs when there is difficulty in terms of the relevant timing response (Exp-5).

Keywords: Time Perception, Expectation, N1P2 complex, CNV, Attentional time-sharing

Öz

ZAMAN ALGISINDA BEKLENTİ, BOZUCU ETKİ VE AYIRT ETMENİN DAVRANIŞSAL VE ELEKTROFİZYOLOJİK İŞARETLERİ

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Beklenti, bozucu etki ve zamansal ayırt etme zorluğu insanlarda zaman algısını etkileyen üç önemli faktördür. Bu tezin kapsamı içinde beklenti algılanan zaman aralığındaki ek bir görevin zaman aralığı içindeki yerine göre ortaya çıkabilir. Sonuçlar göstermiştir ki, dikkatin geçen zamanın takip edilmesinden ek görev performansına kayması sonucunda zaman algısında dikkatsal zaman paylaşımı teorisi ile uyumlu biçimde zaman algısında bozulma ortaya çıkmıştır (Deney-1-2-3). Fakat, aktüel ve önceden kaydedilmiş aralıkların bir içsel eşik ile Deney-3'deki gibi karşılaştırılmasının zorluk içermediği gösterilmiştir. Beklenti etkisi ayrıca elektrofizyolojik işaretler ile de çalışılmıştır (Deney-4-5). Bir zaman aralığının iki ucu arasındaki Olasılıksal Negatif Varyasyon (CNV) artan beklentinin bir işaretidir. CNV rotasındaki değişim beklenenden uzun zaman aralıkları için subjektif zamanlamayla ilgili cevapları öngörmektedir. Dahası, aralığın sonu beklenmiyorsa beklendiği duruma göre N1 tepe potansiyelinin daha büyük bir genliğe sahip olduğu gösterilmiştir.

Zaman algısı ve ek görev arasındaki bozucu etki bütün davranışsal deneylerde gösterilmiştir (Deney-1-2-3). Bundan bağımsız olarak tekrar-üretme aşamasında zamanlamanın ve ek görevin merkezi tepki gereksinimlerindeki çakışmayı işaret eden bir inhibisyon etkisi bulunmuştur (Deney-3). Dahası, görevler arasındaki çakışma, tekrar-üretme aşamasında ise, inhibisyon etkisinden bağımsız olarak zaman aralığının sonuna doğru ek bir bozulmaya neden olmuştur.

Zamansal ayırt etmedeki zorluk, zamansal bir olayın beklentisinin açık bir tepkiyi işaret etmediği durumlarda ortaya çıkar. Açık bir cevabın mümkün olmadığı zaman aralıklarında P2 tepe potansiyeli subjektif olarak verilen kısa veya uzun cevaplar ile module edilir (Deney-4). Daha da önemlisi, ilgili zamansal cevap belirsiz ise P2 tepe potansiyeli değişimi görev performansının doğruluğu ile orantılı olarak gözlenmiştir (Deney-5).

Anahtar Sözcükler: Zaman Algısı, Beklenti, N1P2 Kompleksi, CNV, Dikkatsal zaman-paylaşımı

To My Family

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LIST OF ABBREVIATIONS

CI	Comparison Interval
CNV	Contingent Negative Variation
EEG	Electroencephalogram
ERP	Event-related Potentials
ISI	Inter-stimulus Interval
MTS	Multiple Time Scale
RT	Reaction Time
RLG	Random Letter Generation
RNG	Random Number Generation
PSE	Point of Subjective Equality
SBF	Striatal Beat Frequency
SCR	Simple Choice Reaction
SI	Standard Interval
SET	Scalar Expectancy Theory
SOA	Stimulus Onset Asynchrony

CHAPTER 1

INTRODUCTION

Anticipation of external events is an essential ability of humans for survival in a complex environment. The anticipatory mechanism of an organism brings an advantage for efficient identification of external stimuli and a quick adaptation of possible actions fitting these identifications. A failure in anticipation of what is likely to happen next creates problems for people in terms of adaptive behavior in their daily life. A functioning anticipation ability of an organism requires an implicit timing mechanism. Addressing timing related phenomena is a promising way to understand how our timing mechanism is influenced by various cognitive and perceptual processes and how well we can arrange them in a proper order. Implicit timing is a rather automatic way of interacting with the environment and in this respect expectation can be considered as an automatic response of a cognitive system rather than a more general anticipatory mechanism which can be taken as a more higher order cognitive system.

Time perception can be studied from various perspectives and with various paradigms. The selection of a particular perspective for investigating timing-related phenomena affects the nature of the model, the theory and even the scale of the durations that are chosen. For instance, the study of the relation between time and memory can direct us to the retrospective paradigm (i.e. Block & Zakay, 1997; Zakay & Block, 1997, 2004; Eisler, et al., 2004) and most studies in this paradigm are concerned with relatively longer durations (Grondin, 2010). In the retrospective paradigm, the participants are not aware that the task is related to timing, thus the most relevant modality in this paradigm is the memory of the time which has passed. In this setting, the scale of the time interval can exceed the minute limit. In contrast to the retrospective paradigm, the scale of prospective studies usually is the supra-second scale which stays under the minute level. Moreover, in the prospective paradigm participants are explicitly instructed about the necessity of timing prior to the task; therefore, attention is more relevant and likely to be involved (Zakay & Block, 2004). Besides the paradigm choice, the relevance of the duration scale should be recognized in terms of the model selection. For instance, the relatively shorter durations – usually on the sub-second scale – are targeted for sensory-based timing phenomena and thus the preferred accounts are mostly modality-specific.

These types of timing models are called “intrinsic models” because they do not require a dedicated clock mechanism for timing (Ivry & Schlerf, 2008). On the other hand, the time perception literature which is interested in “interval timing” targets intervals long enough to become available for (higher-order) processes in the cognitive system rather than shorter durations which are more likely the subject of sensory modulation. On the scale of “interval timing”, the typical dedicated mechanism which is assumed to comply with the experimental methods is the “internal clock”. This thesis aims to study timing phenomena within the scope of the prospective paradigm from the “interval timing” perspective, thus the chosen framework in terms of the methods and hypotheses will be based on the internal clock models.

1.1. Interval Timing and Internal Clock Models

The behavioral findings with regards to interval timing are traditionally explained by internal clock models which includes a pacemaker-accumulator framework (Buhsu & Meck, 2005). In this framework, a pacemaker emits signals at a constant rate which are temporarily stored in an accumulator (Church, 2003). An internal clock model can be based on the information processing framework in which the response in a timing task is given according to the comparison of the current number of signals and the duration of a remembered reference interval (Buhsu & Meck, 2005). Given the many variations of the model in terms of the properties of this inner clock, Allman et al. (2014) differentiate these properties into two kinds of principles. The clock speed and storage of the time signals can be considered under the first order principles and contrasted with the second order principles that include the integrational part of timing such as attentional time sharing. The accumulation of time signals can be affected by both first order and second order principles. The clock speed – which might be modulated by the arousal level – corresponds to the frequency of the emitted signals by the pacemaker, thus it changes the number of time signals which are accumulated within a particular duration. Besides changing the clock speed, the number of accumulated signals can be affected by a disruption of the updating mechanism with an introduction of break or a concurrent task. Lastly, there is a dual-task effect on timing. In the reproduction method, for example, participants have to do a concurrent task during the interval which they later have to reproduce – which makes this paradigm a dual-task paradigm. The explanation of this dual-task effect can be based on attentional accounts or be attributed to an interruption working memory. The interference of a concurrent task with the timing task for either accounts targets the accumulation of pulses.

1.2. Interference Effects and Interval Timing

One possible explanation for the type of accumulation interruption just mentioned is in terms of a switch between the pacemaker and the accumulator which can be influenced by attentional modulation (Fortin, 2003). Divergence of attention from the primary task of timing towards a secondary, concurrent task in a dual-task design would lead to the accumulation of less pulses. The attentional time sharing hypothesis predicts that available resources are divided between timing and external events (Allman et al., 2014). The concurrent tasks can be an example of such an external event which can disrupt timing performance.

Another potential explanation for the disruption of the accumulation of pulses can be based on the interruption in the transfer of the pulses in the accumulator to working memory. Alternatively, one might consider only the working memory related effects of a dual-task on timing rather than including an accumulator. Indeed, the necessity of an accumulator has been criticized in terms of neural plausibility (Kononowicz & Van Rijn, 2011; Van Rijn et al., 2011) and of computational predictions (Van Rijn, et al., 2014). In other words, the disruption in timing which is caused by a concurrent task can be conceived as a working memory related maintenance interruption instead of an attentional modulation of the switch in the internal clock models. Although it has been shown that maintenance of temporal order and item information is represented by different frequency bands (Hsieh et al., 2011), the temporal information maintenance is related to the oscillatory mechanisms of working memory. Moreover, Fougny (2009) suggests that the effect of attention on working memory is mainly relevant for information encoding rather than for the maintenance of information. Barrouillet & Camos (2012) suggest that a central bottleneck leads to a memory decay of maintenance by competing with working memory processes. In other words, a change in the working memory trace is expected when there is a longer occupation of working memory in terms of processing requirements.

In brief, there are two rival perspectives for the explanation of the interference effect on timing: 1) the modulation of a switch between pacemaker and accumulator through divided attention in the presence of a concurrent task, 2) the loss of accumulated pulses because of interference with temporal information maintenance.

The first account predicts that sharing of attention between the timing and the concurrent task should lead to a disruption in timing due to the concurrent task performance which prevents the accumulation of time pulses. Moreover, the more attention is spent for the concurrent task the more the encoding of time should be interrupted. In this account, a proper accumulation of pulses is prevented due to the shifts in attention. In other words, when there is a concurrent task requirement within

an interval, pulses which are emitted from the pacemaker do not pass towards the accumulator since the switch is opened as a consequence of an attention shift for the concurrent task performance.

The second account is based on a problem in maintenance of temporal information rather than a disruption at the encoding of an interval. In this account, the pulse accumulation is not disrupted but the number of pulses which are accumulated is open to be lost due to a memory decay. Therefore, a disruption in timing is predicted due to a bottleneck between maintenance of temporal information and working memory requirements of the concurrent task such as processing the stimulus properties and selecting an appropriate response. However, in contrast to the previous account, since the disruption in timing is not related to the encoding of the interval, the length of the overlap between timing and the concurrent task does not matter much for explaining timing related phenomena. However, the decay rate has more substantial effect to explain the rate of accumulated pulses. In other words, even though the higher rate of decay which is applied for the accumulated temporal information can explain the possible differences in terms of the concurrent task difficulty, the duration of the decay – due to the overlap between the timing and the concurrent task – does not have profound effects at least in the brief differences of the task overlap duration. Thus, we can expect an equal disruption for both easy and difficult concurrent tasks – in the presence of a dual-task condition which has almost equal length of the overlap – because of the loss of accumulated pulses in the working memory with the same decay rate. This account differs from the attentional switch account because a direct influence of attentional shift in the difficult concurrent task would cause a disruption in the encoding of pulses during the overlap in the attention based account.

1.3. Temporal Location Effects and Interval Timing

Expectation is another crucial phenomenon to consider in a timing study using a dual-task method. In this respect, the temporal location of the concurrent task is what makes the difference in terms of timing performance. The expectation of a gap or break is suggested to cause attentional interruptions during the timing task (i.e. Fortin & Tremblay, 2006; Fortin et al., 2009). From this break a disruption of timing arises if the break or concurrent task is included somewhat later within an interval. Fortin et al. (2009) proposed that this finding can be explained by the attentional shifts between keeping track of time and monitoring of non-temporal concurrent task stimuli. These shifts are the result of a shifting of the switch between the opened and closed states. The findings in the literature are in line with the accumulation framework (i.e., Brown, 1997; Buhusi & Meck, 2006; Zakay, 2000; Zakay & Block, 1996) which claims that the encoding of an interval is disrupted by the concurrent task since the attention is diverted

away from timing. This attentional account also predicts a performance increase in the concurrent task since the attentional monitoring of the concurrent task is expected to facilitate its performance. Another prediction of this account is that the disrupted timing is also modulated by the expectation of the gap/break not just by its real occurrence (i.e. Fortin et al., 2009).

Buhusi & Meck (2009a+b) proposed that timing is dependent upon the maintenance of accumulated pulses in the context of a distractor or gap. Moreover, this effect is shown to be dependent upon the contrast of the distractor within the interval. An account which is based on the maintenance of attentional and memory resources predicts that the loss of pulses would be proportionate to the length of the interval which has elapsed before the point where the disruption occurs. More specifically, because monitoring and reallocating resources between the tasks (see Buhusi & Meck, 2009a) should decrease the amount of resources for timing, the maintenance of the accumulated pulses would be more affected due to the higher rate of memory decay. In short, in this account, the higher degree of disruption in timing – in conditions where the concurrent task is involved later during an interval – is the result of a problem in working memory related temporal information maintenance. In this account, in contrast to the switch hypothesis, the expectation of the distractor itself would not influence timing since the hypothesized disruption is a result of a maintenance problem, not an expectation or encoding problem.

1.4. Response Inhibition Effects and Interval Timing

Within the scope of internal clock models, timing should be considered to cover all aspects of a timing task. In other words, in addition to the clock level which is studied from the perspective of expectation, it is necessary to address the other levels of the internal clock models – the working memory level and the decision level – for a more comprehensive view on the topic. The decision level consists of a comparison process in which the current temporal context is compared to a threshold that is obtained from the memory distribution and the outcome of this comparison determines the relevant response (Wearden, 2004). Although attention is considered either in terms of a switch on the clock level or in terms of time-sharing on the working memory level, the decision stage of a timing task is often overlooked. This is mainly the result of Scalar Expectancy Theory (SET) (i.e. Church, 1984) which is based mostly on tasks which require responses after the interval presentation has been completed. However, the consideration of both the passage of time in the current context and the previously learned representation of the interval (i.e. Wearden, 1999, 2004) is necessary for other timing tasks – such as time reproduction – since the participants need to control their own responses during timing itself instead of deciding after the interval of experience is complete. The potential response inhibition related effects can be studied by the introduction of a concurrent

task which requires response inhibition into the timing task which requires a central executive kind of process – monitoring the performance of both tasks under voluntary control – to create a central overlap. The central overlap corresponds to the processing requirements which requires a top-down regulation on the relevant task performance. For instance, inhibiting a response since it is not yet time to respond which is expected to be observed in a timing task and inhibiting a response – which is triggered by a low-level stimulus properties – in a conflict resolution task due to a conflict in the low-level stimulus properties and response rules. A potential overlap of timing and the concurrent task is expected to cause a timing disruption resulting from the requirements of the decision level in an internal clock model.

1.5. Comparison Process on the Decision Level of Interval Timing

Although the potential response inhibition effect – which is expected to be a consequence of the overlap between the response inhibition requirements of the timing task and the conflict resolution task – is a result of decision level requirements, it is rather an indirect consequence of the reading of the outcome in the comparison process. We should also consider the possible effect of the demands of this comparison process on timing. Van Rijn et al. (2014) claim that this comparison is based on the ratio-rule which is considerably demanding for working memory resources. The ratio-rule corresponds to the typical threshold comparison rule between the experience of an interval and the reference memory. Instead they propose a coincidence-detection mechanism from the perspective of computational and neural plausibility. Following this line of thinking, if the comparison process is a demanding process in terms of working memory requirements, we should observe more disruption in timing if there is an overlap between this comparison process and the concurrent task monitoring than in the case when there is no overlap in terms of comparison requirements between the two tasks in terms of comparison requirements. In other words, if the comparison process is not demanding and it occurs in a rather automatic way like in a coincidence detection, we would not expect an extra timing disruption due to this overlap between the two tasks. On the other hand, if the comparison process is rather more working memory resource consuming, we would expect more disruptions in parts of an interval which comes later. The attentional-time sharing hypothesis predicts that resource sharing between timing and the concurrent task leave less attentional resources for timing in later parts of the interval due to the monitoring of an approaching concurrent task. Thus, if there is a demanding nature of the comparison process in the decision level of the internal clock, we would expect more disrupted timing performance in which the conditions there exists a decision requirement for timing in comparison to the cases where there is no decision requirement for timing task.

1.6. Neural Markers of Expectation and Decision Related Timing Phenomena

So far, a behavioral perspective is presented to differentiate the attentional switch hypothesis and the attentional time-sharing hypothesis in terms of their predictions for interference and expectation effects. These hypotheses roughly correspond to the pacemaker-accumulator and the coincidence-detection perspectives of internal clock models, respectively. Moreover, investigating whether the comparison process on the decision level of the internal clock is resource-demanding or not is also relevant for supporting either the pacemaker-accumulator or the coincidence-detection mechanism.

Besides evidence from behavioral studies, a similar differentiation can follow from studies of the electrophysiological markers of the processing of interval time. The classical internal clock models, namely the pacemaker-accumulator framework – can be appropriated to neurobiological findings (Allman et al., 2014). However, coincidence detection models (i.e. Matell & Meck, 2000; Matell & Meck, 2004) or dynamic non-linear systems (Large, 2008; Schöner, 2002) – which are built upon oscillatory processes – might be considered as a better account for the decision-related part of the timing mechanism since they do not assume an additional threshold comparison process as assumed in pacemaker-accumulator models. For instance, interval offset ERPs such as the N1 peak can be informative in terms of expected or unexpected events (Chennu et al., 2013; Annic et al., 2014). A finding of an N1 peak which is a marker of a relatively automatic process would support the coincidence-detection mechanism. Moreover, investigating slow potentials, namely CNV (Contingent Negative Variation), is relevant since the CNV is suggested to be a marker of growing expectation. The expectation of an imminent action is usually associated with a threshold to make a response thus it is crucial to take such motor-related processes into account as well. Indeed, due to their anticipatory nature implicit timing and reaction time tasks have been proposed to rely on similar operations in terms of preparation (i.e. Praamstra et al., 2006). A finding in favor of expectation in terms of a threshold for a response and in connection with a CNV (Ng et al. 2011) would indicate a mechanism other than a mere association of the CNV with the accumulator. A further relation of interval offset ERPs to the temporal discrimination difficulty on the decision level can be studied by another interval offset component, namely the P2 peak. With this component the decision level processes of timing can be further elaborated. Lenartowicz et al. (2010) suggest that when there is a difficulty – such as a difficulty in discrimination – in terms of subsequent activity, an attentional burst is necessary for the approaching working memory related process. The P2 peak is a candidate indicator of this top-down attentional manipulation.

In summary, this thesis aims to investigate three different timing phenomena – namely expectation, interference and temporal discrimination – by behavioral and

electrophysiological methods. Since we want to study these subjects in terms of the prospective paradigm on a supra-second scale, the investigation of these subjects will be based on the internal clock models. Interference and expectation in timing will be studied by comparing two hypotheses, namely the switch hypothesis and the attentional time-sharing hypothesis, which are mainly related to the clock level and working memory level of the internal clock model. In this part of the present study, our aim is to build an intrinsic connection between the two levels of the pacemaker-accumulator type internal clock models. Expectation related effects on timing will be considered together with the interference related phenomenon in timing by considering resource sharing between the temporal and non-temporal context, i.e., tasks. As another interference related effect, the response inhibition requirement of a concurrent task will be investigated by considering the overlap of similar requirements which are necessary for both timing and concurrent task. This part of the thesis will reveal the disruptive effect of inhibition requirements at various stages of a timing task. Thirdly, the nature of the comparison process in a timing task will be investigated by comparing the two stages of a reproduction task, namely the encoding and reproduction stages, to reveal whether this process adds a resource demanding load on accurate timing. This will help us to reveal decision level related effects in the internal clock model by manipulating interference and expectation of a concurrent task at different points within the interval. For this particular investigation, our aim is gain insight into the relation of the clock and decision level of a typical pacemaker-accumulator type internal clock model. Further investigating the nature of the decision level in timing, we will investigate an electrophysiological marker which is associated with expectation, namely the N1 peak and CNV, at the interval offset to build a relation between the expectation phenomenon and automatic discrimination in timing. This part of the study will build a connection between the clock level and the decision level of a traditional internal clock model. Lastly, the discrimination process in a temporal context will be further investigated to see whether there is an additional explicit discrimination process when there is a difficulty in the discrimination task. For this purpose, we will focus on the interval offset P2 peak since the amplitude regulation of this peak is associated with difficulty as a marker for subsequent difficulty related processing (e.g. Lenartowicz et al., 2010). Based on the neurophysiological analysis, we will propose an N1 peak related fast and automatic discrimination and a difficulty dependent explicit discrimination process which are complementary in terms of leading to accurate temporal discrimination. The order of the experiments was arranged, firstly, to study the temporal location and interference effects which will provide us a basis for considering expectation as an interference dependent phenomenon presenting us a picture of clock and memory level together. Secondly, the decision level of a timing task will be added to this picture by providing behavioral support. Thirdly, as a follow up to this approach, we will investigate the nature of

decisions further by providing electrophysiological support for our findings in the previously presented behavioral perspective. In this way, in the present study, we achieve a comprehensive picture of the three levels of a typical internal clock model by building relations between the levels. In this context, a coincidence detection type of internal clock models which favors working memory functions in a more plausible way and which presents a rather automatic way of time based decisions will be discussed as an alternative to the typical pacemaker-accumulator framework.

The organization of this thesis is as follows: Chapter 2 presents a literature review which provides a detailed consideration of time perception models in terms of the aforementioned topics of expectation, interference and temporal discrimination from the behavioral and electrophysiological perspective. In chapter 3, two experiments, Exp-1 and Exp-2, on the comparison of the switch hypothesis and the attentional time-sharing hypothesis will be presented. This comparison will be achieved by presenting the expectation-related change in timing performance and the interference effect – which is caused by the presence of a concurrent task. Chapter 4 investigates the decision level of the internal clock model in one further experiment, Exp-3 in addition to the findings regarding the clock level in Chapter 3. This is achieved by addressing the expectation effect in detail in terms of the timing task requirements and by the investigation of the concurrent task effect from the perspective of a rather more central overlap of task requirement. In chapter 5 (Exp-4 and Exp-5), expectation-related ERP markers will be investigated from a neurophysiological perspective, complementing the previously presented behavioral perspective. As a last subject in this chapter, an interval offset marker will be proposed as an indicator of discrimination difficulty in terms of a timing-related discrimination difficulty. Chapter 6 will consist of the general discussion and the conclusion of this dissertation.

CHAPTER 2

LITERATURE REVIEW

The internal clock models have dedicated/central mechanism in contrast to the intrinsic models of timing (i.e. Ivry & Schlerf, 2008) which are modality specific (Grondin, 2010). Interval timing in supra-second scale can be explained better by the internal clock models since these models allow us to consider time-keeping mechanism embedded in a general cognitive system and that is necessary to explain central task overlapping effects. Moreover, the internal clock models are appropriate to explain a direct attentional modulation of the general cognitive system and this is another necessary property of a model to explain expectation phenomena in timing. There are many variations of the internal clock models and they can broadly be categorized as the linear pacemaker-accumulator models (i.e. Gibbon 1992; Wearden, 2003; Church, 2003) and as the oscillatory models (i.e. Large, 2008; Schöner, 2002) with a dynamical non-linear perspective (Grondin, 2010). Despite the differences between these perspectives in terms of whether a time interval is represented by a linear information processing or by non-linear neural patterns, Allmann et al. (2014) suggests that the oscillatory patterns of the cortical neurons can provide a basis for the ticks which are theorized in the pacemaker-accumulator models as well. At the beginning of this literature review, we will focus on the pacemaker-accumulator framework of time perception about the parts of this framework such as switch, accumulator/working memory and decision. The behavioral findings in the time perception field which support this framework will be provided by referring to these parts respectively. However, at the same time, we will discuss some lacks of this framework by addressing both the most studied level of this model, namely the clock level, and the relatively less studied part, namely the decision level, via providing more plausible versions of the internal clock models with a neurobiological perspective. First, the interaction of pacemaker and accumulator will be introduced from the switching perspective along with hypotheses against it.

2.1. Switch in the Pacemaker-Accumulator Framework

In an internal clock model (i.e. Church, 1984; Gibbon et al., 1984; Treisman 1963), the onset of an interval causes a switching between a pacemaker and an accumulator to close (Figure 1). The switching is modulated by attention and the temporal value of the current context in the working memory is compared to a previously represented value in the reference memory (Allmann et al., 2014). The switch is triggered by the significance of the temporal information and the latency of the switch closure is higher at the beginning of an interval than its opening at the end of the interval which can be attributed to a temporal expectation difference at the two ends of an interval (Lejeune, 1998).

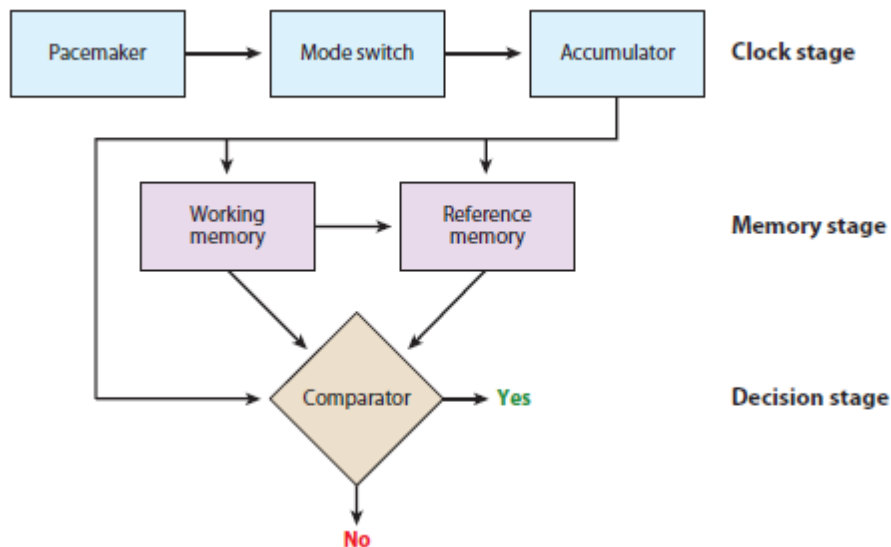


Figure 1. The interval timing in an information processing background by adopting pacemaker-accumulator framework (Almann, 2014, p. 745. Adapted from Church, 1984; Gibbon et al., 1984; Meck, 1984; Treisman, 1963;1984).

An internal clock can have different modes depending upon the modes of switch. In animal studies, it is found that events which include gaps or distractors (i.e. Buhusi & Meck, 2006) or multiple events to be timed at the same time (i.e. Buhusi & Meck, 2009b) can force the internal clock to function under some modes such as “run”, “pause” or “repeat” (Allmann et al., 2014). The pacemaker-accumulator framework is an information processing framework adapted version of the scalar expectancy theory (i.e. Gibbon 1977; Gibbon & Church, 1984) and it is mainly based on the animal studies and usually they provide a memoryless parsimonious system (Reid & Allen, 1998). However, Buhusi & Meck (2006) found that this pacemaker-accumulator system which is

controlled by a switch is not the best account if we take gaps and distractors into account. Instead, they provided evidence for the working memory decay mechanism which delays timing in proportion to the saliency of the distractor events. Buhusi & Meck (2009a) claimed that the contribution of a distractor on the animal timing is dependent upon attention and memory resources and it is concluded that the findings can be explained better by a time-sharing account rather than by a switch account. In the switch based accounts of human timing, the monitoring of an extra signal – which is not a signal to be timed necessarily – creates a change from a close state (i.e. timing goes on) to the open state (i.e. interruption of timing) of the switch (i.e., Penney et al., 2000). If there are gaps or breaks within an interval to be timed, the switch can work either in the stop mode in which the timing continues only during the “to be timed durations” but not during the breaks, or it can work in the run mode in which the timing continues until the end of the interval irrespective of the breaks within the interval. Moreover, it is hypothesized that a flickering is possible between the closed and the open states of the switch which can explain the tradeoff between the timing and the non-temporal stimuli processing (Lejeune, 1998) (Figure 2). Gap location effects – in which the gaps that occur later within an interval cause more timing disruption than the earlier gaps – can be explained by the attentional shifts that affects the switch part of the internal clock (Fortin & Tremblay, 2006; Fortin et al., 2009). This explanation is based on the expectancy account that is dependent upon the accumulation rate of the pulses during timing.

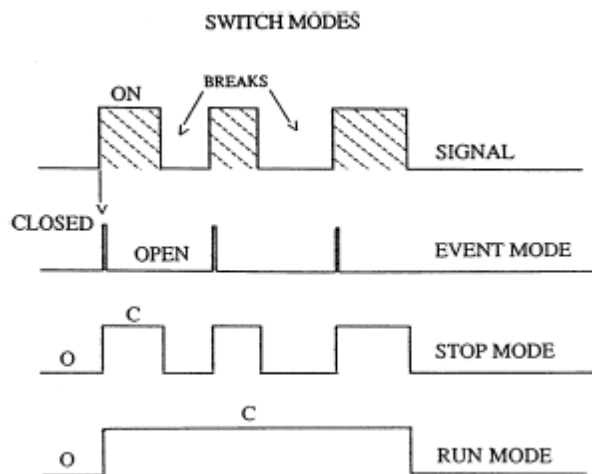


Figure 2. The switch modes in an information processing model of interval timing (Lejeune, 1998, page. 139)

On the other hand, although time-sharing account (i.e. Buhusi & Meck, 2009a) does not provide a discussion on the details of the pacemaker-accumulator framework or its

neural plausibility, this account provides an explanation which is based on a resource sharing between the temporal information – which is processed and maintained in the working memory – and the current context within the interval. In other words, the findings are explained by a working memory decay rather than a switch flickering. In this account, the decay rate is determined in proportional to the relative contrast between the gap/distractor and the current context. If the non-temporal properties of the intruder such as relative intensity and/or saliency is higher, the decay rate increases. Thus, the rate of decay is higher when a gap is introduced during an interval than the occurrence of a distractor. Moreover, the working memory decay rate decreases with the temporal contrast. The temporal contrast is found to be based on the relative duration of the intruder to the ITI (inter-trial interval) in a peak procedure (Figure 3).

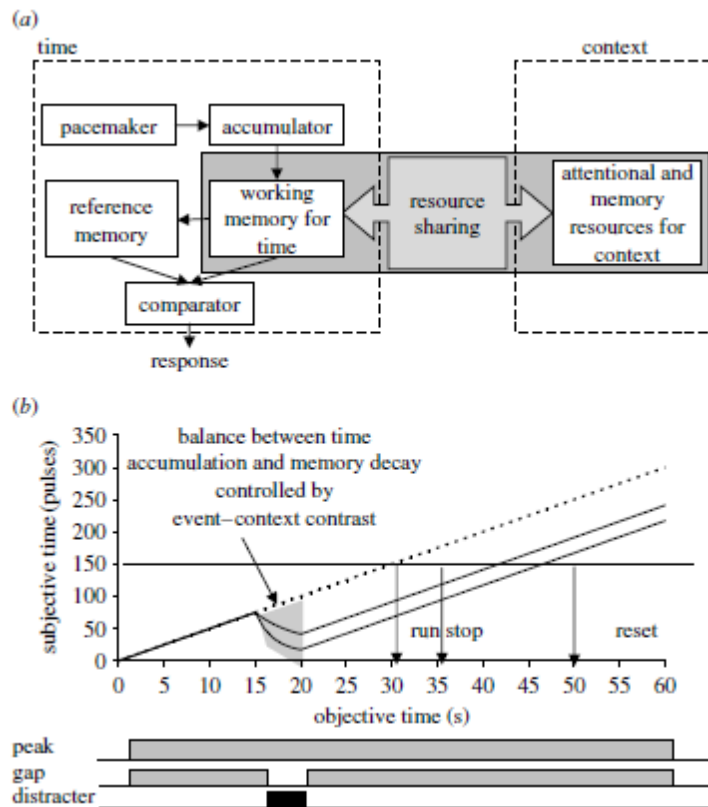


Figure 3. The relative time-sharing Hypothesis and working memory mechanism for the gap occurrence during timing: dashed line, peak; thin solid line, peak + distractor; thick solid line, gap. (Buhusi & Meck, 2009b, p. 1880).

2.2. Accumulator and Working Memory

Lejeune (1998) defines the accumulator as a counter that makes increments in the perceptual temporal storage. In this framework, the accumulator has equivalent role to the short-term memory (working memory) and the working memory component in this framework holds the value which is accumulated in the accumulator when there is a delay between the experience of to-be-timed interval and the timing response for this experience. Dual-task experiments showed that an interference during timing leads to an experience of interval as shorter than its objective length (i.e. Brown, 1997; Buhusi & Meck, 2006; Zakay, 2000; Zakay & Block, 1996). In the attentional sharing perspective, the interference effect on timing is either theorized by its disruption at the accumulation level or at the working memory level after the accumulation (Buhusi & Meck, 2009b). If a particular internal clock model version favors an attentional modulation on the switch between the pacemaker and accumulator (i.e. Lejeune, 1998), attention is taken as a component which works on the accumulation level that is rather independent from the maintenance related phenomena in the working memory. In other words, as Lejeune (1998) suggests, the accumulation is accepted as a perceptual stage of a temporal task which is in line with the claim that the relation of attention is more relevant to the information encoding rather than the information maintenance (i.e. Fougny, 2009). Block & Zakay (1996) suggested a slightly modified version of a typical pacemaker-accumulator type internal clock model, namely the Attentional Gate Model, with an extra gating mechanism to provide explanation the as regards to the findings especially about the intentional attentional resource allocation. Independent from the plausibility or the explanatory powers of these two models (i.e. Lejeune, 1998; Zakay, 2000), both models provide a perspective which are focused on the accumulation level and they explain the interference effects on timing either by a gating or by a switching mechanism. On the other hand, Buhusi (2003) proposed a sharing of the working memory resources between the timing and the context. This perspective is different because the mechanism which is responsible for the loss of pulses is the working memory decay rather than an accumulation of less number of pulses. The context refers to the occurrence of a contrasting event in Buhusi & Meck (2009b) and the sharing of the resources is related to the maintenance interruption in the working memory. In contrast to the encoding based explanation of the switch/gating accounts in which the manipulation of the attentional resources affects the perceptual storage, the working memory decay in the interference situations is based on the impaired ability to hold or do multiple performances at the same time. Indeed, an interference to the working memory process leads to a decay in the presence of a form of bottleneck (Barrouillet & Camos 2012).

Buhusi & Meck (2009b) claim that a divergence of attentional and/or memory resources should be valid in cases which require multiple task performances and the sharing should be independent from the details of the timing mechanism. In other words, the predictions of resource sharing do not strictly require a presence of a pacemaker-accumulator framework in a timing model. Staddon & Higa (1999) pointed out the problems in the pacemaker-accumulator framework of SET in terms of the ways for making the model compatible with the experimental findings. For instance, they argue that additional assumptions about the trial to trial variations of the pacemaker were added to make the model in line with the results even though the timing mechanism has no any intrinsic way to distinguish the trial onsets. Similarly, they noted the accumulator's limitless upper boundary in SET which makes difficult to reconcile it with the idea of a limited working memory capacity. Instead, they proposed a multiple time scale (MTS) habituation model of interval timing – which is based on the memory dynamics – and it is claimed that this model is successful to explain a wide variety of experimental findings from temporal discrimination to Weber law. In this model, a time marker which states the onset of an interval is assumed to share similar properties with any other stimulus in terms of the short-term memory effects. In other words, some aspects of this marker get weaker and this corresponds to the decay of the relevant interval onset. In this account, which is based on an event based working memory model, the habituation is assumed to be the main element of the stimulus presentation. Rate sensitivity – which is accepted to be the dynamic feature of the habituation – is an element of a surprising act. Rate sensitivity provides constraints into the working memory such as the presence of a higher rate of habituation in the short interstimulus intervals (ITI) than in the longer ones, along with a rapid recovery from the habituation after the short ITIs (Staddon & Higa, 1999). A memory trace is used for keeping track of time in this model (Luzardo et al., 2013). The memory decay function in the MTS model is determined by the number of fixed intervals in a habituation series (Figure 4). The presentation of a reward causes an increase in the activity of the decaying units which forms a memory trace and thus a response threshold – which corresponds to the decaying level – is determined (Luzardo et al., 2013). Reinforcement is achieved by instant rewards of the time markers and the trace decays between one marker to the other one (Figure 5). The effect of introducing a gap within a fixed interval is rather debatable in animal studies since this sometimes causes a reset of the clock while indicating a continued timing during the gap in other times. Cabeza de Vaca et al. (1994) proposed a hybrid perspective since they found a support for a gradual loss of the accumulator value which can explain the intermediate conditions. Thus, they provide an account for the shifts in the peak time procedure by adding the memory decay to the pacemaker-accumulator framework. (Higa, 2008) (Figure 6). In this account, both duration of the gap and the pre-break duration are taken into account to be able to provide explanations for the different durations and different temporal locations effects. The decay function is dependent upon the pulses which are accumulated before the gap.

Thus, the loss of pulses would be higher when the gap is later during an interval than the gap is earlier (Cabeza de Vaca et al., 1994).

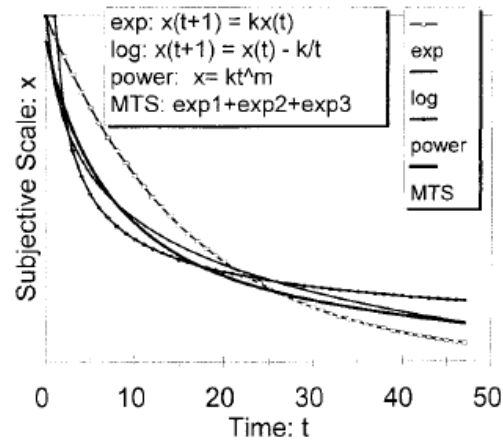


Figure 4. Different memory decay functions: exponential, logarithmic, power and Multiple Time Scale models with three fixed intervals (Staddon & Higa, 1999, p. 220)

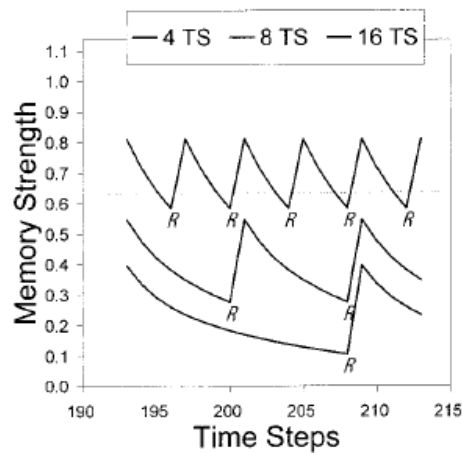


Figure 5. Rewards and monotonous decay in the different fixed intervals (Staddon & Higa, 1999, p. 232)

However, it is claimed that the gap location effect can also be explained by the MTS model. For instance, the gap location effect is dependent upon the differences between the trace of the interval onset and the gap onset. Since the early gap occurrence causes smaller differences, there should be relatively less responding in a peak procedure in contrast to the late gap conditions in which responding after a gap increases because of the greater trace differences (Higa, 2008).

2.3. Comparison and Response Related Processes in Interval Timing

In the decision level of an internal clock model in a pacemaker-accumulator framework, a comparison process should be applied to respond. The comparison is made between a standard interval – which is sampled from the reference memory – and the current interval in the working memory. The comparison process is task dependent and the response can only be executed after the comparison process is complete (Wearden, 2004). In the comparison level, a threshold value – which is updated from trial to trial - is compared to the difference between the standard and the comparison interval. Task dependence of the comparison process is mainly based on the definition of the reference value. Wearden (2004) defined this reference value as the standard interval which is given in a temporal generalization task in which the comparison is about deciding whether the current interval is shorter or longer than the standard interval.

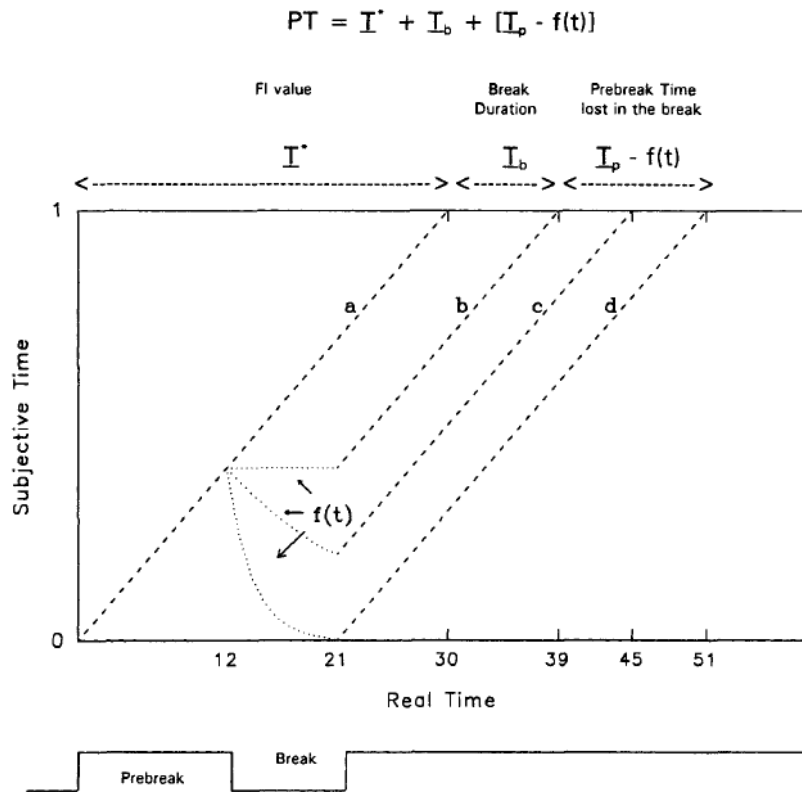


Figure 6. Pacemaker-Accumulator Framework with a memory decay account: (a) No Break (b) No Decay (c) Intermediate Decay (d) Complete Decay (Reset) (Cabeza de Vaca et al., 1994, page 190).

However, the reference value is slightly different in a bisection task in which there are two standard references such as short and long standard intervals. In this case, the

reference can be taken as either the arithmetic mean (Wearden & Ferrera, 1996) or the geometric mean (Allan & Gibbon, 1991) of the two standards. However, in this framework, the general idea of the comparison process is based on the sequential nature of the comparison and response steps. The key issue in this account of the decision process in a temporal task is the presence of a temporal point which determines the relative sections of the subjective responses. This point is called as the bisection point in which the likelihood of responding either short or long is equal. Levy et al. (2015) stated that the location of the bisection can be affected by the ratio of the standards (i.e. Wearden & Ferrara, 1996; Allan, 2002b) and it corresponds to the arithmetic mean if the ratio is closer to 4 or more and to the geometric means if the ratio is close to 2 (i.e. Kopec & Brody, 2010).

The scalar property of timing in the typical temporal generalization and bisection tasks is usually attributed to the transformation of the temporal value by a function which is either applied during the transfer from the working memory to the reference memory or at the reference memory (Wearden & Bray, 2001). We cannot mention a reference memory in some timing tasks such as reproduction, production or verbal estimations in a strict sense. However, Wearden & Bray (2001) showed that the scalar property can arise even if the comparison is achieved in a trial based bisection task – roving bisection – in which the interval to be compared is given in a single trial. The reproduction task – in which the interval to be timed is given just before the execution of the reproduction of that interval – is similar to the roving bisection task in that sense. However, the violations of the scalar property are usually observed in the data from the reproduction method. For instance, in the reproduction task, the shorter durations are overestimated in contrast to an underestimation of longer durations and usually there is an indifference point at the middle (Lejeune & Wearden, 2009). However, it is suggested that the reproduction task requires a response initiation-time and a response execution-time and this fact makes it different from the timing tasks that were previously mentioned. Indeed, in Wearden (2003)'s study, a modelling which considers these parameters (i.e. response initiation and response execution times) can explain the scalar property violations. However, other mechanisms and/or models such as memory mixing (Penney et al., 1998; Gu & Meck, 2011), Bayesian memory models (i.e. Jazayeri & Shadlen, 2010) and Internal Reference Model (i.e. Bausenhardt et al., 2014; Dyjas et al., 2012) were also proposed for an explanation of violations in the reproduction method (Van Rijn, 2016).

2.3.1. Effects on Decision Processes

In the internal clock models which are derived from the scalar expectancy theory, a comparison process must exist in both reproduction and temporal generalization tasks. It is found that this comparison process can be affected by differential payoff

manipulations (i.e. Wearden & Grindrod, 2003). In this study, the standard in a temporal generalization task is changed by different encouragement levels. Similarly, in another study (i.e. Wearden & Culpin, 1998), differential payoffs for errors are applied for the different comparison intervals (Wearden, 2003). In these types of effects on the comparison process, Wearden & Grindrod (2003) indicated that the threshold value is changed in the models in accordance with the scalar timing. A further example of an effect on the comparison process is the task difficulty (i.e. Ferrara et al., 1997) in which the discrimination is found to be better in the difficult condition and it is once again can be explained by a threshold change (Wearden, 2003). Wearden (2003) favored a threshold change account instead of an attentional explanation to explain the difficulty effect since it is claimed that the attentional accounts are more appropriate in the presence of a concurrent interference and the mechanism behind the discrimination facilitation is not explained by attributing higher attentional resource allocation in the difficult discriminations. There is no study which directly attributes the interference of a concurrent task on the comparison process requirements. The concurrent task effects on timing is mainly discussed in the dual-task framework. Thus, the findings are attributed to the general interference of the two tasks either in terms of an attentional sharing or a working memory related decay. Wearden (2004)'s study suggests an understanding of decision processes by a presence of two stages – namely the comparison process and response – in a sequence and the potential effects on this level of the internal clock should be investigated into two parts. Van Rijn et al. (2014) claims that the comparison process – which is based on the threshold rule – is considerably demanding for the working memory resources. For instance, there should be a current value retrieval from the accumulator and the reference value from the reference memory in every check of the value along with a threshold comparison of the ratio of these two values. In other words, if this is a demanding procedure for the working memory, we can expect a working memory interference which can be assigned just for the disruptions that arise from the comparison process. Rattat & Fortin (2011) suggests that the comparison process of threshold/accumulation is applied towards the end of the interval. This idea is consistent with the self-paced nature of the reproduction task. The very beginning of an interval is unlikely to be a target for an explicit comparison. It is possible to theorize an increasing level of a comparison process which is in line with growing expectation.

The second part of the decision process in a reproduction timing is execution of the response. Reproduction task must include a response initiation – after the comparison process is complete – which should be completed (i.e. Wearden, 2003, 2004) by the response execution which has an effect necessarily on the length of the reproduced interval. A “yes” outcome (i.e. threshold is passed) from the comparison process must

be followed by a response activation process. Thus, there is possible response execution overlap effect due to an interference between the timing task and the concurrent task in a dual-task design. This effect should be considered separately from the effect which is claimed to be the result of an overlap between the comparison process of a temporal generalization task and another discrimination task which is found in Rattat & Fortin (2011). Because, in a reproduction task, there is a further task requirement share between timing and the concurrent task in terms of the motor response related requirements.

2.3.2. Response Inhibition Effects

Other than the response initiation effects, we need to address the potential effects which can arise due to the inhibition requirement which is an intrinsic part of the reproduction task. The motor inhibition in a reproduction task should be considered because it is necessary to avoid a premature response during the period where there is no need for response activation due to a “no” outcome (i.e. threshold is not passed) from the comparison process. Zhang et al. (2016) showed that PD (Parkinson Disease) patients responded prematurely in a time discrimination task in a way which can be dissociated from other timing deficiencies. In this example, the failure at a properly working response inhibition process in PD patients leads to a rapid response. This leads to a performance disruption due to the rapid comparison processes which is constrained by the failure of the response inhibition. Wittmann et al. (2011) showed that greater activation in the cortical regions – in which the impulsivity is associated – corresponds to the underestimations of the reproductions. Premature responding of impulsive or patient populations at any task is related to the preparatory inhibition failure. In the Greenhouse et al. (2015)’s study, it is suggested that this inhibition can be related to the task relevant muscles (i.e. Duque et al., 2010) or to a more general motor inhibition (i.e. Badry et al., 2009).

2.4. Neural Correlates of the Internal Clock Model

A separate consideration of the clock, the memory and the decision levels of the pacemaker-accumulator models is supported by the pharmacological findings in the literature which indicate a dissociation of the clock and the memory stages by dopaminergic and cholinergic systems respectively (Buhusi & Meck, 2005). Dopaminergic system is found to affect the clock speed and a leftward shift in a peak procedure indicates that the clock becomes faster when a dopamine agonist – such as cocaine, methamphetamine or nicotine – is administered (Allmann et al., 2014). On the other hand, the cholinergic activity is found to be mainly related to the memory related predictions of the pacemaker-accumulator information processing models because the

findings indicated a presence of an absolute error and this error corresponds to the temporal memory translation constant between the working memory and the reference memory (Buhusi & Meck, 2005). The biological substrate of the milliseconds and supra-second range timing is claimed to be different since the cerebellum is associated with the motor timing which is embedded in a bottom-up system whereas the interval timing is mainly related to a cortico-striatal-hippocampal circuit that includes a top-down mechanism (Meck, 2005). In line with this dissociation, Allmann et al. (2014) indicated that the hippocampus activity is shown to be proportional to the absolute error in the temporal memory (i.e. Meck, 2002a+b, 2006). Besides a cholinergic regulation of the hippocampal regions on timing, the dopamine system is also restricted to a specific region, namely the striatum. In other words, the clock speed is a function of the regulation by the dopamine receptors which are located in the nigrostriatal pathway (Allmann et al., 2014). In this schema, the relation of the frontal cortex/hippocampus is achieved through the striatal regions and the changes in the functioning of the internal clock is regulated by neurotransmitters such as acetylcholine and dopamine which mainly corresponds to the effects related to the working memory/reference memory translation and the clock speed respectively (Figure 7).

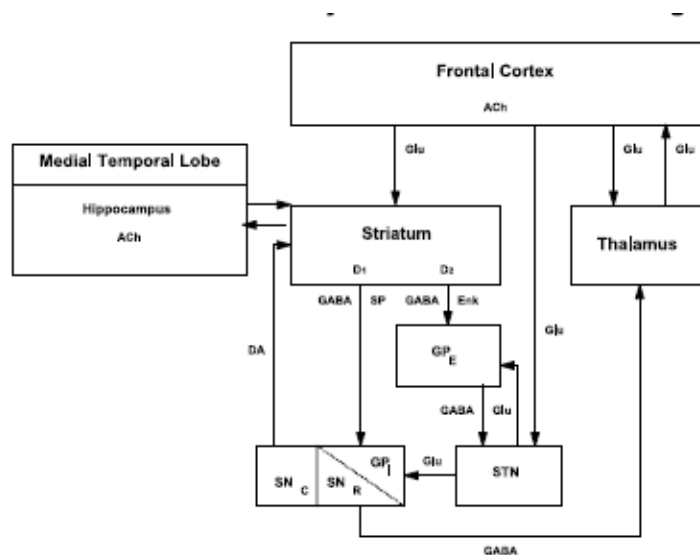


Figure 7. Cortico-Striatal Circuit and the Neurotransmitters (Meck, 2005, page. 4).

Apart from the pharmacological findings, striatal firing is shown to be sensitive to the different intervals in a reproduction task (i.e. Matell et al., 2003). Similarly, a ramp like activity in the striatum is found during the intervals (i.e. Apicella et al., 1992; Schultz et al., 1992) in which there is a delay of the relevant information (Buhusi & Meck, 2005).

As for the decision mechanism, which is based on the ratio comparison, Gibbon et al. (1997) states that this type of process – which takes ratios as inputs – is difficult to reconcile with the neurobiological network. Matell & Meck (2004) indicates that one implication for the decision related timing phenomena in the hippocampus is that there is a feedback-control mechanism in rats which ensures a minimization of the error by relying on a selection of the reference memory from the opposite sides of the mean at the consecutive trials (i.e. Meck, 1988; Meck et al., 1984).

2.4.1. Event Related and Slow Potentials in Interval Timing

Mismatch Negativity (MMN) – with a fronto-central distribution – is found to be in line with the scalar property of timing in an oddball paradigm since the ERP component amplitude for the deviant interval changes as a function of the ratio of the standard and the deviant intervals (i.e. Brannon et al. 2004; Brannon et al., 2008). Macar & Vidal (2009) suggested that the pulse accumulation within the pacemaker-accumulator framework is represented by a slow potential named as Contingent Negative Variation (CNV). Similar findings which associate the CNV with the duration length (i.e. Pouthas et al., 2000; Pfeuty et al., 2008; Macar et al., 1999) are in line with the idea that CNV amplitude represents the length of the interval (Grondin, 2010). For instance, Macar et al. (1999) claimed that the correspondence of higher CNV amplitude to an experience of a standard interval as longer than the standard seems to support the accumulation-CNV association. However, the same results could not be replicated by another study (i.e. Kononowicz & Van Rijn, 2014) and the habituation effects were suggested to be responsible for the CNV amplitude differences for the subjective responses. Although the relation of CNV peak and the interval length is controversial, the relation of the CNV slope-change and the interval timing is a relatively robust finding (Ng. et al., 2011). For instance, Macar & Vidal (2003) proposed that the CNV course change – after a CNV peak at the standard – is a representation of the encoded duration memory trace, thus CNV peak is an index of decision making in a temporal generalization task. Moreover, the peak time of CNV rather than the CNV amplitude, thus the slope of the CNV ramping is suggested to be the index of the memorized standard duration (Pfeuty et al., 2005). Although this study includes an explicit judgement about timing, the durations were at the sub-second scale and the motor preparation related mechanisms might be the cause of these results instead of a directly pacemaker-accumulator based interval timing. Tarantino et al. (2010) also provided evidence for a change of CNV course just before the end of an interval along with a faster reaction times for the intervals which are longer than the standard. Van Rijn et al. (2011) argued against the relation of the CNV and the pulse accumulation since the performance dependent variations of CNV cannot be explained by the changes in the pacemaker speeds. Thus, two alternative accounts are proposed

for the relation of CNV and timing: 1) the relation of the oscillatory processes and CNV in which growing CNV activity is the consequence of the higher number of neuron population firing, and 2) CNV as a marker of time-based preparation process. Temporal preparation hypothesis is in line with the Ng et al. (2011) study since two durations – namely the short standard and the geometric means of the short and the long standard in a bisection task – are indicated as the relevant points for the preparation requirements (Van Rijn et al., 2011).

Moreover, N1P2 amplitude at the onset of an interval can be associated with the precision of initiation of timing and this component might be a marker for a start-gun in a timing task (Ng et al., 2011). In this study, the correlated N1P2 amplitude and higher CNV amplitude is suggested to be a result of a reduction in the latency jitter. Similarly, in Bendixen et al (2005)'s study – which is a replication of Macar et al. (1999) study – it is suggested that the higher negativity of N1 peak at the interval onset is an indication of the enhanced processing and this corresponds to a higher number of accumulated pulses which may be accepted as a marker for the durations to be perceived as longer.

2.4.2. Oscillation and Coincidence Detection in Interval Timing

The multiple oscillator models (i.e. Church & Broadbent, 1990;1991; Miall, 1989; Meck et al., 2008) are not restricted by an unbound integration problem due to the accumulator which arises in the pacemaker-accumulator models. The integration of the spikes for the long intervals is not in line with the findings about the dopaminergic control at the basal ganglia (Matell & Meck, 2004). The oscillation based models do not require an integrator and the neurobiological role of the dopamine is more plausible in these models.

For instance, in the striatal beat frequency model (i.e. Meck et al., 2008) (Figure 8), the synchronization of the oscillating neurons at the PFC (Prefrontal Cortex) is achieved by a dopaminergic input at the interval onset. Moreover, an expected reward and a related dopamine change in the concentration can be the correlate of the decision level of an internal clock (Matell & Meck, 2004). In this model, dopamine specifies the temporal points in which there is a reward by strengthening the particular oscillation patterns. Thus, during timing a similar interval, the spiny neurons in the striatum can detect the same temporal location by comparing the current pattern with the already encoded pattern. The match of the patterns is determined by a coincidence detection function of the spiny neurons (Meck et al., 2008). In this framework, CNV can be a representation of the synchronization of the wide neural populations since the random firings of the neuron populations at the interval onset leads to a base activity and this activity can

increase due to a more synchronized firing with elapsing time (Van Rijn, et al., 2011). Indeed, Ng et al. (2011) found a correlation of the onset ERPs and the subsequent CNV which might be taken as a support for the relation of the synchronization at the onset and the ramping activity that follows it. Van Rijn et al. (2014) states that the main difference between the pacemaker-accumulator framework and the striatal beat frequency model (SBF) is their assumptions about the decision rules. In the pacemaker-accumulator models, a general decision rule – which is implicitly assumed – requires a retrieval during a continuous comparison of the current time and the encoded time. However, in the SBF model, the event durations are considered as unique – which are represented by the unique patterns of the oscillation – and each spiny neuron responds to a particular pattern thus this type of coincidence detection does not require a general decision rule (Van Rijn, et al., 2014).

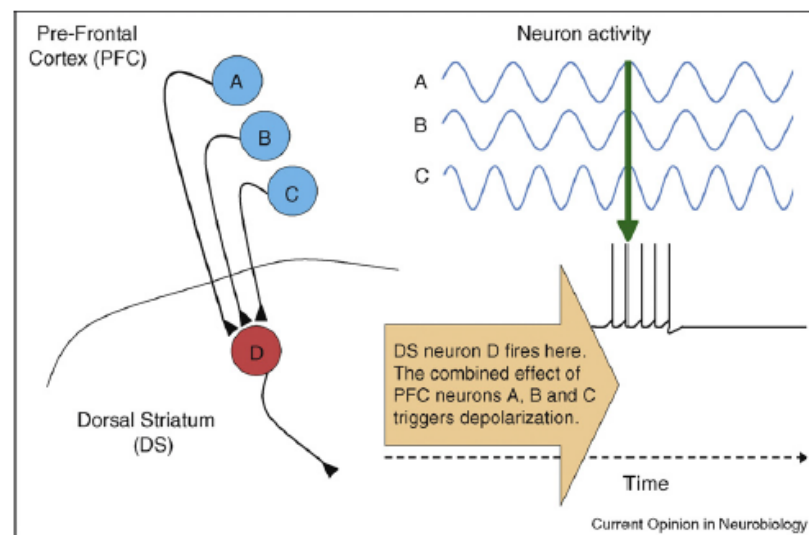


Figure 8. Striatal Beat Frequency Model (Meck et al., 2008, page. 147)

2.5. What is missing in the interval timing literature?

One of the problems of the interval timing literature is that the studies mostly neglect the decision process level of the typical internal clock model and focus on the clock and memory level. Although there are some studies which directly target the decision process in a timing task (e.g. Wearden, 2003, 2004), this level of the internal clock model was not studied as detailed as the clock level or memory level so far. Thus, in the following chapters, decision/comparison related processes form a part of the set of our research questions, especially in chapters 4+5, to target this gap in the interval timing

literature. In fact, this relative ignorance of the decision level of the internal clock within a pacemaker-accumulator framework indicates an erroneously separate conceptualization of the levels in this model. This thesis is an attempt to build an experimental and theoretical connection between these levels by providing both behavioral and neurophysiological evidence. For this purpose, coincidence detection models (e.g. Striatal Beat Frequency) will be discussed as a biologically and conceptually plausible alternative to the traditional pacemaker-accumulator models since the coincidence detection can combine the time keeping and time based decisions in principle by introducing an automatic discrimination process through event detection. Thus, in the chapters in which we will investigate some of the behavioral and neurophysiological markers of these automatic discrimination and expectation processes, we will present a view which will be based on an event based timing mechanism.

CHAPTER 3

EXPECTATION AND INTERFERENCE EFFECTS ON ENCODING OF TIME

This chapter covers the effects of expectation and interference on timing performance within the scope of typical internal clock models of time. The first subject of this chapter is the study of attentional sharing between temporal and non-temporal tasks in a dual task design. The manipulation of the temporal location of the non-temporal task within an interval is chosen as the method for investigating this subject. A manipulation of the temporal location is included for the sake of investigating the effect of expectancy on timing performance. The temporal location effect stands for the higher levels of timing disruption when a concurrent task is present later within an interval than it is presented earlier within that interval. The experimental manipulation is targeting the first level of a typical internal clock model, namely the clock process. In this chapter, the first research question is about the source of the temporal location effect. The question is based on the different predictions of two hypotheses which provide different accounts for the temporal location effect. The first hypothesis is called as “switch hypothesis” (i.e. Fortin et al., 2009) and it is based on the attentional shifts/switches between the concurrent task and timing. The explanation of the temporal location effect in this hypothesis is based on the divergence of attention away from the temporal information towards the concurrent task requirements. However, “attentional time-sharing” hypothesis (Buhusi & Meck, 2006; Buhusi & Meck, 2009a+b) predicts that the source of the timing disruption is the working memory maintenance disruption as a result of time-sharing rather than the attentional switches. Firstly, to test the predictions of these hypotheses, we manipulated expectancy levels by changing the temporal location of the concurrent task within the time interval. The first experiment is designed to establish the disruptive effect of expecting an interference while experiencing an interval by comparing the situations of less extended or more extended periods of expectation. Expectation is related to the preparation for the non-temporal task, and the more a participant has to monitor the approach of the concurrent task that the more the duration of expectation will increase in terms of preparation. For both hypotheses, the preparation requirement for the concurrent task will cause an increase in attention for the concurrent task monitoring, which in turn causes a decrease of attention for timing. In short, one of the aims of the experiments in this chapter is to investigate the expectation in terms of the

predictions of two hypotheses. These two hypotheses have different predictions for the control conditions in which there is no concurrent task and this will be discussed below.

Secondly, the interference effect on the accumulation of temporal signals will be the other subject of these two experiments. To be able to introduce an informative variation on the accumulation, a concurrent task – which is reliably known in the literature in terms of its demand characteristics – is chosen. The presence of at least two types of stimuli in a concurrent task is useful to investigate the interference effect on the accumulation of time signals. By this way, we would have a chance to compare two different types of stimuli, and thus two different levels of difficulty/demands. Moreover, it is also worth to consider the task demand itself independent from the difficulty levels of particular trials by comparing the time estimations of intervals with a concurrent task with a control condition where there is no task interference. Thus, our second aim for these experiments is investigating the connection between the clock level and the memory level. The possible loss of accumulated signals in working memory because of the presence of an interfering concurrent task during timing will therefore be investigated in this chapter. Once more, the loss of accumulated signals will be investigated from either the perspective of divergence of attention from timing to the concurrent task – switch hypothesis – when there is a performance requirement for the concurrent task or from the attentional time-sharing hypothesis perspective which focuses on the maintenance of the temporal information in the working memory. These two hypotheses have different predictions in terms of easy or difficult concurrent tasks which will also be discussed below.

The findings as regards the shared allocation of attentional resources to both timing and the expectation of a non-temporal task stimulus is in line with the internal clock framework (e.g., Brown, 1997; Buhusi & Meck, 2006a+b; Zakay, 2000; Zakay & Block, 1996) and the scalar expectancy theory (e.g., Gibbon, 1977; Gibbon & Church, 1990; Gibbon, Church, & Meck, 1984). This sharing leads to a decrease in the number of accumulated signals for timing which is attributed to the manipulation of the switch part of the clock (Fortin et al., 2009) (Figure 9, red box). Resource sharing between two types of processes – temporal and non-temporal – can be taken as a general point of departure for interpreting dual-task paradigms in which timing is a part. However, a resource sharing should not presume that the only way to divide attention is to introduce a switch between the pacemaker and the accumulator. Switching predicts a change in the accumulation rate (i.e. Fortin & Tremblay, 2006) in the presence of an expectation even in the absence of the occurrence of a gap (i.e. Fortin et al., 2009). Therefore, the switch hypothesis predicts a timing disruption even in the control conditions where there is a concurrent task.

The expectation of a stimulus to be responded to should cause a sharing of attention between the primary timing task and the concurrent task before the appearance of that task. Although the expectation-related disruption of timing that is hypothesized in the context of this chapter does not actually originate from the overlap of two tasks, we can think of this expectancy effect as a resource-sharing between the two tasks, namely timing and the concurrent task. This is because the concurrent task – a Simon task in this case – requires the performance to be as fast and accurate as possible, thus the attentional sharing due to the monitoring of the approaching task can be considered as a sharing of resources already.

1. *Switch Hypothesis*
2. *Attentional Time-Sharing Hypothesis*

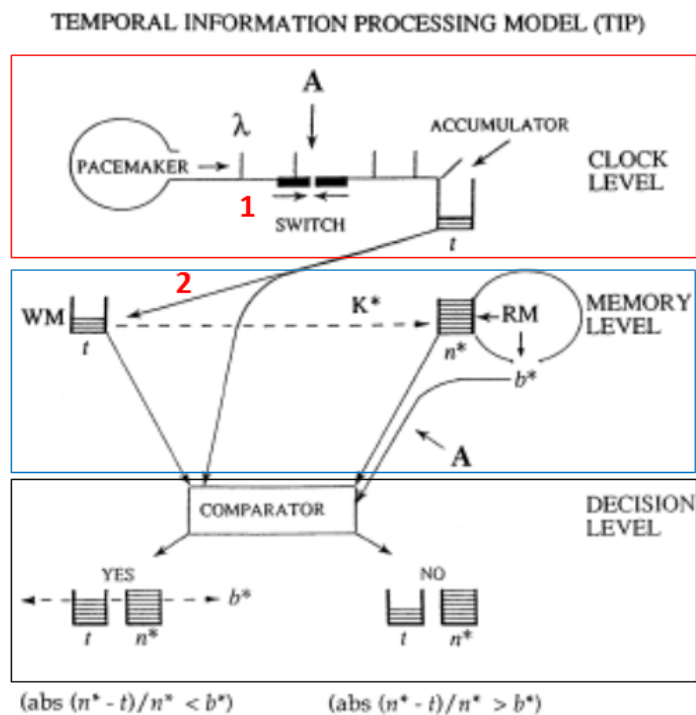


Figure 9. Internal Clock Model in an information processing background (Lejeune, 1998, page. 132).

The second hypothesis, namely the attentional time-sharing hypothesis, can predict the attentional sharing between the two tasks without assuming a switch between the pacemaker-accumulator. The monitoring of the gap/distractor can lead to a resource sharing – both attentional and working memory related – which explains the temporal location effect by referring a memory decay. The timing disruption in conditions where the concurrent task is presented later is based on the working memory decay of the

accumulated temporal information in a proportionate to the length of the already experienced interval. In other words, sharing of resources leads to a less available resources for timing which in turn results a more profound loss of accumulated pulses because of the maintenance disruption in working memory. This account, namely the attentional time-sharing, is based on the interaction of accumulator and working memory in a typical internal clock model (see Figure 9). Thus, it does not predict a timing disruption in the control condition (empty trials) since the loss of accumulated pulses is dependent upon the actual occurrence of the distraction in contrast to the switch hypothesis where the sharing of attention directly affects the accumulation of pulses.

The interference effect on timing is different in nature in comparison to the temporal location effect because it emerges from the requirements of the concurrent task such as perception of color and spatial location, response inhibition and motor responses. This interference is the result of the demands arising by the execution of the task itself. Once again, the two hypotheses – which are distinguished previously in terms of their predictions for temporal location effect – have different accounts for the interference effect. The switch hypothesis predicts that attention shifts from timing to the performance of the concurrent task when it is appeared on the screen. Thus, a disruption in timing is expected when there is a necessity of a concurrent task performance. Moreover, this hypothesis predicts that if the concurrent task takes longer time – because of its difficulty in terms of response – this should be followed by more profound timing disruption in difficult concurrent tasks since the switch is opened longer than the case in which an easier task must be performed. The switch hypothesis is mainly based on the passage of the pulses from a pacemaker to an accumulator, thus the longer distraction in difficult concurrent task should be accompanied by a hindrance of pulse accumulation for a longer duration. In other words, in situations where there is central executive requirement – i.e. difficult task – the shifting back and forth between timing and the concurrent task should lead to a stable divergence of attention during the attentional bottleneck. The reaction time difference between the easier and difficult concurrent tasks – assuming the task needs a resolution of a central conflict – should be totally reflected on timing disruption.

However, the attentional time-sharing hypothesis does not predict a difficulty effect in this extend. Because the interested part of the internal clock model in this account is the relation of accumulator and working memory and the predicted interference effect due to the occurrence of a concurrent task arise from the working memory decay of the already accumulated temporal information. Although the duration of memory decay is longer in the difficult concurrent task than the easier concurrent task, the decay of the temporal information is affected by the total duration of the concurrent task, not just

the duration difference between easy and difficult concurrent task RTs. In other words, the extend of the task difficulty difference in duration is subject to be ignored if one considers the total duration of the concurrent task during an overlap between timing and the concurrent task.

In summary, the two experiments in this chapter are designed to investigate the disruption of timing if there is a concurrent task at different temporal locations of the timing task. Therefore, two different temporal locations are determined for the presentation of the concurrent task within a given interval. These two temporal locations are defined as “early” and “late” since the concurrent task stimuli are given to the participants either early in the time interval or later and closer to the end of the interval. The temporal location effect which is defined above corresponds to the timing disruption in late occurrence of the concurrent task. Besides a temporal location effect, an interference and a concurrent task difficulty effects will be investigated from the perspectives of two hypotheses, namely switch hypothesis and attentional time-sharing hypothesis. We have chosen the Simon task as the concurrent task. Because it has well defined characteristics in terms of response selection requirements which allows us for difficulty related manipulations. The difficulty of concurrent task will be achieved by single trial insertion into a time interval. Given the asynchrony between the start of the interval and the start of the Simon trial, the temporal locations are named as ‘Early SOA’ or as ‘Late SOA’. In addition, as regards with the two different types of stimuli of the Simon task, namely the congruent and the incongruent ones, we will compare the effect of congruency on timing in terms of their different executive demands and difficulty. The congruent trials are considered as easier and the incongruent trials are accepted as relatively difficult in terms of executive demands.

3.1. Experiment-1

A concurrent task besides the primary timing task is necessary to be able to introduce both interference and expectation. We chose the Simon task for its reliability in terms of producing a stable effect (the Simon effect) and its nature which is open to manipulating the ratio of congruent vs. incongruent trials. The Simon effect is the difference in response time to the two types of stimuli, namely congruent and incongruent trial stimuli: congruent stimuli are responded to faster as compared to incongruent stimuli. Although there are no intrinsic differences about these two stimulus types in terms of the relevant stimulus dimension (color), the match or mismatch between the spatial location of the response and the irrelevant stimulus dimension (spatial location) differs for these two trial types. If the response mapping is determined by colors and horizontal dimension of the key presses – e.g., red color/left key press and

blue color/right key press – the overlap between the (irrelevant) spatial presentation of the stimulus (at the left or right) and the (relevant) color mapping corresponds to congruent trials and leads to relatively faster RTs. On the other hand, a mismatch between the color and the location codes of the stimulus corresponds to incongruent trials, which are more difficult to respond to because the automatically triggered response tendency towards the location of the stimulus needs to be inhibited (Simon, 1969). In short, the presence or absence of this task with its different trial types which potentially have different effects on timing, is chosen for the temporal location manipulation. A Simon trial with its particular congruency condition is embedded within an interval at some temporal location. As a timing task, we use the reproduction method. In this method, there are two stages: the initial stage in which participants experience an interval to be re-produced and the second stage in which the participants estimate the interval according to their experience of time by pressing a button two times determining the beginning and the end of the interval. We can place the concurrent task either during the initial stage where the participants experience the length of the interval or during the reproduction stage. In both experiments described in this chapter, the concurrent task is embedded in the experience stage of the reproduction task.

The temporal location manipulation of a concurrent task creates expectancy differences for the non-temporal stimuli (i.e., Casini & Macar, 1997). To test the effect of expectancy on timing, we used two types of SOAs (Stimulus onset asynchrony), namely Late SOA and Early SOA. In addition, we administered an empty interval timing condition in which there is no interference. The hypothesized expectancy-related difference in timing between Early and Late SOA conditions is the one of the focuses in this chapter. Since the task-related demands of the concurrent task will be the same for both expectancy conditions, we will have a chance to compare just the temporal location effect while keeping constant the amount of interference. If there is a temporal location effect as it is hypothesized to cause an underestimation in the encoding stage, this effect should be stronger in late SOA in comparison to early SOA since more pulses will be lost in the late SOA temporal location and, consequently, a lower number of time signals will be accumulated (i.e., Zakay, 1989; Block & Zakay, 2006; Casini & Macar, 1997). However, the mechanisms which are introduced for this loss of accumulated pulses in the temporal location effect differs in the switch hypothesis and attentional time-sharing hypothesis. The switch hypothesis predicts an attentional shift which changes the accumulation rate in the late SOA condition. The monitoring of the concurrent task within an interval in the late SOA condition would lead to more attentional shifts in this condition. Therefore, the accumulation of pulses – which are emitted from the pacemaker – in the late temporal location is more disrupted. After the completion of the concurrent task, the rate of accumulation returns to the normal level. However, the final value of temporal signals

will be lower in the late SOA condition which in turn leads to an underestimation of timing (Figure 10).

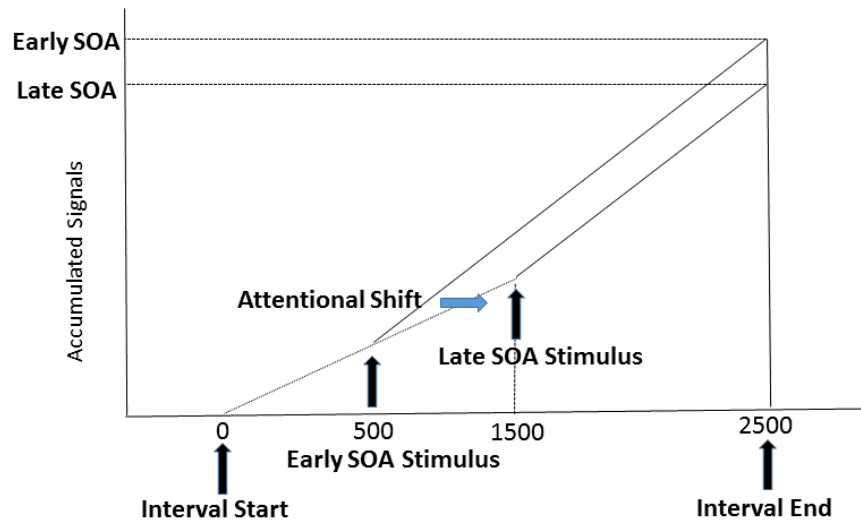


Figure 10. Attentional Shift due to the expectation of the concurrent task at the late SOA temporal location: The accumulation rate turns to its normal range in the late SOA only after the concurrent task performance

This hypothesis has another prediction in terms of the expectation of a concurrent task without its occurrence. In this experiment, the empty trials in which there is no concurrent task are presented in a mixed design, thus the monitoring of concurrent task stimulus is also present even if a particular trial turns out to be a control which does not include a concurrent task. In other words, the switch hypothesis predicts that there should be an underestimation in the empty trials due to an expectation related attentional switches even if there is no concurrent task. This proposed underestimation should be compared to the objective length of an interval because an interval can be reproduced rather more accurately without an expectation related disruption on timing (Figure 11). The same underestimation which is predicted in the late SOA condition is explained by a different mechanism in the attentional time-sharing hypothesis. In this account, the monitoring of the concurrent task in the late SOA condition causes a sharing of both attention and memory resources. However, this resource sharing is not dependent upon a switch (i.e. Buhusi & Meck, 2009a). The passage of the pulses from the pacemaker to the accumulator depends on the context, thus the presence of a concurrent task is necessary to observe a timing disruption. In other words, since the attentional and working memory resources are shared because of the monitoring requirements of the concurrent task, when a distractor – namely the Simon task

– appears, the diminished resources would lead to more disruption in timing in the late SOA condition. Because, the temporal information memory decay would be more profound due to the lack of resources for temporal information maintenance in this condition (Figure 12).

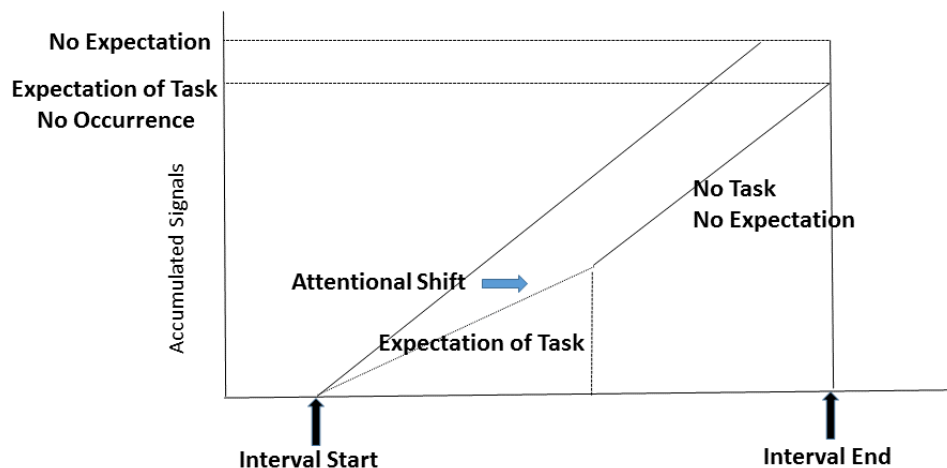


Figure 11. Attentional Shift due to the expectation of the concurrent task without the occurrence of the concurrent task: The expectation of the concurrent task resolves after some point, thus the accumulation rate turns to its normal range

However, this hypothesis does not predict an underestimation in the control trials in which a concurrent task is expected until some point within an interval but does not occur because the timing shrinkage is dependent upon the working memory maintenance disruption not upon the attentional switches. In addition to expectation-related timing inaccuracy, trials with empty intervals, i.e., without a task, will serve as a reference to evaluate the interference effects of the overall task requirements. We expect a break in the accumulation or a loss of accumulated timing signals which results a shorter experience of the interval compared to the experience of an interval without any interruption by a concurrent task. The disruption of timing is hypothesized to lead to a loss of accumulated signals for the overall timing task since the updating mechanism is affected by the abrupt appearance of the concurrent stimuli although it is irrelevant to the timing task. The switch hypothesis explains this interference effect by proposing an attentional switch during the overlap of timing and the concurrent task. Thus, an underestimation is predicted due to a break in the passage of pulses from the pacemaker to the accumulator (Figure 13). Similarly, the switch hypothesis predicts rather more extended underestimation for the incongruent conditions in comparison to the

congruent condition. Since the incongruent trials of Simon task are difficult than the relatively easier congruent trials, they take more time to complete – which leads to a Simon effect – and thus the overlap between the Simon task and timing would be even more disruptive in these trials.

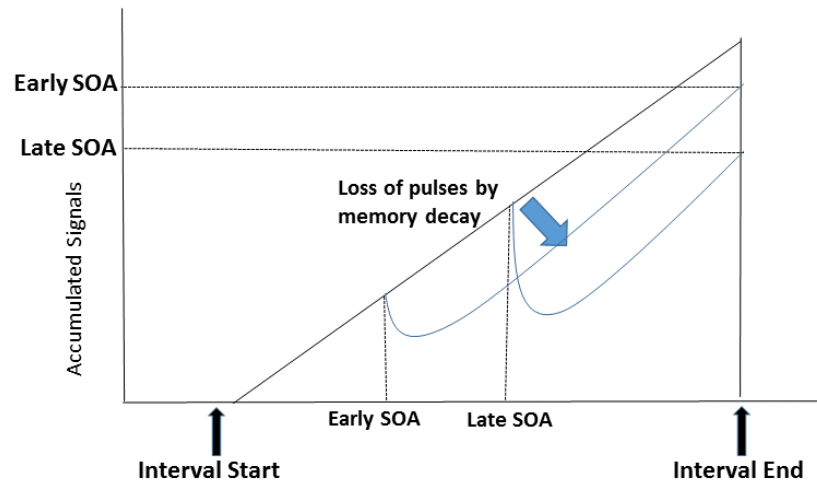


Figure 12. Temporal location Effect by Attentional Time-Sharing Hypothesis which predicts different decay rates for SOA conditions: A more dramatic decay is predicted since there is less amount of attentional resources in the late SOA.

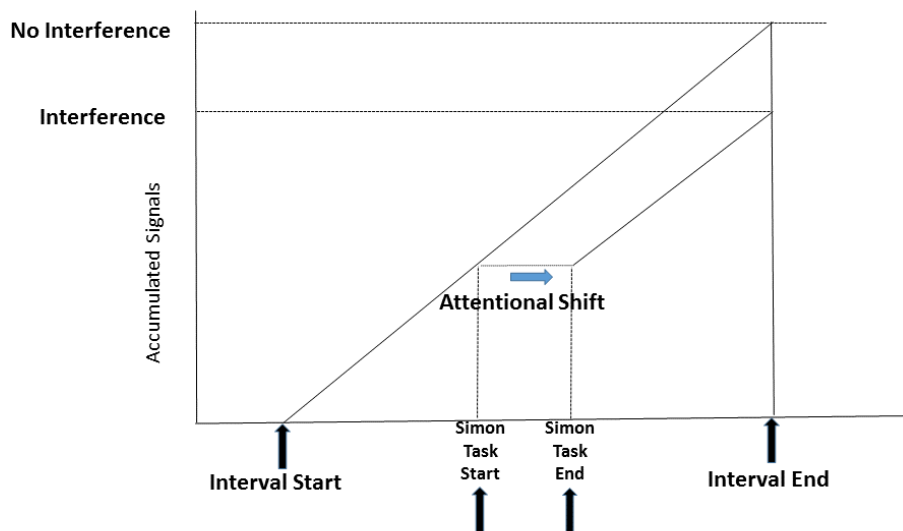


Figure 13. The mechanism which is predicted by the switch hypothesis for the interference effect

More importantly, if we take the nature of Simon task requires an attentional control and this control can be modulated by the working memory capacity and load

(Vandierendonck, 2014) the conflict resolution in the incongruent trials is subject to an attentional bottleneck. Ruthruff & Pashler (2010) propose a similar account in terms of a bottleneck for the concurrent task and timing overlap. Moreover, considering the stable nature of Simon effect although the extend of the effect is subject to be manipulated, the necessity for the response selection in the incongruent trials seems to hold attentional resources until the response conflict is resolved. In other words, if there is an attention switch for this conflict resolution during timing, we should expect an underestimation in timing which should correspond to the extent of Simon effect (Figure 14).

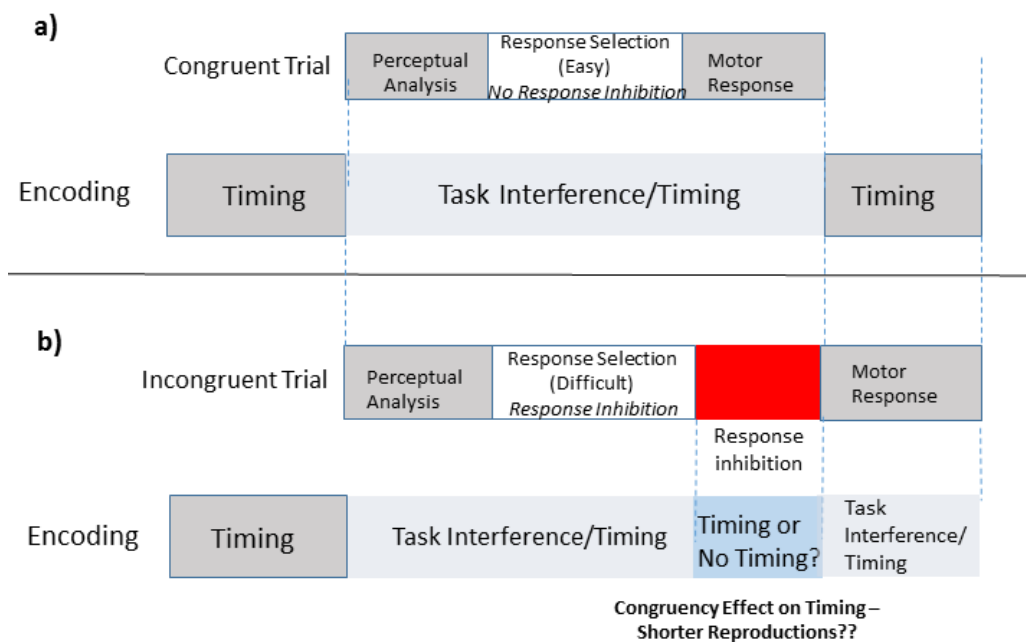


Figure 14. Potential difference between timing in intervals which include the congruent and the incongruent trials: a) The overlap of timing in the encoding stage and the congruent trial of Simon task b) The overlap of timing in the encoding stage and the incongruent trial of Simon task

This line of thinking within the scope of switch hypothesis predicts an elongated overlap between Simon task and timing in the incongruent trials in comparison to the congruent trials, therefore the accumulation of pulses in the congruent trials is more disrupted in the difficult trials in a way corresponding to the duration of Simon effect (Figure 15). On the other hand, the interference effect is explained by a working memory decay in the attentional time-sharing hypothesis.

The requirements of the concurrent task cause a loss of accumulated pulses during the overlap of two tasks.

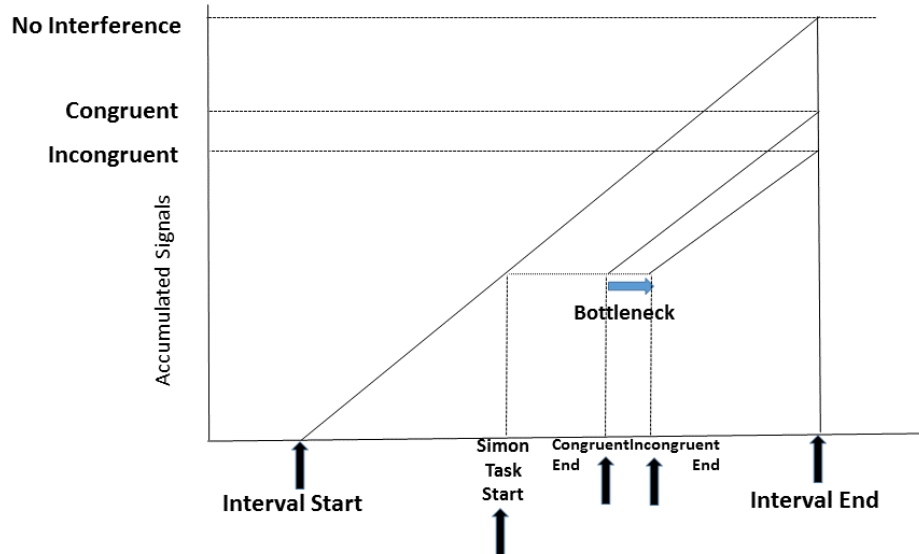


Figure 15. The Prediction of Switch Hypothesis on Congruency: A bottleneck due to the attentional shift for the conflict resolution in the incongruent trial causes more disrupted pulse accumulation.

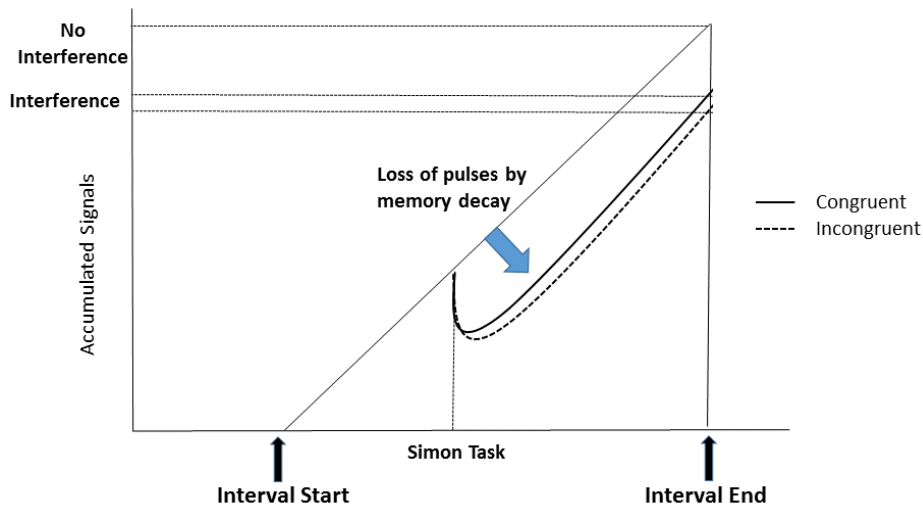


Figure 16. Congruency Effect Prediction by Attentional Time-Sharing Hypothesis with the same memory decay rate with slightly differing duration

However, this hypothesis has a different prediction for the difficulty of the concurrent task. In this hypothesis, the incongruent trials do not have to lead to a more disrupted timing in comparison to the congruent trials. Because, the predicted effect of interference is expected to be dependent upon the already accumulated pulses in

contrast to the prediction of switch hypothesis which predicts a break in the accumulation of pulses during the task overlap. The amount of accumulated pulses would be the same for both types of congruency conditions. In this account, the duration of memory decay would be longer in the incongruent trials than the congruent trials. However, since the loss of pulses is not dependent upon a strict bottleneck as in the case of switch hypothesis, we expect no clear differences between incongruent and congruent conditions. The memory decay of temporal information is dependent on the total duration of overlap between timing and Simon task, thus the additional effect of longer overlap in the incongruent trials is subject to be ignored within the total overlap of Simon task (Figure 16).

3.1.1. Participants

A total number of 15 subjects participated in this study voluntarily. (Mean age=25.3, $SD=3.6$). All subjects had normal or corrected-to-normal vision. The study is approved by the Ethics Committee at METU.

3.1.2. Experimental Procedure

The experiment was run in a silent room at METU and conducted with E-prime 2.0. It started with a practice stage including 12 trials for one sample duration length (2750 msec). The purpose of the practice stage was to familiarize participants with the subsequent experimental block by covering each SOA condition and timing with and without a concurrent task. In the test stage, a total of 180 trials are randomly presented to the participant. The three independent variables – each having multiple levels – were *congruency* (congruent/incongruent/NoSimon), *SOA* (Early/Late) and *durations* (2000, 2500 and 3000 msec). Please notice that by referring congruency condition it is meant ‘time reproductions’ with different congruency situations, it should not be taken as RTs of Simon task. Each of the levels with a concurrent task consisted of 60 trials which makes a total number of 180 trials, including empty trials. All participants were instructed not to count loudly or silently and not to use any strategy during their performance, and they were told that the experiment was about their experience of time.

3.1.2.1. Encoding Stage of an Interval

In the procedural flow of a trial in the Early SOA condition, a fixation cross specifies the beginning of an interval and stays on the screen for a brief duration (500 msec). Then, the concurrent task stimulus appears on the left or right side of the screen while the fixation cross is still on the screen. The participants are expected to perform the concurrent task, namely the Simon task, while they are still keeping track of the passage of time.

3.1.2.2. Simon Task Mapping Rules

We defined the mapping rules between color and the required key press as follows: “red-left/blue-right”. The subjects are instructed to ignore the spatial location of the stimulus on the screen which means that the spatial location was task-irrelevant. They must react to the stimuli in accordance with the pre-specified rule as quickly and as accurately as possible (Figure 17).

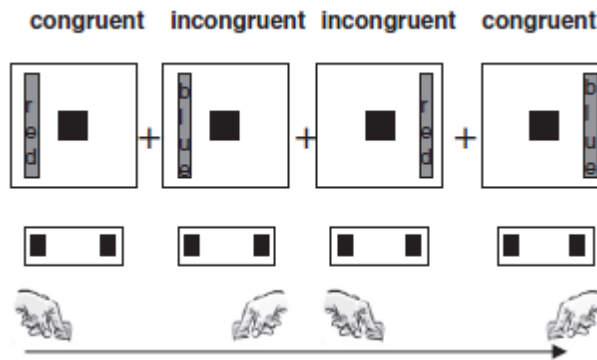


Figure 17. The Color and key mappings of the Simon Task which had to be performed during the encoding stage of the timing task (Duzcu & Hohenberger, 2014, page 38)

The percentages of the two task conditions (congruent/incongruent) are equal in the classical Simon Task (50%- 50%). Although a particular reproduction of an interval includes only one instance of the Simon task stimuli, the percentage of the overall Simon task conditions has an effect on the timing. In order to keep the difficulty of the concurrent task is in its normal range, we therefore preferred the classical proportion of congruent/incongruent cases in this experiment. However, notice that the percentage of congruency is an experimental variable in the second experiment.

3.1.2.3. Reproduction Stage of an Interval

The disappearance of the fixation cross indicates the end of the time interval. It is followed by the appearance of the text (“Start”) on the screen. When the participants see the “Start” signal, they press a predefined key to start their re-production of the experienced duration. After this key press, a black square is presented at the middle of the screen as the visual counterpart of the passage of time, and different from the fixation cross of the encoding stage. A different stimulus (black square) other than the fixation cross was preferred in order to avoid a possible confusion as regards the two different stages of a trial. For finishing their estimation, they pressed the same key with

which they had started the reproduction interval once more. A text display (“New Trial”) is presented for one second on the screen to warn the participants of a new trial. An example of a trial with an Early SOA is visualized below (Figure 6). The temporal location was different for the Late SOA condition but always occurred 1000 msec before the end of the interval. Therefore the specific SOAs in this condition are variable because of the different lengths of the intervals used in the experiment. These varying SOAs are 1000, 1500 and 2000 msec for the three duration types of 2000, 2500 and 3000 msec, respectively. The structure of a trial in this SOA condition is the same as in the previous condition except for the place of Simon task stimulus (Figure 18).

3.1.3. Results

Linear mixed effect models are used for the analysis because of its superiority in accounting for the individual trial variations, not just the means of the conditions, while calculating the effects. It allows to eliminate a particular independent variable if it has no effect on the dependent variable. The elimination method is used to simplify the full models by discarding those independent variables or interactions between variables that do not explain a significant amount of variance in the data. The selection of the superior model is done by considering both Akaike Information Criterion (AIC) and the log likelihood in the comparison of any two models.

3.1.3.1. Time Reproduction Analysis

Reproductions less than 800 msec and more than 4200 msec (% 3), reproductions that have incorrect Simon task responses (% 3.3) and reproductions that have no Simon task responses (% 4) are removed from the data analysis. In the full model, three independent variables and their three-way interaction are included. The dependent variable is the ratio of reproduced estimations and the corresponding duration length. One of the independent variables is temporal location which has two levels: Early SOA, late SOA. The second variable is congruency which has three levels: Congruent, incongruent and NoSimon. As last variable in the analysis, interval length is added – not as factors that includes three levels of different intervals but by coding them as -1, 0 and 1 from the shortest interval to the longest one since duration length is added as continuous variable not as factors. The comparisons which are based on the AIC reveal that the full model is not better than the model which discards the three-way interaction of duration length with the other two variables ($\Delta AIC = 1.8$; $\chi^2 = 0.17$, $p = .67$).

Moreover, we have found no effect of two-way interaction between congruency and duration length ($\Delta AIC = 1.8$; $\chi^2 = 0.08$, $p = .77$) and two-way interaction between SOA and duration length ($\Delta AIC = 0.7$; $\chi^2 = 3.3$, $p = .19$).

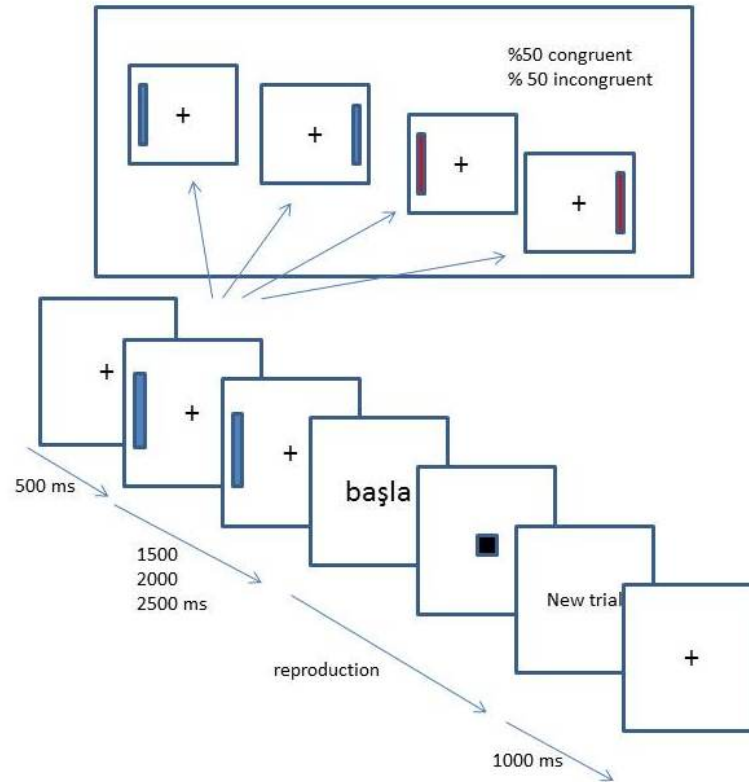


Figure 18. Experimental Flow of an Early Interference Condition (Experiment-1): Early SOA for 3 different intervals (2000, 2500 and 3000 msec)

In the final model (Table 1) in which the intercept term corresponds to the congruent Late SOA condition, this intercept effect is significant ($\beta = 0.97$, $p < .001$). Furthermore, the congruent trials at Early SOA condition are less underestimated than the ones at the Late SOA condition ($\beta = 0.06$, $p < .001$) (Figure 19). The duration length effect was significant, indicating more underestimation at longer intervals ($\beta = -0.065$, $p < .00$). (Table 1). Although there was no two-way interaction between SOA and duration length, we calculated the SOA effect in msec for each interval. For each interval, namely 2000-2500-3000 msec, the mean SOA effect was 62 (0.031×2000), 98 (0.039×2500) and 249 (0.083×3000) msec, respectively.

In terms of ratios, the overall ratio difference of early – late SOAs (0.051) was distributed over the different intervals as 0.031, 0.039 and 0.083 (see Table 2) (see Appendix A for the analysis of duration length-SOA interaction in raw reproductions).

Table 1. Linear Mixed Effect Model: Beta Values of Task, Temporal location and duration length effects of a concurrent task on timing (Exp-1)

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	9.713e-01	4.276e-02	1.430e+01	22.717	1.30e-12
incongruent	2.514e-03	8.723e-03	2.310e+03	0.288	0.773
NoSimon	2.870e-02	4.052e-03	2.311e+03	7.082	1.88e-12
Early SOA	5.688e-02	1.224e-02	2.310e+03	4.648	3.54e-06
durR	-6.545e-02	6.047e-03	2.310e+03	-10.823	< 2e-16
congruency:Early	1.347e-03	1.221e-02	2.310e+03	0.110	0.912

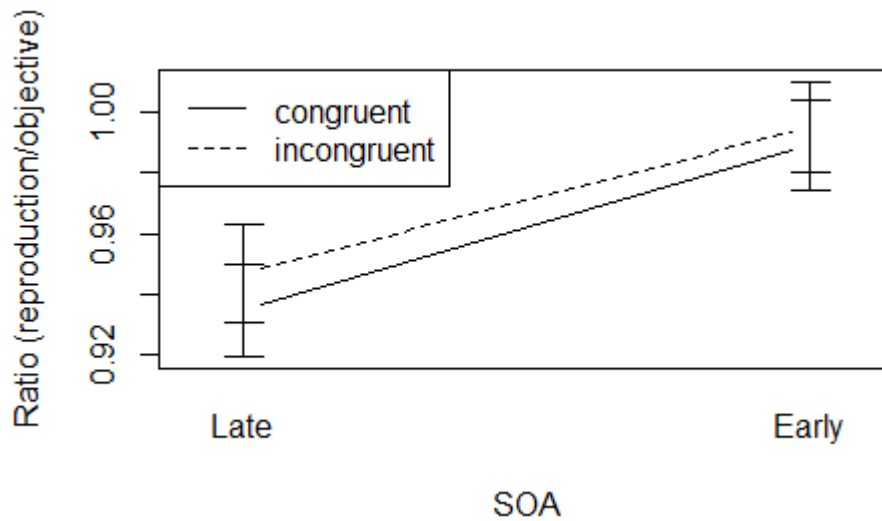


Figure 19. Effects of Congruency and SOA on time reproductions. Error bars represent Standard Error (SE)

The interaction between congruency and SOA terms was not significant ($\beta = 0.001$, $p = .91$). A Helmert contrast revealed that the reproductions of empty trials (NoSimon condition) turned out to be longer than the reproductions that include a concurrent task in the congruent condition ($\beta = 0.03$, $p < .001$) (Figure 20).

However, we found no main effect of congruency which means that reproduction ratios of congruent and incongruent trials were the same ($\beta = 0.03$, $p = .77$) (see Table 2 for descriptive statistics).

Table 2. Descriptive Statistics of ratios (reproduction/objective duration) for Congruency and SOA conditions

SOA	congruency	ratio (rep/obj)	SE
Early	congruent	0.989	0.015
Late	congruent	0.935	0.015
Early	incongruent	0.995	0.015
Late	incongruent	0.947	0.016
NoSimon		1.026	0.0010
Early – Late SOA ratio difference = 0.051			
Overall Early–Late SOA Reproduction difference = $0.051 \times 2500 = 128$ msec			

Congruency Manipulation on Time Reproductions

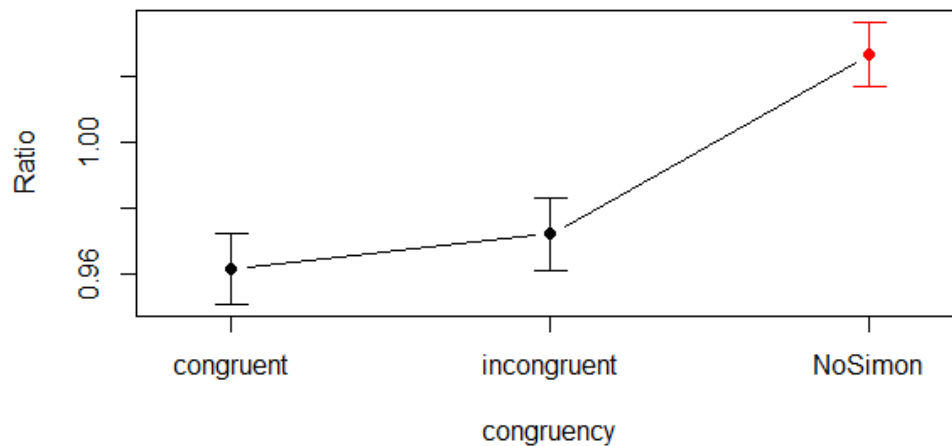


Figure 20. The effect of Congruency on time reproductions with three levels: Congruent, incongruent and empty trials. (Error bars: SE).

We can calculate the approximate differences in milliseconds between any levels by using the intercept and the respective β values. For instance, the intercept corresponds to the congruent trials at the late SOA condition covering all three intervals. The difference between reproductions in the early and late SOA condition corresponds to the effect of expectancy.

3.1.3.2. Simon Task Analysis

Incorrect responses of Simon task are removed from the data analysis (% 6). Beside the results of the primary task – the temporal reproductions – also the results of the concurrent task – the Simon task – are of interest here. Note that the Simon effect is the difference in response times between incongruent and congruent trials. The full model for the analysis of the Simon effect includes the following three variables: congruency with two levels (congruent, incongruent), SOA again with two levels (early, late) and duration length (2000-2500-3000 msec) together with their three-way interaction. In addition, in this analysis a further independent continuous variable (Trial number) is added to capture the potentially growing expertise at the Simon task throughout the experiment.

Table 3. Linear Mixed Effect Model: Beta Values of the Simon effect (Exp-1)

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	771.36772	32.83114	17.00	23.495	2.20e-14
Late	-39.46561	11.22936	1509.50	-3.515	0.000454
incongruent	27.21252	11.26081	1509.20	2.417	0.015786
durR	19.67266	4.99946	1509.30	3.935	8.70e-05
Trial	-0.42405	0.07763	1510.70	-5.462	5.49e-08
Late: incongruent	-16.41903	16.08727	1509.20	-1.021	0.307597
SOA = Early:					
contrast	estimate	SE	df	t.ratio	p.value
incongruent – congruent	27.21252	11.26087	1506.1	2.417	0.0158
SOA = Late:					
contrast	estimate	SE	df	t.ratio	p.value
incongruent - congruent	10.79350	11.49268	1506.1	0.939	0.3478

The reduced model (Table 3) which lacks the interaction of duration length with the other two multiple leveled variables is appropriate to go on with the analysis ($\Delta AIC = 1$; $\chi^2 = 4.4$, $p = .22$). When we remove the Trial order variable, this has a significant effect on the model, thus we decided to keep this variable throughout the further analysis ($\Delta AIC = 17$; $\chi^2 = 29.6$, $p < .001$).

The final model in which the intercept effect – which corresponds to the congruent condition at Early SOA – is significant ($\beta = 771.43, p < .001$). This result shows that the RTs at late SOA are shorter than the RTs at early SOA for congruent trials ($\beta = - 39.4, p < .001$).

Table 4. Descriptive Statistics of Simon RTs for congruency and SOA conditions

congruency	SOA	Reaction Time (msec)	SE
congruent	Early	727.4	11.1
incongruent	Early	753.9	12.3
congruent	Late	670.1	7.8
incongruent	Late	685.7	6.9

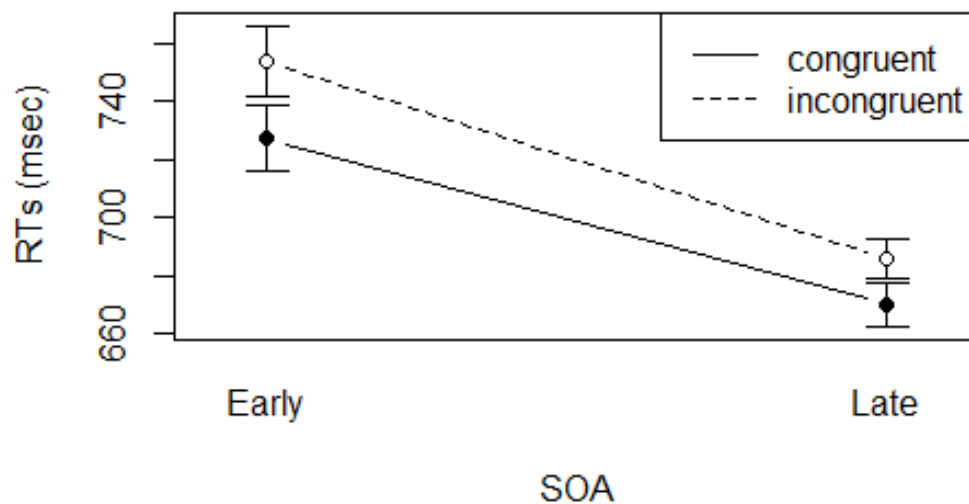


Figure 21. Reaction times for two different temporal locations of the Simon task: Early and Late SOAs for each type of congruency condition: congruent, incongruent (Error Bars: SE).

Moreover, incongruent trial RTs are longer than congruent RTs ($\beta = 27.2, p < .05$) at Early SOA. Post-hoc tests revealed that the difference between congruent and incongruent reproductions is not significant at late SOA (estimate = 10.7, t ratio = 0.93, $p = .34$) (Figure 21).

Trial number had a speed-up effect on the Simon task RTs ($\beta = - 0.42, p < .001$) – which indicates faster RTs with increasing trial numbers – and duration length significantly

affects Simon task RTs resulting in longer RTs at longer intervals ($\beta = 19.6, p < .00$) (Table 3). See Table 4 for the descriptive statistics.

3.1.4. Discussion

Attentional interruptions during a timing task (e.g., Fortin & Tremblay, 2006; Fortin et al., 2009) are suggested to explain the underestimation of intervals when there is a concurrent task towards the later temporal locations of an interval. The interval is perceived as shorter when an interference/second task is expected as compared to a condition without an expectation of this kind. One possible mechanism is favored by the switch hypothesis in which timing disruption is a consequence of attentional shifts between keeping track of time and monitoring of the non-temporal task stimuli (Fortin et al., 2009). Attentional shifts from the passage of time to the monitoring the concurrent task stimulus can be imagined as a change in the slope of accumulation (see Figure 10). Thus, expectation (i.e., late SOA) decreases the slope of accumulation by causing a deviation from the actual number of accumulated signals in the absence of any expectation. Indeed, our results showed a loss of accumulated signals at late SOA of approximately 150 msec on average as a result of attentional shifts during the expectation prior to the concurrent task.

However, this mechanism is not sufficient to explain the absence of any underestimation in the empty trials in which there is no concurrent task but an expectation is present until the point where the concurrent task appears in the late SOA condition even if there is no occurrence of Simon task in these trials. Although, Fortin et al. (2009) provided that the effect of gap expectation cause timing disruption even if the gap does not occur within an interval, our results do not indicate this situation. On the other hand, our results are in line with the prediction of attentional time-sharing hypothesis since the loss of pulses in timing is based on the occurrence of a gap/distractor. The introduction of a second task or gap during timing give rise to a working memory decay during this break. Moreover, the extent of the decay is proportional to the duration in which the concurrent task is expected because a resource sharing is necessary for the monitoring of the concurrent task in the late SOA condition during this expectation duration (see Figure 12). However, this hypothesis does not predict a working memory decay (i.e. Buhusi & Meck, 2009a+b) in the presence of a concurrent task expectation without its occurrence. Indeed, our results showed that empty trials are reproduced closer to the objective length of the intervals which indicates no underestimation even there is an expectation which is similar to the late SOA condition.

The difference in findings of Fortin et al. (2009) and our results might be explained by the average location of the gap and/or concurrent task. In their experiment (Exp-2-Fig-

3), it is possible to observe a difference between 75% condition (gap location within the interval) and no gap condition due to the run mode (even if there is a gap) in the % 75

gap location condition since it is close to the end of the interval or the remaining part of the interval after the gap might be added – after the reset of the clock – by a simple addition to the previously accumulated part. Indeed, Van Rijn & Taatgen (2008) suggests that simple additions can cause biases if the pacemaker is non-linear. For instance, in an already started pacemaker, the frequency of pulses decreases until the gap location in a % 75 condition, however if there is a simple addition of the post-gap duration this indicates a reset in the clock at the gap location. This would be cause a relative increase in the estimate since more pulses accumulated in the post-gap duration in contrast to the actual value it should be. Therefore, more pulses are added to the pre-gap duration to reproduce the experienced duration in the % 75 condition. This bias can explain the relatively overestimated intervals in the 75 condition of Fortin et al (2009) study. However, in our experiment, the late SOA condition is not that close to the end of the interval in terms of the relative percentages of the interval. The average late SOA duration was approximately % 60 of the total duration. Thus, it is unlikely to reset the clock in our experimental design and this makes it free of simple temporal additions.

An alternative explanation for the temporal location effect might be a clock onset related disruption on timing instead of an expectation related resource sharing. An interval onset disruption may cause an aroused state in the Early SOA trials which can lead to a faster signal emitted from the pacemaker. Indeed, Matthews & Gheorghiu (2016) mention some studies which indicate that an unexpected stimulus may cause pacemaker acceleration (e.g. Tse et al., 2004; New & Scholl, 2009). In this alternative explanation, if we assume that there is no expectation effect but just a pacemaker acceleration in the Early SOA in comparison to the late SOA, we should expect an additive effect in proportion to the duration length. We found a 62 msec SOA effect in the shortest duration (2000 msec). A possible pacemaker acceleration effect in the middle interval length (2500 msec) and the longest interval (3000 msec) should be proportional to the difference in their length, respectively. For instance, in the longest interval, the predicted SOA effect should include an extra effect which corresponds to the half of the 62 msec found in the shortest duration assuming the pacemaker emits signals linearly. However, we found a quite extended SOA effect in the longest interval which is around 249 msec. This extended effect suggests a multiplicative effect which is in line with an expectation related interpretation instead of a pacemaker based explanation since the attentional time-sharing account is based on a memory decay function which can be exponential or

logarithmic (see Staddon & Higa, 1999) and has a multiplicative property. In the attentional time-sharing account, the expectation effect is associated with the monitoring requirement of the approaching task and thus the duration during which the

participants were expecting a concurrent task stimulus can be taken as the late SOA duration in each interval assuming they did not have enough time to build an expectation at early SOA conditions. Thus, for each interval from the shortest to the longest, the expectation length was 1000, 1500 and 2000 msec, respectively. In this picture, the memory decay should be twice in power in the longest interval since the duration of expectation was twice in comparison to the shortest interval. Assuming the decay function is multiplicative, we should expect an exponential like loss of pulses at the longest interval. Indeed, the SOA effect was found to be 249 msec which fits this interpretation since the SOA effect in the shortest interval was only 62 msec.

Moreover, we have found that a speeding-up of the Simon task RTs (see Figure 21) and this supports the resource sharing between the Simon task and timing. The Simon RTs are shorter when the Simon Task occurs later within the interval (late SOA) than the reaction times at early SOA. This effect can be called “preparation effect” and it is an indicator of the monitoring of approaching stimulus. The stronger you expect the stimulus to arrive as time advances, the better you are prepared and the faster you are able to respond to it. In addition, the results show that there is a difference between incongruent and congruent conditions of the Simon task at the Early SOA condition – namely the Simon effect – as in a standard Simon task. However, we did not find a Simon effect at the late SOA condition which suggest that the preparation effect eliminated the Simon effect at the late SOA. This finding can indeed be claimed to be a marker of monitoring the concurrent task-related response options. Thus, the expectation which corresponds to the preparation for the Simon task at the late SOA is a candidate for the explanation of the temporal location effect on timing. This preparation effect is consistent with both hypothesis, namely the switch and attentional time-sharing since they both predicts a monitoring effect thus a better performance in the Simon task even though their explanations for the timing disruption differs.

In addition to that, the results suggest that the higher RTs in the incongruent Simon condition at Early SOA (as compared to the congruent condition) have no effect on the overall timing performance. In other words, we did not observe a congruency effect on timing performance: the same amount of underestimation occurred in both congruent and incongruent conditions (see Figure 20). Thus, we can claim that although the incongruent trials of the concurrent task show worse performance as an indication of task difficulty, this concurrent task difficulty did not cause any disruption of the timing task. The fact that the interference of the Simon task is not specific to one particular type

of congruency suggests that the response selection demands, namely the inhibition requirements, of an incongruent trial does not have an additional effect on timing besides the overall response requirement of the task. The absence of congruency effect

on timing supports the prediction of the attentional time-sharing hypothesis rather of the switch hypothesis. Because, in the switch hypothesis, the longer duration of overlap

between the Simon task – incongruent trials to be precise – and timing would be reflected in the timing disruption as an underestimation which should correspond to the Simon effect length because of the attentional bottleneck (see Figure 15). However, our results did not provide an evidence for this carry over effect (i.e. Ruthruff & Pashler, 2010) from the Simon effect to the time estimations. On the other hand, time-sharing hypothesis is compatible with this finding since the duration of the decay for both incongruent and congruent trials do not change in a significant way if one considers the total duration of the concurrent task and timing overlap as a source of the memory decay. In brief, the absence of congruency effect also supports the working memory decay mechanism of the attentional time-sharing hypothesis. However, since the extent of Simon effect is around 30 msec in average, we should further investigate the issue to eliminate the switch hypothesis. For this purpose, the second experiment aims to increase the Simon effect in length. Moreover, the absence of Simon effect in the late SOA condition should be also dealt with to prepare a better experimental design. By this way, a creation of a potential more deepened attentional bottleneck between the incongruent trials of the Simon task and timing can be achieved.

Our finding is consistent with Ogden et al. (2014)'s study because the results indicates that reproduction of a time interval relies mainly on updating, access and shifting processes but not inhibition requirements. In line with this finding, response selection in incongruent trials requires inhibition of the automatically triggered response tendency in these trials, and we found no difference for the reproductions of the intervals that include either type of Simon task stimuli. The general interference of the concurrent task during the encoding stage of a reproduction task is evident in both types of trials and can be addressed as 'overall task effect'. The hypothesis which states that the memory updating tasks affect the updating mechanism of timing (i.e. Ogden et al. 2011) is in line with our results as well. Miyake et al. (2000) defines updating mechanism as an online process and the overall concurrent task effect is based on the disruption of this updating mechanism. Our findings provided evidence in support of the working memory decay mechanism to explain the disruption in the updating mechanism of timing (see Figure 16). However, the finding of a relatively weak Simon effect and the fact that this effect was found only for the Early SOA indicates a need for further investigation. Therefore, we decided to conduct a second experiment to investigate a possibly unnoticed effect of congruency in a design in which the Simon effect is more profound.

In conclusion, this experiment revealed the that both the temporal location of the concurrent task within the time intervals and overall task requirements cause a

disruption on timing which manifests itself as an underestimation of the intervals. More importantly, attentional time-sharing hypothesis predictions are found to be better in

comparison to the switch hypothesis predictions with regards to the findings about the control condition and the congruency effect. Following up on these results, a second experiment is conducted with quite the same design except for the proportion of congruent and incongruent trials which will be changed. A further support in favour of the attentional time-sharing can be obtained by a further investigation of the congruency effect. The attentional control which explains the Simon effect will be augmented by changing the frequency of the incongruent trials within the total number of Simon task trials.

3.2. Experiment-2

In Experiment-2 the percentage of incongruent trials are decreased to 20 % of all trials of the concurrent task. This manipulation is expected to affect the overall preparation requirements of the Simon task and thus enhance the Simon effect. If it is the case that the inhibition effect of the concurrent task could not be observed because of a relatively weak Simon effect in the previous experiment, this change is expected to influence timing. The less frequent number of incongruent trials would increase the inhibitory burden on these rather unexpected trials and increase their RT. This increase would affect the late SOA condition which did not show a Simon effect in Experiment-1. Furthermore, the increase of the inhibition requirements would be expected to increase the attentional bottleneck, thus we should catch an underestimation in the timing task in the same extent with the observed Simon effect.

The attentional time-sharing hypothesis predicts that this rare occurrence of the incongruent trials is hypothesized to affect only the concurrent task performance but not the timing accuracy related with the disruption arising from the appearance of the incongruent trials. However, the switch hypothesis predicts that attention should be diverted away from timing towards the incongruent stimulus of Simon task since it is now rare and it captures more attention. In other words, the appearance of this divergent concurrent task stimulus would lead to a more profound attentional shift which in turn is expected to lead a more disrupted timing in the incongruent trials.

The overall number of timing trials which include a concurrent task (both congruent and incongruent trials) is the same as in the previous experiment, since we only decrease the percentage of incongruent trials in the total number of trials that include a concurrent

task. Therefore, we hypothesize that the change of the percentage of incongruent trials in the concurrent task would not give rise to any different extent of monitoring of the Simon task stimuli and thus we expect approximately the same degree of the temporal

location effect which is in line with both switch hypothesis and attentional time-sharing hypothesis.

3.2.1. Participants

A total number of 14 subjects participated in this study voluntarily. (Mean age=26.7, SD=2.8). All subjects had normal or corrected-to-normal vision.

3.2.2. Experimental Procedure

The experimental procedure was almost the same with the previous design. The practice stage with only one sample interval length was performed to familiarize participants with the experimental flow. The interval length in the practice stage was different from the ones that are used in the experimental block, though. In the experimental stage, each level of temporal location had 60 trials including the empty trials which had no concurrent trials in them, which makes 180 trials in total. Each temporal location condition had either a congruent or incongruent Simon task stimulus, according to the percentage of incongruent trials (20 %). All participants were instructed not to count loudly or silently and not to use any strategy during their performance, and they are told that the experiment was about their experience of time.

3.2.2.1. Encoding Stage of an Interval

In the procedural flow of a trial with the Early SOA condition, a fixation cross specifies the beginning of an interval and stays on the screen for a brief duration (500 msec). Then, the concurrent task stimulus appears on the left or right side of the screen while the fixation cross is still on the screen. The participants are expected to perform the concurrent task, namely the Simon task, while they are still keeping track of the passage of time.

3.2.2.2. Simon Task Mapping Rules

The Simon task requirements are same as in the previous experiment and thus the color red is associated with a left press of a key while the appearance of the blue color requires a right key press. Participants are instructed to ignore the spatial location of the stimulus on the screen which means that the spatial location was task-irrelevant. They have to react to the stimuli in accordance with the pre-specified rule as quickly and as accurately as possible.

The key difference which relates to the rationale of this experiment is the percentages of congruent and incongruent trials. As opposed to the equal percentages of the congruent

and incongruent trials in the classical Simon task (50 % - 50 %), this percentage is different in the current experiment, namely 80 %-20 %, respectively.

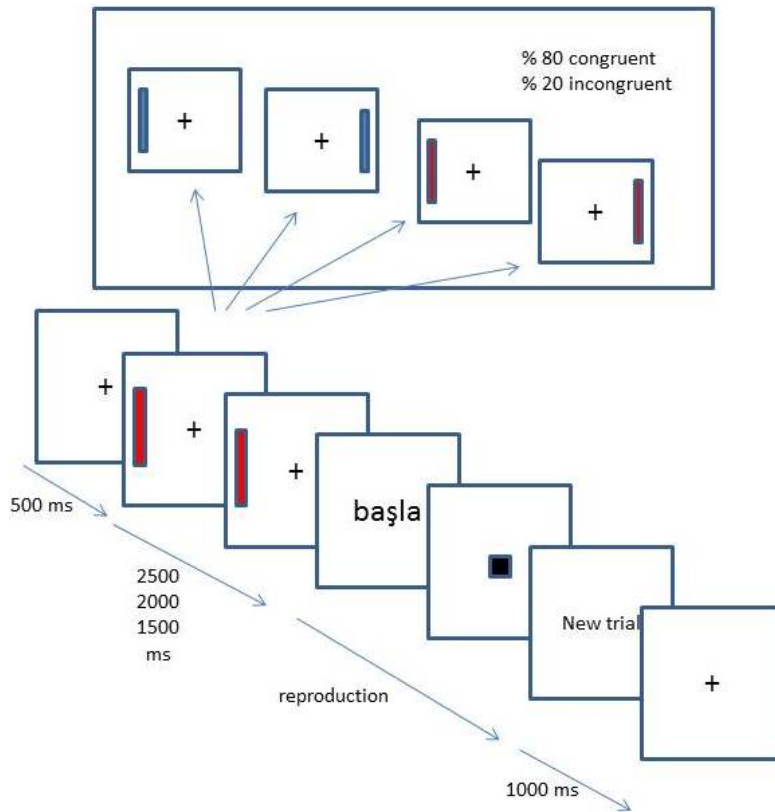


Figure 22. Experimental Flow of a trial in the Early Interference Condition with different percentages of congruency, namely 80 % congruent and 20 % incongruent trials (Experiment-2).

Although a particular reproduction of an interval includes only one instance of a Simon task stimulus, the percentage of the overall Simon task conditions has an effect on timing. Therefore, in this experiment, our manipulation of the percentages changes the difficulty of the incongruent trials which is expected to be reflected in the attentional bottleneck extent. For a visualization of the experimental flow with different percentages of Simon task stimuli in the Early SOA condition as an example, see Figure 22).

3.2.2.3. Reproduction Stage of an Interval

The disappearance of the fixation cross indicates the end of the time interval and is followed by the appearance of the text ("Start") on the screen. When participants see

the signal (“Start”) to begin their estimation, they press a predefined key to start their re-production of the previously experienced duration. After this key press, a black square

is presented at the middle of the screen as a visual counterpart of the passage of time, corresponding to the fixation cross of the encoding stage. A different stimulus (black square) than the fixation cross is preferred in order to avoid any confusion as regards the different stages of a trial. So, in the reproduction stage, participants are waiting for a certain time until they think the previously experienced duration has elapsed and finish their estimation by pressing the same key with which they started the reproduction. A text display (“New Trial”) is presented for one second on the screen to warn the participants of a new trial. The temporal location was different for the Late SOA condition but always occurred 1000 msec before the end of the interval. Therefore the specific SOAs in this condition are variable because of the different lengths of the intervals used in the experiment. These varying SOAs are 1000, 1500 and 2000 msec for the three duration types of 2000, 2500 and 3000 msec, respectively. The structure of the trial flow at this SOA condition is the same as in the previous condition except for the temporal location of the Simon task stimulus within the interval.

3.2.3. Results

Linear mixed effect models are used for the analysis because of its superiority in accounting for the individual trial variations, and not just for the means of the conditions, while calculating the differences. The elimination method is used to simplify the full models by discarding those independent variables or interactions between variables that do not explain a significant amount of variance in the data. The selection of the superior model is done by considering both AIC and log likelihood in the comparison of any two models.

3.2.3.1. Time Reproduction Analysis

Reproductions less than 800 msec and more than 4200 msec (2.6 %), reproductions that have incorrect Simon task responses (1 %) and reproductions that have not Simon task responses (1 %) are removed from the data analysis). In the full model, three independent variables and their three-way interaction are included. The dependent variable is the ratio of reproduced estimations and their corresponding duration length.

The first independent variable is temporal location which has two levels (Early SOA, late SOA). The second variable is congruency which has three levels (congruent, incongruent and NoSimon task). As for the last term in the analysis, interval length is added but not as a factor that include three levels of different intervals but by coding them as -1, 0 and 1 from the shortest interval to the longest one.

Table 5. Linear Mixed Effect Model Beta Values of Task and Temporal location effects of the concurrent task on timing (Exp-2).

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	9.250e-01	5.430e-02	1.330e+01	17.034	2.08e-10
incongruent	6.848e-05	1.003e-02	2.352e+03	0.007	0.994
NoSimon	3.859e-02	4.182e-03	2.352e+03	9.228	< 2e-16
Early	4.790e-02	1.397e-02	2.352e+03	3.429	0.00061
durR	-8.349e-02	5.397e-03	2.352e+03	-15.471	< 2e-16
congruency:Early	5.031e-03	1.397e-02	2.352e+03	0.360	0.71877

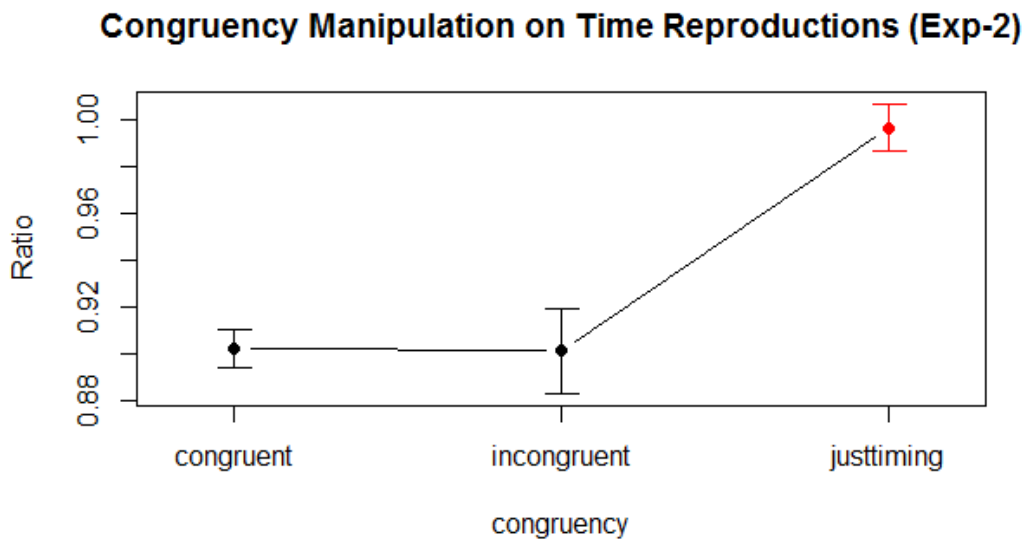


Figure 23. Congruency manipulation on time reproductions with three levels including timing while performing congruent or incongruent Simon task trial and empty trials in which the only task is timing (Experiment-2) (Error Bars: SE).

The comparisons which are based on the AIC reveal that the full model is not better than the model without the interaction of duration length with the other two variables (ΔAIC

= 2; $\chi^2 = 5.6$, $p = .22$). Thus, the final model is the one which has SOA with two levels (Early, Late), congruency with three levels and duration length term along with their 3-way interaction.

Table 6. Descriptive Statistics of ratios (reproduction/objective duration) for Congruency and SOA conditions

congruency	SOA	ratio	SE
congruent	Early	0.922	0.01
incongruent	Early	0.929	0.03
congruent	Late	0.882	0.01
incongruent	Late	0.872	0.03
NoSimon		0.997	0.01
Early – Late SOA ratio difference = 0.049			
Overall Early–Late SOA Reproduction difference = $0.049 \times 2500 = 121$ msec			

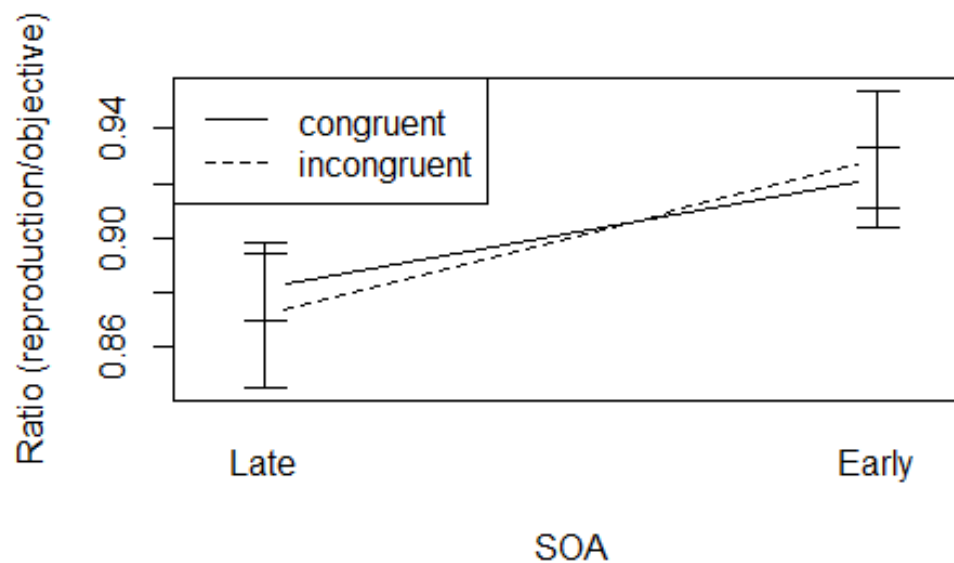


Figure 24. Effect of temporal location on time reproductions at early or late SOAs for congruent and incongruent conditions (Experiment-2) (Error Bars: SE)

In this model the intercept term corresponding to the late SOA condition is found to be significant ($\beta = 0.93$, $p < .001$). The reproductions of empty trials (NoSimon condition) turned out to be longer than the reproductions that include a concurrent task in a Helmert contrast design ($\beta = 0.04$, $p > .001$) (Figure 23) (Table 5). Moreover, results indicated that the reproductions at the Early SOA condition are longer than the ones at

the Late SOA condition ($\beta = 0.05$, $p < .001$) (Figure 24) (See Table 6 for the descriptive statistics). It is shown that duration length was significant indicating more underestimation at shorter intervals ($\beta = -0.08$, $p < .001$). The average reproduction difference was 121 msec for all intervals (see Table 6). For each interval, namely 2000-2500-3000 msec, the mean SOA effect was 54 (0.027×2000), 40 (0.016×2500) and 267 (0.089×3000) msec, respectively (see Appendix A for the analysis of duration length-SOA interaction in raw reproductions). The calculation of the effects of temporal location and concurrent task requirements in milliseconds indicated an effect of SOA (the difference between early and late SOA conditions) which amounts to approximately 121 msec (0.049×2500).

3.2.3.2. Simon Task Analysis

Incorrect Simon task responses are removed from the data analysis (3 %). The full model for the analysis of the Simon effect includes congruency with two levels (congruent, incongruent), SOA again with two levels (Early, Late) and duration length (2000, 2500, 3000 msec) together with their three-way interaction. In addition, in this analysis a further independent variable: Trial order is added to capture the potentially growing expertise throughout the experiment.

Table 7. Linear Mixed Effect Model Beta Values of the Simon effect (Exp-2)

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	728.42592	23.39306	17.50	31.139	< 2e-16
incongruent	59.11544	14.62677	1491.00	4.042	5.58e-05
Late	-65.10251	9.15043	1491.00	-7.115	1.74e-12
Trial	-0.23933	0.07978	1491.20	-3.000	0.00275
incongruent: Late	12.80336	21.26663	1491.10	0.602	0.54724
SOA = Early:					
contrast	estimate	SE	df	t.ratio	p.value
incongruent - congruent	59.11544	14.626	1496.06	4.042	0.0001
SOA = Late:					
contrast	estimate	SE	df	t.ratio	p.value
incongruent - congruent	71.91881	15.44	1496.34	4.656	<.0001
congruency = congruent:					
contrast	estimate	SE	df	t.ratio	p.value
Late - Early	-65.10251	9.150	1496.12	-7.115	<.0001
congruency = incongruent:					
contrast	estimate	SE	df	t.ratio	p.value
Late - Early	-52.29915	19.201352	1496.22	-2.724	0.0065

The full model (Table 7) is not found to be better than the reduced model which lacks the interaction of duration length with the other two variables is ($\Delta AIC = 6$; $\chi^2 = 0.35$, $p = .94$). The duration length variable was omitted from further analysis as the comparison of the reduced model with the model including duration length was insignificant ($\Delta AIC = 2$; $\chi^2 = 0.02$, $p = .89$). In the final model the intercept effect – which corresponds to the congruent condition at Early SOA – is significant ($\beta = 728.4$, $p < .001$). RTs of incongruent trials are significantly longer than congruent RTs at Early SOA ($\beta = 59.1$, $p < .00$) (Figure 25). The interaction of congruency and SOA is found to be non-significant ($\beta = 12.8$, $p = .54$).

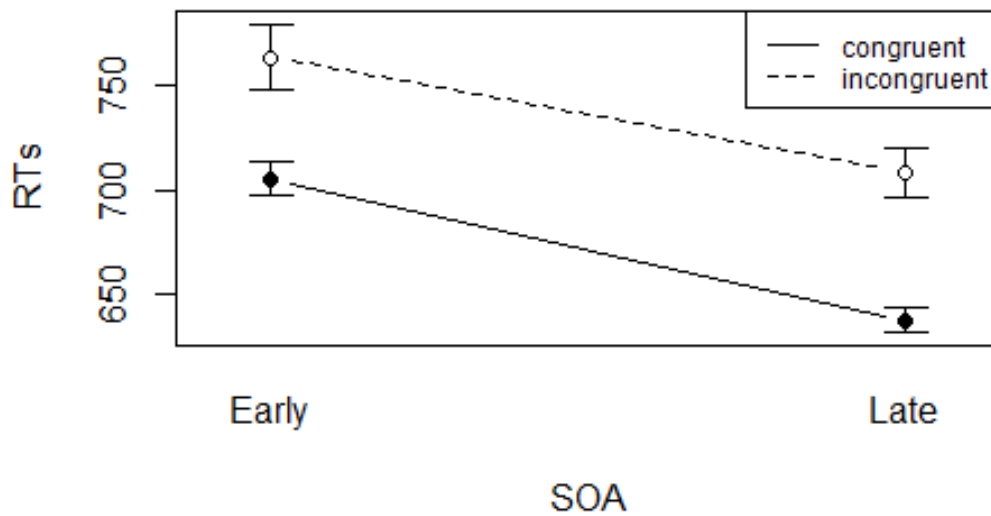


Figure 25. Effect of Temporal location (Early, Late SOA) and congruency (congruent, incongruent) on Simon RTs (Experiment-2) (Error Bars: SE).

Post-hoc tests reveals that incongruent RTs at Late SOA are significantly higher than congruent RTs ($\beta = 71.9$, $p < .001$). Moreover, RTs at the Late SOA condition are shorter than RTs at the Early SOA condition for congruent trials ($\beta = - 65.1$, $p < .001$) and incongruent trials ($\beta = - 52.3$, $p < .001$) (Table 7). See Table 8 for the descriptive statistics.

Table 8. Descriptive Statistics of Simon RTs for congruency and SOA conditions (Exp-2)

congruency	SOA	Reaction Time (msec)	SE
congruent	Early	705.6	8.4
incongruent	Early	763.6	15.9
congruent	Late	637.7	5.8
incongruent	Late	708.2	11.7

2.2.3.3. Bayes Factor Comparison for the Congruency Effect

A Bayes factor comparison allows us to support null effects by providing a likelihood factor as evidence against the alternative explanation for a difference between the measurements. Thus, in this analysis we compared the null hypothesis – that the congruent and incongruent conditions have a similar effect on timing – with the alternative hypothesis which states that they differ in terms of their effect on timing. The results reveal that the null effect is 14:1 times more likely than the congruency effect to explain the ratios of the timing task. This result supports the conclusion that congruency does not affect time reproductions (Table 9).

Table 9. Bayes Factor Results of Congruency and Null effect comparison

Bayes factor analysis

[1] Intercept only: 14.19292 ±0.03%
Against denominator:
ratio ~ congruency

2.2.3.4. Group Comparison for SOA

After presenting the results of both experiments, Exp-1 and Exp-2, separately, here we want to compare both experiments in an overall model, with respect to the effect of SOA. The mixed effect model which includes three levels of SOA (Early, Late and NoSimon), group with two levels (Exp-1 and Exp-2) and random intercepts for subjects revealed that the intercept effect – which corresponds to the Early SOA in the Exp-1 – is significant ($\beta = 0.99$, $p < .001$). In Exp-1, the difference between Early and Late SOA is found to be significant ($\beta = -0.07$, $p < .001$) and the absence of an interaction between Group and SOA ($\beta = 0.02$, $p > .05$) indicates that the Early-Late SOA comparison shows a similar change in ratios in both experiments (Table 10).

Table 10. Effects of Group (Exp-1, Exp-2) on SOA (Early, Late; NoSimon)

	Estimate	Std.Error	df	t-value	p-value
(Intercept)	0.99970	0.0434	14.697	22.990	0.000
Late	-0.06579	0.0114	4896.24	-5.722	1.0492e-08
NoSimon	0.02993	0.0117	4896.22	2.549	1.0774e-02
Group2	-0.06913	0.0694	26.30	-0.995	3.1964e-01
Late: Group2	0.02024	0.0164	4896.13	1.227	2.1974e-01
NoSimon: Group2	0.04149	0.0166	4896.13	2.492	1.2683e-02

2.2.4. Discussion

The findings from the previous experiment – effects of expectancy and interference on timing – are replicated in this experiment as well. Moreover, we provide further support for the hypothesis that inhibition requirements – stemming from the incongruent Simon trials – have no effect on timing, at least while participants are encoding an interval. According to the switch hypothesis, the rare occurrence of incongruent trials in this experiment should capture the attention for the Simon task performance – and this is reflected in the observation that the estimated Simon effect increased significantly in Exp-2 in comparison to Exp-1 from 30 msec to 60 msec. – and this situation should leave less available resources for timing in these trials. The attentional shift due to the switch opening in the pacemaker-accumulator structure predicts that incongruent condition should be more underestimated. However, the results indicate otherwise which supports the attentional time-sharing hypothesis. Because, in this account, the working memory decay is dependent upon the whole duration of the overlap between Simon task and timing. In other words, rare occurrence of the incongruent trials does not add an additional extent to the interference effect that is emerged from the disruption of accumulated temporal information in the working memory. The longer duration of the decay due to the increased RTs in the incongruent trials is rather limited to be reflected on timing inaccuracy. Because the contribution of the incongruent trials – namely 60 msec duration (Simon effect) – is small in comparison to the total overlap of timing and the Simon task that is around 750 msec. Moreover, the expected decay in the attentional time-sharing hypothesis is not a like “none or all” as it is predicted by the switch hypothesis – the attention shifts completely towards incongruent trial conflict resolution which creates an attentional bottleneck – but the decay is a temporal function of the distractor’s duration. In brief, the absence of the attentional bottleneck effect on timing can be explained by the attentional time-sharing account.

As regards the expectancy effect, we showed that the temporal location effect exists to the same extent even if the percentage of the concurrent task-specific stimuli is changed while keeping the total percentage of the concurrent task trials stable with respect to the percentage of empty trials. We interpret this result in the sense that the preparation requirements of the concurrent task stay the same in both experiments. This is because the expectation of the interruption or break within an interval is modulated by the frequency of interference relative to the trials without interference. Indeed, Fortin (2003) showed that the high expectancy of a break throughout an interval production experiment – which is achieved by the relative frequency of breaks and no-breaks – causes more serious loss of signals since attentional shifts are more frequent in the high expectancy condition. In line with this account, we observed the same amount of

underestimation at late SOA in comparison to the Early SOA in both experiments.

The sameness of the total expectation for the Late SOA, and thus the same degree of the temporal location effect in both experiments, can also be inferred from the extension of the Simon effect to the Late SOA in the present experiment. If an increase in the expectation existed (e.g., paying more attention for the sake of resolving more difficult incongruent trials), we would find a similar absence of the Simon effect at Late SOA as observed in the previous experiment. Through increased expectation, thus increased preparation, the Simon effect in the late SOA in this experiment would be cancelled as well. However, as claimed before, the hypothesized sameness in the total expectation level in Exp-1 and -2 does not rule out higher RTs for incongruent Simon trials when the ratio of congruent to incongruent Simon trials is changed from 50%-50% in Exp-1 to 80%-20% in Exp-2, respectively. Since incongruent trials in the concurrent task of Exp-2 are less expected, they are processed slower. If there is no increase in attentional sharing in favor of the Simon task in general as it is compared to the previous experiment (e.g., not sufficiently increased preparation which should be enough to eliminate Simon effect in the late SOA), this would mean similar amounts of attentional resources for maintenance of accumulated temporal signals in the working memory. This kind of similarity in the temporal location effect through same amount of attentional sharing is supported by our results with the absence of interaction between SOA and group variables.

As for the discussion related to the possibility of an onset related timing disruption instead of an expectation based explanation of the temporal location effects in Exp-2, we have observed a difference of the SOA effect for the shortest and the longest interval similar to the finding in Exp-1. In other words, the expectation effect was the most profound in the longest interval which fits with the hypothesized multiplicative functions. However, in this experiment unlike in Exp-1, we did not observe an extended expectation effect in the middle interval in comparison to the shortest interval. This finding suggests the same amount of the temporal location effect for these two intervals and thus it seems to support an onset related effect. However, if we compare the temporal location effect in the longest interval (267 msec) with the 54 and 40 msec effects in the other intervals, we cannot explain this difference with only onset related disruptions in timing. Moreover, an offset registration disruption type of explanation cannot be an option either since the distance from the end of the interval was the same for all intervals. An interval offset related disruption can be based on the different modes of the switch apparatus in an internal clock model. For instance, if a stop mode would be the case for the longest interval but not for the other intervals, this would explain our findings, namely a more profound timing disruption in the longest interval. However, assuming the distance to the end of the interval was the same for all intervals, there is

no direct reason to suppose this potential stop mode only in the longest interval. One possibility is that the participants might choose to stop timing to perform the concurrent task in the longest interval due to the difficulty of the registration of the interval end and performance of the concurrent task at the same time. However, explaining why it is more difficult to perform these two types of requirements in the longest interval – although these two types of requirements were existing in all intervals – requires an assumption that there were less attentional resources in the longest interval. This is consistent with the attentional time-sharing account predictions for explaining expectation effects since there can be less available resources in the longest intervals. In this schema, resource sharing was still evident without a need for a decay function based explanation, and thus just a stop mode in the internal clock model would be enough. However, even in this interpretation, ignoring the Exp-1 results which are consistent with a multiplicative function, our results are not in line with the attentional switch account since this account predicts that expectation itself causes a higher disruption in the longest interval, not a permanent opening of the switch in the longest interval due to an interval offset related disruption. In other words, there can be an early offset registration (i.e. opening of the switch) in the longest interval which can lead to more profound timing disruption, however, to assume a switch opening, we somehow need to refer to the necessity for this switch opening. If there is no sufficient amount of attentional resources at the moment when the participants need to perform both the offset registration of the timing task and the concurrent task, this explanation can be defended. For this purpose, we need to assume that the expectation of a concurrent task causes a critical decrease of resources to perform both the offset registration and the concurrent task. In this way, we can explain the less extended SOA effect in the shorter intervals. In these shorter intervals (i.e. the shortest and the middle interval), performing both the offset registration and the concurrent task are required, thus an explanation which is only based on a switching at the time of overlap between timing and the concurrent task, cannot explain this SOA effect difference in the different intervals.

In brief, there is a possibility that more extended attentional sharing between timing and the context (i.e. expectation of the concurrent task) can cause a relatively early opening of the switch at the end of the longest intervals – which causes higher timing disruption – in comparison to the shorter intervals due to the shorter periods of this sharing in these intervals. However, this attentional sharing due to the expectation is not in line with the predictions of the attentional switch account since this account almost equalizes attention and timing by proposing that expectation itself leads to the contraction of time perception which was not supported by our results from the empty trials that were reproduced accurately.

On the other hand, these findings do not suggest any mechanism for how attentional sharing before the appearance of the concurrent task was made possible, for instance by a switch based framework or not. Our results are differentiating the switch account in an internal clock from the memory decay account and favor the latter one. However, our interpretation does not speculate on a mechanism for the question on how attentional sharing takes place since the attentional time-sharing account does not assume a mechanism for this sharing, but just predicts that there should be less available resources for timing (e.g. maintaining stored temporal value) at the time of the appearance of the concurrent task stimulus due to the expectation of this stimulus.

In conclusion, these results provide further support for the attentional time-sharing hypothesis of time perception in terms of expectation and interference of the concurrent task within the framework of internal clock models. In these models time pulses as a measure of temporal information are accumulated and updated in working memory throughout the experience of an interval. Moreover, the results of the two experiments which both investigate the inhibition effect (congruency effect) on timing by producing different magnitudes of the Simon effect from a subtle (Exp-1) to a more extended Simon effect (Exp-2) do not cause a difference in temporal underestimation. These findings provide new evidence for the controversial interpretations of executive task effects on timing in the literature (Brown et al., 2013; Brown, 2006; Ogden et al., 2011). On the other hand, the clear effect of the presence of an overall concurrent task during keeping track of time indicates that the relevant interference is more likely to be related to the updating mechanism of the accumulation process during timing as suggested in the literature before (i.e. Ogden et al. 2011). In addition to that, the inaccuracy in timing in our results – due to a disruption towards the updating mechanism – is better explained by the attentional time-sharing account in contrast to the switch account of attentional shifts.

These two experiments are thought to cover the encoding stage of a time reproduction task. Both expectancy and interference manipulations were included while participants were experiencing the passage of time. In the reproduction stage, there was no necessity for making any decision or responding other than starting and ending the trial, i.e., there was no concurrent task in the reproduction stage. We intend to investigate the role of both temporal location and interference in the reproduction stage in the next experiment, Exp-3, in terms of differing requirements on timing such as making a decision and a motor response in the reproduction stage.

CHAPTER 4

ATTENTIONAL TIME-SHARING AND RESPONSE INHIBITION IN TIMING:

THE COMPARISON OF THE ENCODING AND THE REPRODUCTION STAGES

People form temporal representations of particular intervals and these representations can be used by a decision process later. In the decision process, the internal representation is compared with the stimulus duration in the context. Encoding a time interval can be considered as the perceptual stage of a temporal reproduction task in the sense that a feature (“duration” in this case) of a stimulus must be extracted. Keeping track of an interval (corresponding to the accumulation process in the internal clock models) must be at work in both stages of a reproduction task. Indeed, a concurrent task within a timing task – both during encoding and reproduction – is expected to interfere with timing performance (e.g., Brown, 1997; Zakay & Block, 2004; Fortin & Rousseau, 1998). However, in Scalar Expectancy Theory (SET) (e.g., Church, 1984) a decision process is present in the reproduction part. It is necessary to complete the task by considering both the passage of time in the current context and the previously formed representation of the interval (Wearden, 1999, 2004) and to decide to press a key when they are found equally long. In other words, a decision process is only applied in the reproduction stage in order to complete the estimation of the most recent interval encoded. Thus, the reproduction method is an appropriate candidate for a comparison of different requirements of a timing task in terms of accumulation and/or decision processes. In the encoding stage of a reproduction task, a representation of the interval –without any decision to finish the estimation – is formed, and then in the reproduction part, the comparison of the already formed representation with the reproduced one informs an explicit decision completing the time estimation. This task structure is an appropriate way for an evaluation of a potential overlap between timing and concurrent task response requirements of both response decisions and motor responses.

The hypothesized decision process can be conceptualized as a demanding process that requires an explicit comparison between the inner representation and the accumulated signals in the reproduction context as in SET. Thus, by introducing a concurrent task which has two different types of trials in terms of their demands of response selection difficulty, we can investigate a potential effect of overlap between response selection of the concurrent task and decision requirements of the timing task. We want to observe whether there is a difference in terms of the congruency effect between the encoding and reproduction stage of an interval timing task. The attentional time-sharing account predicts that working memory decay rate of the incongruent trials is higher than the decay rates of the congruent trials in the reproduction stage (Figure 26). In other words, although we did not find an extra effect of incongruent Simon trials in the encoding stage in the previous experiments, we want to investigate this within the reproduction stage as well.

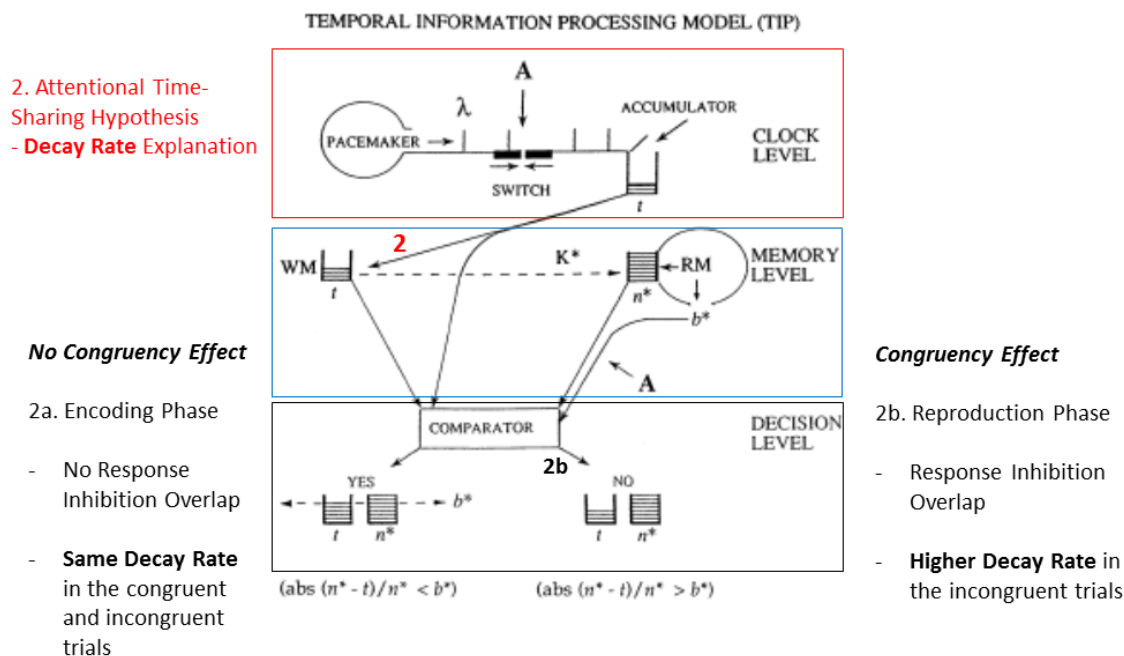


Figure 26. Time-Sharing Hypothesis on Overlap between Response Inhibition Requirements of Simon Task and Timing (Lejeune, 1998, page. 132).

The theory of scalar timing is mainly based on the temporal generalization and bisection methods. In these methods, a tripartite process is involved: (1) a reference duration (the standard) is learned by participants, (2), comparison duration is presented, (3) a decision is applied which is defined in terms of a threshold/ratio rule. In the generalization task

the participant must decide whether the comparison duration was the same as or different from the standard. In the bisection method, the participant must decide whether the comparison duration was shorter or longer than the standard. However, there is a substantial difference between the decision processes in temporal generalization and reproduction tasks. In reproduction tasks, since the ongoing duration which is to be compared to the previously experienced duration is not given to the participant, but rather is under the control of the participant. Therefore, the decision stage in scalar timing theory is not particularly clear for the time reproduction method. In other words, SET-compatible models of the reproduction method should include a distinction between the encoding and reproduction stages of the task in terms of the comparison process.

We propose to consider the decision process in a reproduction task as it includes two issues of the overall decision-related effect on timing: the first is about the response inhibition requirement during the comparison process. The comparison process should follow a response inhibition process when there is a “not yet” outcome (see Figure 16: 3rd level of “congruency”). As regards with the relation of timing and response inhibition, Zhang et al. (2016) showed that Parkinson Disease (PD) patients respond prematurely in a time discrimination task such as temporal generalization and bisection tasks. Considering the difficulties of PD patients in response inhibition, this is an indication that temporal decision requirements and response inhibition are related. In a similar sense, we can propose that there is some overlap of the inhibition requirement of timing in a reproduction task and a concurrent task in healthy participants. The investigation of the potential interference between response inhibition of a conflict task (e.g., Ridderinkhof et al., 2004) such as the Simon or Stroop task and the response inhibition related to the timing task would present an opportunity to reveal the nature of the comparison process in timing.

In this experiment, when the concurrent task is presented during the encoding stage, reproductions are expected to be more underestimated in case of an interference. On the other hand, an overestimation is expected in case the concurrent task is embedded in the reproduction stage. However, assuming that there is an additional comparison process in the reproduction stage, we can expect different outcomes of underestimation and overestimations in terms of response inhibition for the encoding and reproduction stages. Because, if the concurrent task is in the reproduction part, the difficult (incongruent) trial of the concurrent task might cause more disruption in timing due to the possible overlap between the response inhibition of timing compared to the case when the concurrent task is included in the encoding part. More precisely, response inhibition demands of the concurrent task can create a disruption in timing performance

due to an overlap with the response inhibition part at the decision level of the internal clock model. Since there is no response inhibition related process for timing in the encoding stage, we would not expect such an effect as observed in the previous chapter. However, since the decision requirement of determining the end of a reproduction is under voluntary control of the participant, the response inhibition requirement of the concurrent task can interfere with the response inhibition requirements of reproducing the interval. Thus, we expect to find a congruency effect on timing when the concurrent task is introduced in the reproduction part of timing task but not when it is introduced in the encoding part. This kind of effect can be theorized by a central bottleneck (e.g., Ruthruff & Pashler, 2010) since the overlap between the two tasks corresponds to a more central type of requirement (see Figure 27), as opposed to the previously investigated general task interference in Exp-1-2 – which is a result of possible interference with the updating mechanism of timing that is expected to be effective in both stages. We propose that the memory decay in the incongruent trials is expected to be more dramatic because of this central bottleneck (Figure 28).

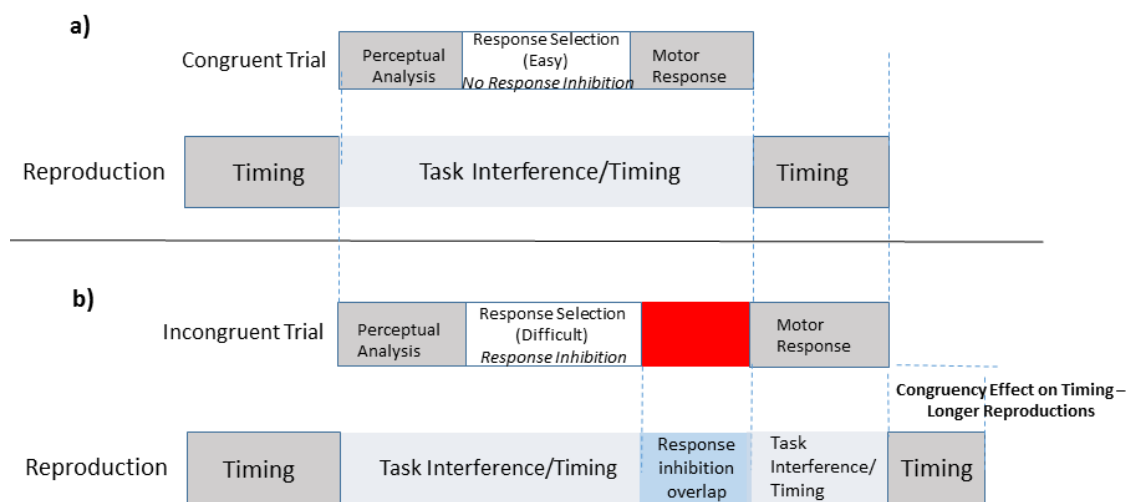


Figure 27. Response inhibition overlap of two tasks- Congruency Effect on Timing in the Reproduction Stage. a) Overlap of timing and congruent Simon task trial b) Overlap of timing and incongruent Simon task trial

Since one of the aims of this chapter is the effect of inhibition on timing, we preferred a concurrent task in line with Miyake et al. (2000)'s classification of cognitive tasks such as inhibition, shifting and updating. The central executive requirements of a Stroop task stimulus in the incongruent trials –which has well defined response selection

requirements (i.e., Maanen et al., 2009) – is a typical instance of response inhibition. In summary, we expect a congruency effect on the accumulation process in the reproduction stage and we hypothesize that it should be independent of the duration of the inhibition process which is required for the timing task. Importantly, the response inhibition to prevent a premature response to end the estimation itself does not cause a disruption on timing – otherwise we would always observe an overestimation in a typical empty reproduction trial – but rather the overlap of the response inhibition with the concurrent task response inhibition would give rise to the inaccuracy in timing. In other words, a potential response inhibition effect, namely the congruency effect, should be observed in all temporal locations in the reproduction stage of the timing task.

In addition, the overall task interference is also expected for both stages of the reproduction task (encoding and reproduction stages of a reproduction task) since the disruption of the updating mechanism of timing would apply to both stages of the timing task. Therefore, the presence of the effect of the general task requirements of the Stroop task on timing in the two stages will be the second research interest in this chapter.

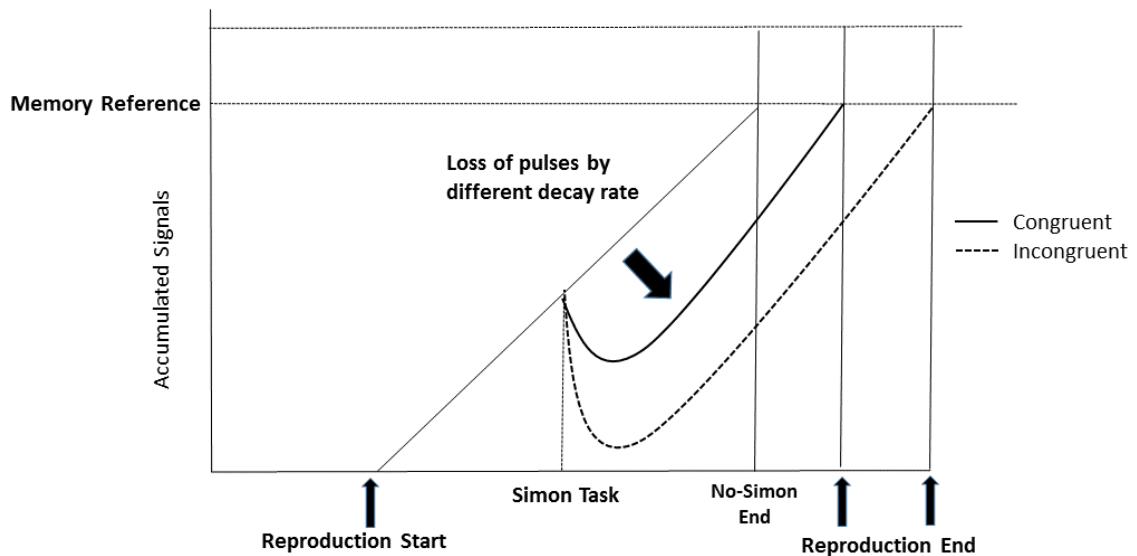


Figure 28. Congruency effect in the reproduction stage: Different memory decay rates in the accumulation process of congruent and incongruent trials

As a second part of this chapter, we will investigate the question whether the comparison process of threshold in the reference memory and the accumulation of pulses within the current context is applied towards the end of the interval as it is

suggested by Rattat & Fortin (2011) or not. If the overlap between the time discrimination and a concurrent task discrimination (digit discrimination in that study) demands apply more towards the end of the interval, we would expect a temporal location effect varying with the degree of overlap between the two tasks. In other words, the temporal location effect which is modulated by the expectancy should be observed more profoundly towards the end of the interval since there would be an additional loss of accumulated signals. This effect can be distinguished from the expectancy effect which holds between the Early and Late SOA – due to the overlap of decision requirements (the comparison of the threshold and the current signals) of timing and response selection of the Stroop task. In other words, if the comparison process in the decision level of interval timing have a demanding nature, we should expect an extra timing disruption by elapsing time if the concurrent task is included in the reproduction stage. This hypothesis is based on the idea that the decision should be easy – less demanding – if the current number of pulses is farther (i.e. earlier SOA conditions) to the threshold value in the reference memory. However, we can expect more demanding working memory processes if the time elapses up to a point (i.e. later SOA conditions) where the result of the comparison process is not that obvious. Thus, if the nature of the comparison process is demanding, we expect more dramatic timing disruptions in later SOA conditions in the reproduction stage in comparison to the encoding stage because there is no need for a comparison process in the encoding stage. On the other hand, if the comparison process is not a central process which requires a deliberate comparison process, but on the contrary if the comparison is rather an automatic process, we should not expect an extra disruption in the reproduction stage since the overlap of timing and the concurrent task does not a further disruption.

Besides a possible comparison process effect which is elaborated above, there can be further overlaps between the timing task and the concurrent task in the reproduction stage. The timing task should include a response activation process if the test of the threshold and the current number of time signals yields a “yes” outcome (see Figure 26). In other words, after the comparison process gives an outcome which requires a motor response, there are task requirements of a timing task which are common to all reaction time tasks. Similarly, in the Stroop task as well, a response must be activated independently from whether there is any inhibition (as in an incongruent trial) before the response activation or not (as in a congruent trial). In a conflict resolution task that includes a stimulus processing, direct response activation corresponds to the congruent trial requirements of this task. However, if there is an inhibition requirement, the information processing follows an indirect path which is completed with the response activation processes. Response activation processes can include response selection and motor response related processes. In the incongruent case of a conflict resolution task

such as Simon task and Stroop task, an automatic triggering of stimulus related response should be inhibited first and then the correct response can be selected and executed (Figure 29).

The overlap of these two response activation-related activities – when there is a need for a response – should be observed only towards the end of the timing task. We hypothesize that this effect should be independent of the response inhibition requirements (i.e. during the period where there is no need for response activation but there is a need for inhibition of the timing response) since the overlap of the response activations occur only later in the interval.

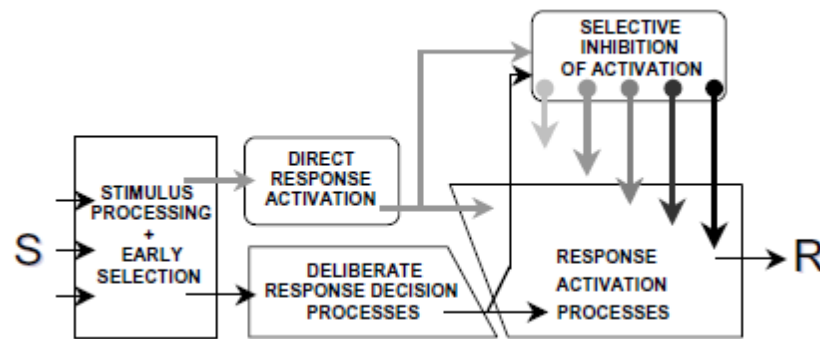


Figure 29. Response selection for both routes of direct and indirect responses in the conflict tasks (Ridderinkhof et al., 2004, page 2)

Thus, in this chapter, as a third aim of the comparison between the encoding and reproduction stage of timing, we will investigate whether the SOA manipulation affects timing in different degrees in these two stages. The expectancy effect which is demonstrated in the previous chapter is dependent upon attentional time-sharing between the timing and the concurrent task and this is a result of the division of attentional resources between two tasks. We therefore hypothesize that this effect would be more profound in the later SOA conditions when the concurrent task is included in the reproduction stage of the timing task. Because, in this case, in addition to the temporal location effect which is observed between early and late SOA conditions due to attentional sharing, we expect another source of the loss of accumulated signals which arises from the overlap between response requirements. In other words, the pattern of increased time estimation from early to late SOA condition in the reproduction stage should be different than the pattern of decreased time estimation in the encoding stage. Thus, we expect a slope of the temporal location effect in both stages even if these

slopes have opposite signs (for reproduction stage: (+), for encoding stage: (-)). If there is an extra disruption in timing performance during the reproduction stage, we can expect a steeper pattern in the trials which include a concurrent task during the reproduction stage as compared to the decreasing pattern in the trials in which the concurrent task is embedded in the encoding stage. This additional interference in the reproduction would cause a more dramatic effect on timing from early to late SOA conditions. In other words, the change in the disruption of timing from early to late SOA conditions is expected to be higher in the reproduction stage if there is an overlap of response activation of timing task and the concurrent task in the late SOA condition. In the present experiment, in a similar design as in the previous chapter, we aim to investigate the similarity or the difference in time reproduction between the effect of a concurrent task in the two stages in a reproduction task, namely the encoding and the reproduction stages. A concurrent task is introduced in different temporal locations of an interval either during the participants are encoding an interval or during they are reproducing an interval.

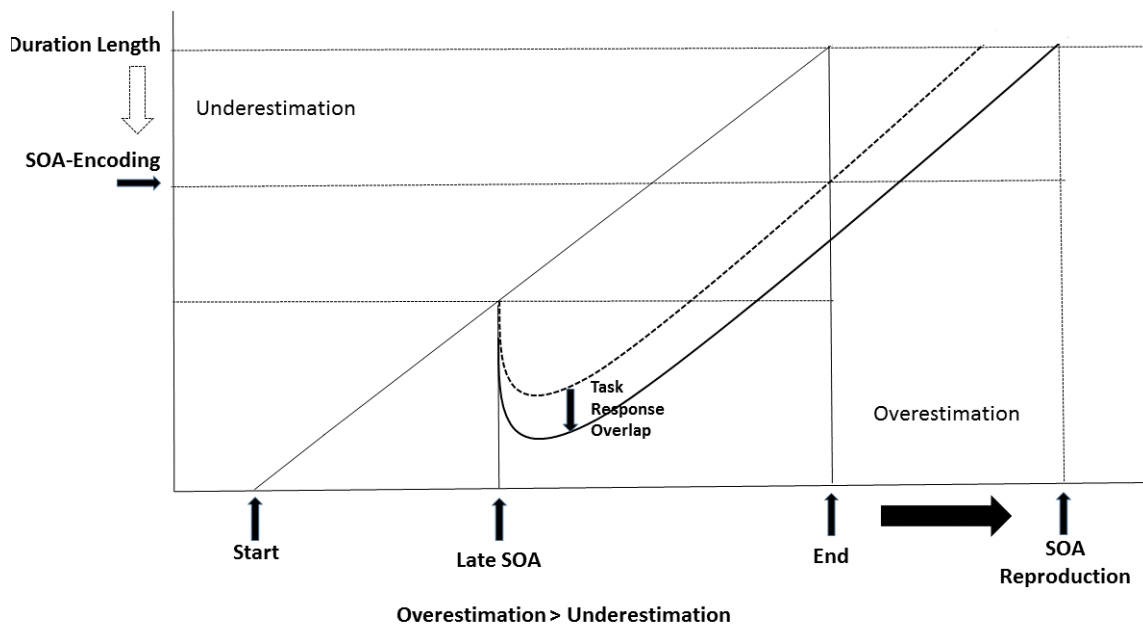


Figure 30. The difference in timing disruption due to the Response Overlap Effects in the Encoding and Reproduction Stage Blocks

This last aim of this chapter is whether there is an effect of task response overlap. When the pulse accumulation starts, it has an accumulation rate which should not change and ends normally if there is no any interference during timing. However, if there is a concurrent task towards the end of an interval (i.e. late SOA) in the encoding stage, this

would cause a memory decay at some extent which leads to an underestimation. The difference between early SOA and late SOA reproductions would be the result of the attentional time-sharing account which is favoured in the previous chapter (Figure 30). However, as it is explained above, since we expect an extra disruption due to an overlap of response activation related processes of timing task and the concurrent task, we expect more profound memory decay in the reproduction stage. In other words, overestimation extent would be more dramatic in the reproduction stage in comparison to the underestimation extent in the encoding stage.

The similarity or the difference of the two stages (encoding and reproduction) of the interval timing was not studied explicitly except in a few studies (Fortin & Rousseau, 1998; Sawyer et al., 1994). In Fortin & Rousseau's (1998) study, the comparison of the perceptual (encoding) and the reproduction stage is achieved by the presence of a concurrent task on different difficulty levels. A memory search task was given to the participants separately both in the reproduction stage and in the encoding stage. The participants had to keep the items in memory during the whole interval. They found that the length of reproduced intervals increased with increasing demands of memory search (increasing memory set size) in the reproduction stage whereas the reproductions decreased as a function of set size in the encoding stage. However, a between-subject comparison of the two experiments was not presented in this study. Similarly, Sawyer et al. (1994) manipulated the different levels of concurrent task difficulty for target intervals in the encoding and reproduction stage. In this study, the participants had to perform a concurrent task in both stages of the reproduction task in the same trial. They found that if the concurrent task which is included in reproduction stage was easier than the one in the encoding stage, a pattern of underestimation was observed. Similarly, an overestimation was found if the participants had been engaged in a more difficult task during the reproduction of the interval. However, again, there was no quantitative comparison of interferences for the two stages in terms of the concurrent task demands in these studies.

The comparison of two stages of the reproduction task can be achieved by the introduction of a concurrent task at different temporal locations within the interval. By this way, we might observe a potential difference in terms of the decision/comparison in the reproduction stage. Previous studies showed that duration judgments are overestimated when the introduced break is later during a production task (Fortin & Masse, 2000; Fortin et al., 2005). Similarly, if an interfering stimulus comes later within an interval, temporal underestimation is observed in the encoding stage of a reproduction task (Gaudreault et al., 2010) or an overestimation when the interfering task is inserted within a time production task (Champagne & Fortin, 2008; Macar, 2002).

The present experiment is aimed at a comparison between two potentially distinct stages of a reproduction task (encoding and reproduction stages) in terms of processes which are required. A general similarity of the effects is expected (timing disruption either in the form of underestimation or overestimation) but the slopes of the decreasing pattern of underestimation and the increasing pattern of overestimations are also expected to change as a function of the temporal locations of the concurrent task in a statistical comparison. Therefore, this approach aims to contribute to the question on whether there is an extra disruption in the reproduction stage which can be attributed to a potential bottleneck effect arising from the overlap between timing and the response demands for the interfering (Stroop) task.

In summary, our first question is whether the response inhibition of the concurrent task would interfere with the response inhibition requirement of the timing task itself in the reproduction stage. As demonstrated in the previous chapter, there is no congruency effect on timing in the encoding block. Thus, we expect to validate the absence of the response inhibition effect in the encoding stage of interval timing but the presence of this effect in the reproduction stage where we expect an overlap in terms of response inhibition. The second question of this chapter is about the temporal location of the comparison process which is hypothesized to be revealed by comparing the two stages of the timing task in terms of the interaction of task interference and SOA manipulation. In other words, we expect more profound inaccuracy in timing at a late SOA of the reproduction stage – due to the response overlap – in comparison to the inaccuracy of timing at the same temporal location in the encoding stage – where no response needs to be made. However, concerning the reproduction stage, we do not hypothesize that the comparison process of timing causes an additional demand on timing performance before a point where there is a need for a response within an interval. In other words, response inhibition – which is a result of the comparison process – before the decision of a timing response would not lead to a change in the overestimation pattern as a result of the temporal location effect.

4.1. Participants

Twenty-four students (15 females) participated in the experiment. They were given partial course credits for their service. Four of these participants were excluded from the data analysis since most of their time estimations were less than 1000 msec which indicates they did not perform the task according to the experimental instructions. Their mean age was 20.4 years ($SD = 1.7$) and all participants had normal or corrected-to-normal vision.

4.2. Experimental Procedure

The experiments were conducted with E-prime 2.0 and a Serial Response Box was used to collect the data for button presses in the timing task and vocal RTs in the Stroop task. The participants started with a practice stage of ten trials for each single task. The Stroop task and the duration estimation task were presented separately for the sake of eliminating misunderstandings about the requirements of both tasks. Then they were instructed to perform both tasks at the same time during the experimental session. There were two blocks of experimental session (the concurrent task occurred either in the encoding stage or in the reproduction stage of the timing task). The order of the blocks was counterbalanced across subjects. Each experimental block was started with a corresponding practice stage of ten trials, which, however, were excluded from analysis.

As Stroop task stimuli, two colour pairs (red/blue and yellow/green) were used to make it difficult for participants to familiarize with the task. Three SOA conditions (early, middle and late) were included to manipulate the temporal location of the Stroop task. Three different intervals (3.0, 3.5 and 4.0 s) were presented. Early SOAs were always 500 msec which means the Stroop stimulus appeared 500 msec after the beginning of the interval to be timed. Middle and late SOAs were different for each interval taking the end of the interval as a reference point. Late SOAs (1.5, 2.0, 2.5 s) were arranged according to the disappearance of the Stroop stimulus 500 msec before the end of the interval. Middle SOAs (1.0, 1.25, 1.5 s) were the average of early and late SOAs. There were two congruency conditions with respect to the type of Stroop task trial: congruent (when the colour name was the same as the colour of the word) and incongruent (when the colour name was different from the colour of the word). Two thirds of the trials in one block (72 trials) were either congruent or incongruent. The remaining 36 trials were duration estimations without a concurrent task. All the combinations of independent variables (SOA, congruency, duration) had equal numbers of trials and were presented randomly throughout the experiment. The duration of the inter-stimulus interval (ISI) was chosen from a uniform distribution from 1 to 2.5 s. At the encoding block, the target interval to be attended was given with the presentation of a “+++++++” stimulus and if there was a Stroop task in that trial, the coloured text was presented later in the middle of the plusses. After a participant had responded to the Stroop stimulus or if there was no response after 1000 msec, the text disappeared and the plusses were back on the screen again until the end of the interval which was defined by the presence of a “?” mark on the screen. Participants started and completed their own reproductions by pressing the middle key on the response box. The reproduction stage of a trial was identified by the characters “#####” (Figure 31).

The flow of a trial was the same in the reproduction block except the Stroop task was given during the presentation of the hash marks. The participants were instructed to respond to the Stroop stimuli vocally as fast and accurate as possible. They were also informed that they had to pay equal attention to both the timing and the Stroop task and not to count or use any strategies to estimate the durations.

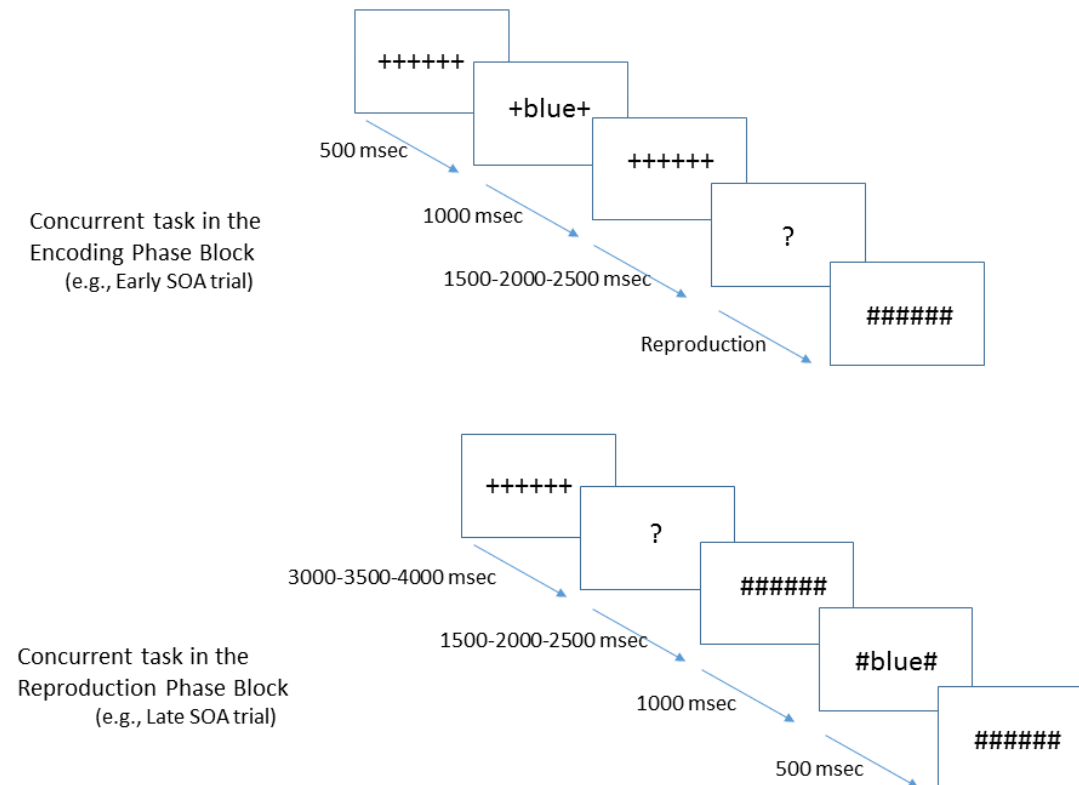


Figure 31. Experimental Flow of the Experiment-3

4.3. Results

Reproductions shorter than 1500 msec and longer than 6500 msec in the timing task (3 %) were removed from the analysis. Because of a problem with capturing the vocal responses in the Stroop task, only one third of the Stroop RT data was included in the analysis. In this data, Stroop RTs faster than 350 msec were excluded from the data analysis (0.3 %). The evaluation of the experimental manipulations was done using linear mixed effect (LME) models (Baayen et al., 2008) since it allowed us to consider the effect of single trial fluctuations. Moreover, along with the fixed effects, a random effect of

intercept per participant was included to account for the inter-individual variability. The implementation of the linear modelling is achieved by *lmer* function in R version 3.02. The *LmeTest* package was used for the estimation of *p*-values that correspond to the factors of the best fitting model. The selection of the best fitting model was achieved with a model simplification procedure. The base model for time estimation was fitted with all the experimental manipulations (SOAs, reproduction task blocks, durations, congruency and trial number) as predictors along with their interactions, and the ratio (estimation/objective duration) – 1 was used as a dependent variable. A subtraction is done in the ratios because of a comparison between the two blocks – which have different directions of timing disruption (underestimation or overestimation) is aimed for an analysis. This operation does not change the actual outcome of any analysis. If a predictor or an interaction had no significant effect on the model fit, it was removed from the model. The removal decision is based on the Akaike information criterion (AIC) and a χ^2 test. Post-hoc tests were conducted using *lsmeans* package (Lenth, 2016).

A Bayesian factor model comparison was performed to compare the “null effect” hypothesis (SOA manipulations effects in encoding and reproduction stages are the same) with the alternative hypothesis that the two distinct stages of the reproduction task had different slopes with increasing SOAs. The evaluation of the evidence in favour of the null hypothesis is allowed in Bayesian analysis as opposed to the traditional statistical analyses. Linear regression fits per participant for the SOA manipulation were used to compute Bayes factors for both models (null and alternative). The directional hypothesis that the slope differences of the two stages was different from zero was tested using the *ttestBF* function in the *BayesFactor* package of R to reveal whether the individual regression fit differences tended to be negatively or positively directed.

4.3.1. Reproductions Analysis

The model comparisons show that the three-way interaction of congruency, SOA and block ($\Delta AIC = 3$; $\chi^2 = 1$, $p = 0.69$) and the two-way interaction of congruency (with three levels: congruent, incongruent, NoStroop) with SOA (with three levels: early, middle, late) ($\Delta AIC = 1$; $\chi^2 = 1$, $p = 0.18$) do not have an effect on time estimations (Figure 32). The results from the best fitting model are shown in Table 11. The intercept which corresponds to the congruent condition for the late SOA in the encoding block is found to have a significant effect ($\beta = -0.015$, $p = .62$). In the encoding block, we did not find a significant difference between congruent and incongruent conditions ($\beta = 0.005$, $p = .35$).

However, post-hoc tests showed that the incongruent condition has greater reproductions than the congruent condition ($\beta = 0.029$, $p < .05$) in the reproduction block.

Table 11. Best fitting model for Time reproductions (Exp-3).

Fixed effects:					
	Estimate	SE	df	t value	p-value
(Intercept)	-1.461e-02	2.930e-02	2.300e+01	-0.499	0.623
incongruent	5.159e-03	5.608e-03	4.127e+03	0.920	0.358
NoStroop	1.945e-02	4.212e-03	4.127e+03	4.618	4.00e-06
Repro-Block	1.254e-01	9.872e-03	4.127e+03	12.698	< 2e-16
Early	8.141e-02	1.382e-02	4.127e+03	5.892	4.11e-09
Middle	1.057e-02	1.374e-02	4.127e+03	0.769	0.442
durR	-8.087e-02	3.960e-03	4.127e+03	-20.422	< 2e-16
Trial	7.784e-04	1.037e-04	4.127e+03	7.509	7.28e-14
incong:Repro-Block	9.423e-03	7.911e-03	4.127e+03	1.191	0.234
NoStroop:Repro-Block	2.936e-02	5.903e-03	4.127e+03	-4.974	6.82e-07
Repro-Block: Early	-2.351e-01	1.934e-02	4.127e+03	-12.156	< 2e-16
Repro-Block: Middle	-7.422e-02	1.943e-02	4.127e+03	-3.820	0.0001

Block = encoding:					
contrast	estimate	SE	df	t.ratio	p.value
Incongruent-congruent	0.01031762	0.011	4127.01	0.920	0.5554
Block = Reproduction:					
contrast	estimate	SE	df	t.ratio	p.value
incongruent-congruent	0.02916427	0.011	4127.01	2.613	0.0175

A Helmert contrast, in the encoding block, revealed that the empty trials were reproduced longer than the trials which include the concurrent task ($\beta = 0.019$, $p < .001$).

The presence of an interaction between block and task effect ($\beta = 0.029, p < .001$) indicates an even more profound task effect in which the empty trials are estimated longer than the trials that include a concurrent task (Figure 33) (see Table 12 for the descriptive statistics).

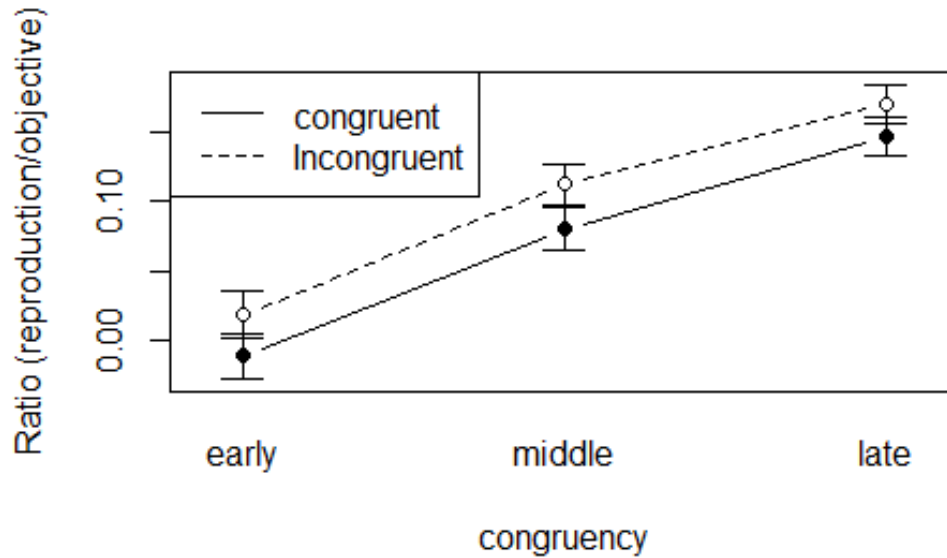


Figure 32. Main effects of congruency and SOA but no interaction in the reproduction block. (Error bars represent SE)

In the encoding block, the Early SOA condition yields higher reproductions than in the late SOA condition ($\beta = 0.08, p < .001$). However, in this block, the difference between the middle and late SOA are not found to be significant ($\beta = 0.01, p = .77$). The presence of a n interaction between block and early-late SOA ($\beta = -0.24, p < .001$) as well as between Block and middle-late SOA ($\beta = -0.07, p < .001$) suggested a post-hoc test for the reproduction block. It turned out that Early SOA reproductions were significantly lower than Late SOA reproductions ($\beta = -0.15, p < .001$) and Middle SOA were lower than the late SOA as well ($\beta = -0.06, p < .001$) (Figure 34) (see Table 13 for the descriptive statistics).

We have calculated SOA effects in msec for each interval and it was found that SOA effect between early SOA and middle SOA was 139, 353 and 271 msec for each interval from the shortest to the longest interval in the encoding stage. In this stage, SOA effect for early SOA and late SOA was -55, 480 and 341 msec for each interval. In the reproduction stage, this effect for early-middle SOA was 240, 258 and 526 msec for each interval. As for the early-late SOA comparison, the effect was 311, 564 and 813 msec for each

interval. See Appendix C for the analysis of interaction between the duration length and SOA for each stage. As for the last effect, the duration factor has an effect on reproductions indicating that the longer intervals were underestimated more compared to the shorter intervals ($\beta = -0.08, p < .00$).

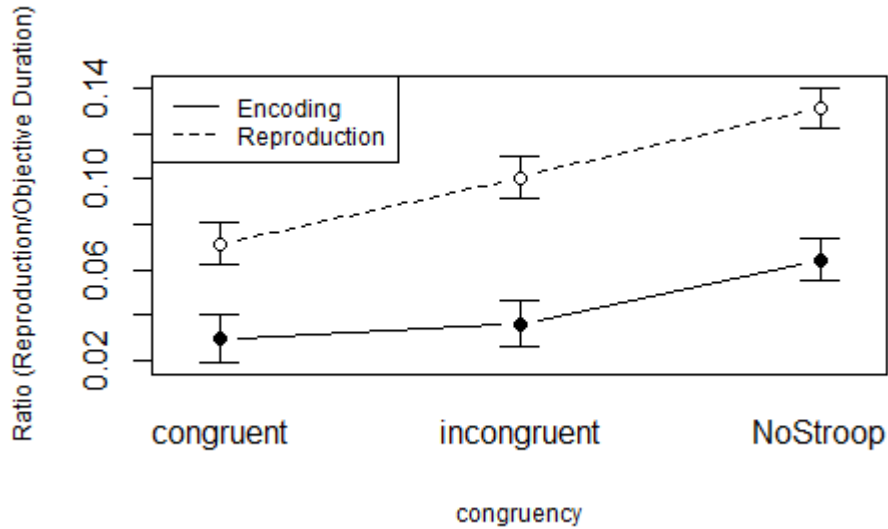


Figure 33. Congruency and Task Effects in Encoding and Reproduction Blocks of Timing Task

Table 12. Descriptive Statistics for Congruency and Overall Task Effects in the Encoding and Reproduction Blocks

congruency	Block	ratio	SE
congruent	encoding	0.0295	0.01
incongruent	encoding	0.0362	0.01
NoStroop	encoding	0.0643	0.009
congruent	reproduction	0.0714	0.009
incongruent	reproduction	0.1007	0.009
NoStroop	reproduction	0.1315	0.009

The difference between early and late SOA which corresponds to the temporal location effect in the encoding block is 280 msec (0.08×3500). The difference between late and middle SOA amounts to an average of 35 msec duration (0.01×3500). Thus, the estimated difference between early and middle SOA conditions is approximately 245 msec ($(0.08 - 0.01) \times 3500$).

In the reproduction block, time estimations increase with increasing SOAs; the intervals are reproduced shorter at early SOA compared to late SOA and the difference between early and late SOA is approximated 525 msec ($-0.15 \cdot 3500$) corresponding to the expectancy effect. In this block, the difference of middle and late SOA is found to be significant and amounts to 210 msec ($-0.06 \cdot 3500$).

Table 13. Descriptive Statistics for SOA effects in the Encoding and Reproduction Blocks

congruency	Block	ratio	SE
early	encoding	0.0794	0.012
middle	encoding	0.0156	0.013
late	encoding	0.0031	0.013
early	reproduction	0.0023	0.012
middle	reproduction	0.0976	0.011
late	reproduction	0.1585	0.010

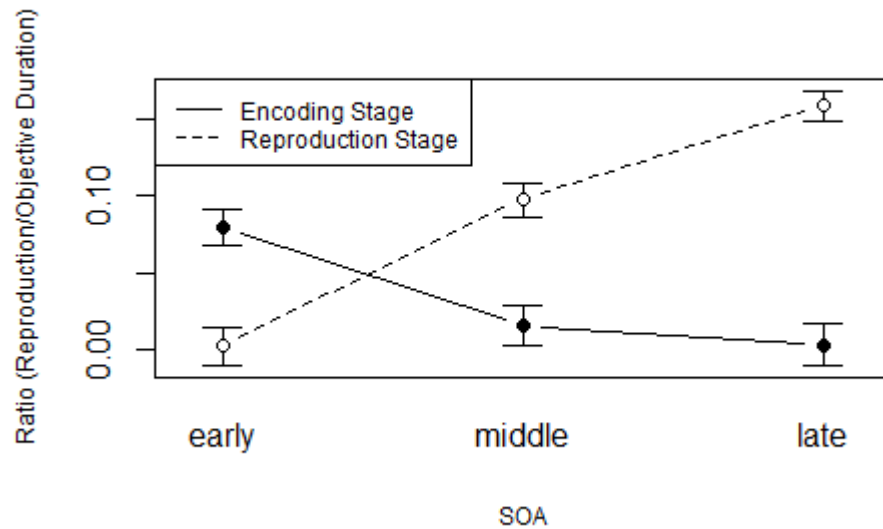


Figure 34. SOA Effect (Early-Middle-Late SOA) in the Encoding and Reproduction Blocks

Finally, the last estimated difference between the early and middle SOA amounts to 315 msec ($(-0.15 - (-0.06)) \cdot 3500$). This estimation for the congruency effect in the reproduction block was around 100 msec ($0.029 \cdot 3500$).

4.3.2. Stroop Task Analysis

The full model contains congruency, SOA and Block along with their three-way interactions and with Trial number. The removal of the three-way interaction from the model does not affect the explanatory variation ($\Delta AIC = 4$; $\chi^2 = 0.19$, $p = 0.90$). Similarly, the SOA and congruency interaction can be removed from the model ($\Delta AIC = 4$; $\chi^2 = 0.17$, $p = 0.91$).

The final model (Table 14) which includes the interaction of block and SOA along with the congruency-block interaction and trial number reveals that there is an intercept effect ($\beta = 704$, $p < .001$) which corresponds to the middle SOA condition of the encoding stage.

Table 14. Best fitting model for Stroop Task RTs (Exp-3).

Fixed effects:				
	Estimate	SE	df	t value
(Intercept)	704.14	16.93	33.80	41.589
Repro Block	7.11	11.71	1771.10	0.607
Early	23.37	10.13	1770.40	2.306
Late	30.31	10.10	1769.30	3.001
Trial	0.07	0.09	1770.90	0.825
Repro Block: Early	-7.10	14.34	1771.00	-0.495
Repro Block: Late	-42.26	14.21	1769.60	-2.974
Encoding Block: Incongruent	48.38	8.29	1769.50	5.834
Repro Block: Incongruent	49.84	8.22	1771.00	6.058

Block = Encoding:					
contrast	estimate	SE	df	t.ratio	p.value
early - middle	23.371	10.136	1770.35	2.306	0.0406
late - middle	30.318	10.103	1769.32	3.001	0.0054
late - early	6.9477	10.196	1769.58	0.681	0.7109
Block = Repro:					
contrast	estimate	SE	df	t.ratio	p.value
early - middle	16.269	10.153	1770.59	1.602	0.1956
late - middle	-11.944	10.000	1770.50	-1.194	0.3873
late - early	-28.213	10.037	1772.98	-2.811	0.0098

Moreover, incongruent trial Stroop RTs are significantly longer than congruent trial RTs ($\beta = 48.4$, $p < .001$) in the encoding stage and in the reproduction stage ($\beta = 49.8$, $p < .00$)

(Figure 35) (see Table 15 for the descriptive statistics). As regards the SOA manipulation, in the encoding stage, RTs are longer when the task is presented at the early SOA within an interval compared to RTs at the middle SOA ($\beta = 23.4, p < .05$). On the other hand, the SOA effect is in a different direction, i.e., we can see that late SOA RTs are also longer than middle SOA RTs ($\beta = 30.3, p < .01$).

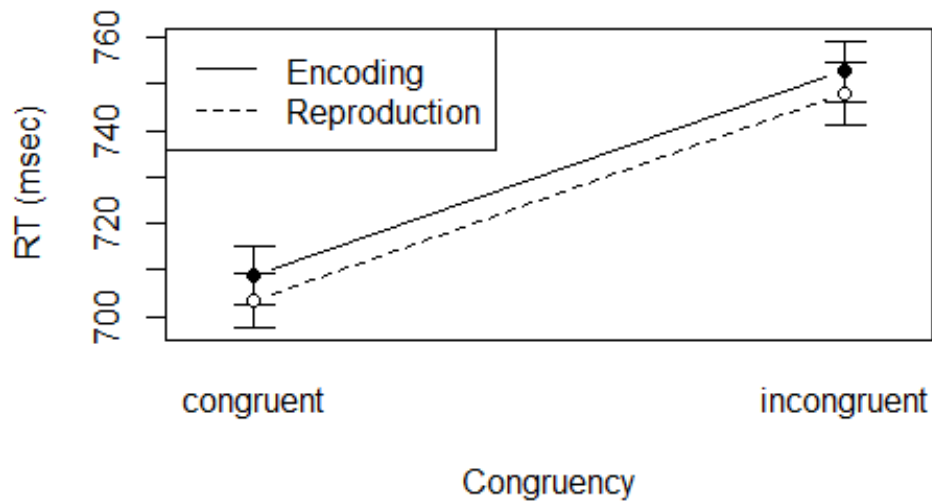


Figure 35. Stroop Effect in the two stages of the timing task: encoding and reproduction (Error bars represent SE)

Table 15. Descriptive Statistics of congruency in the Stroop task

congruency	Block	Stroop RT (msec)	SE
congruent	encoding	709.00	6.22
incongruent	encoding	752.80	6.53
congruent	reproduction	703.44	5.87
incongruent	reproduction	747.82	6.76

As for the reproduction stage, we do not observe a difference between the middle and early SOA as shown by a post-hoc test ($\beta = 16.3, p = 0.19$). However, late SOA RTs are faster than early SOA RTs ($\beta = -28.2, p < 0.01$) (Figure 36) (see Table 16 for the descriptive statistics).

The Stroop effect is found to be around 43 msec in the encoding stage and 44 msec in the reproduction stage.

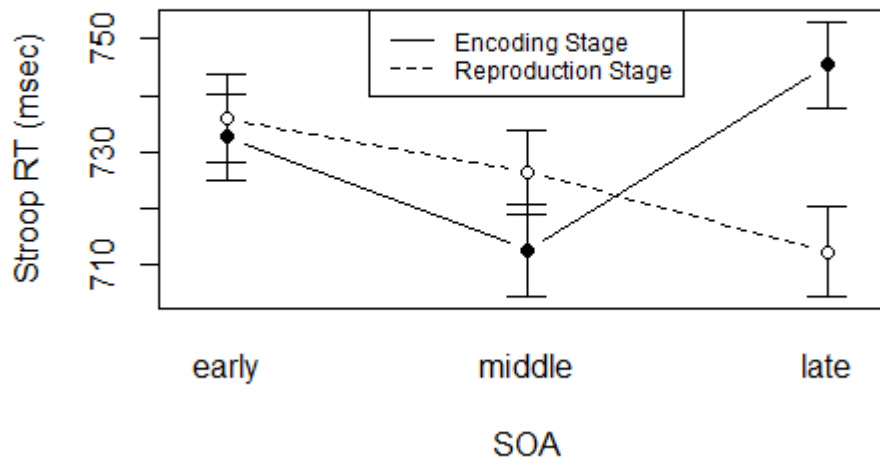


Figure 36. Stroop RTs change with SOA manipulation in the Encoding and Reproduction Stages (Error bars represent SE).

Table 16. Descriptive Statistics of SOA in the Stroop task

SOA	Block	Stroop RT (msec)	SE
early	encoding	732.56	7.63
middle	encoding	712.46	8.19
late	encoding	745.35	7.76
early	reproduction	735.94	7.85
middle	reproduction	726.31	7.50
late	reproduction	712.12	7.99

4.3.3. Early-Middle SOA and Early-Late SOA Comparisons of the Two Stages of the Timing Task

We decided to conduct an analysis by using early and middle SOA conditions for comparing the two blocks in terms of the difference between the increment of underestimation or overestimation. We decided to start with this comparison since it gives us a chance to compare two stages of a reproduction task which are interrupted by

Stroop task in two different blocks. In other words, we could reveal any disruptive effect of a comparison process (threshold-accumulated pulses comparison) due to an overlap with Stroop task requirements. Early-middle SOA comparison is appropriate for this purpose, since we do not expect another response requirement such as response activation in the middle SOA. Thus, we calculated the difference in the means of the Early and Middle SOA conditions for both encoding and reproduction stages to compare whether the increase in the overestimation from early to middle SOA for the reproduction stage is higher than the decrease in the underestimation for the encoding stage. The confidence interval was set to 99 % for the Bonferroni correction. The results showed no significant difference ($M = 0.041$, $SE = 0.019$) between the two stages in terms of timing inaccuracy which is observed by the Early-Middle SOA comparison ($t(19) = 1.927$, $p = 0.069$). The regression fits per individual are shown to illustrate the distribution of underestimation and overestimations for each individual (Figure 37).

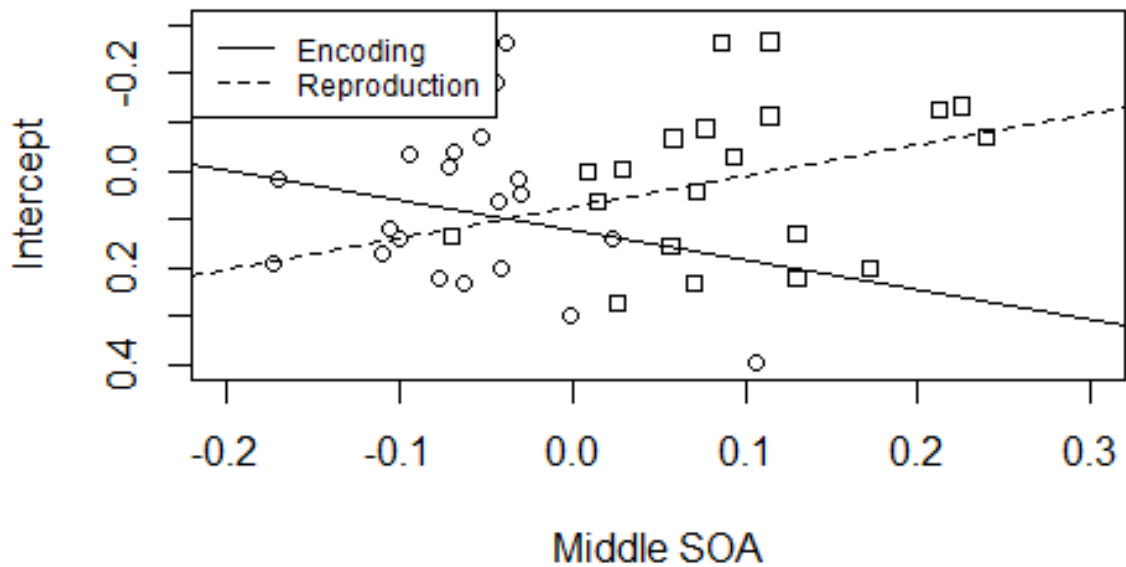


Figure 37. The changes of middle SOA estimates in comparison to early SOA estimates in the encoding and reproduction stages. (Square: Reproduction, Circle: Encoding).

As for the Early and Late SOA comparison between the two blocks, again the mean differences for each individual were calculated to conduct another one-sample t -test. The results showed a significant difference ($M = 0.078$, $SE = 0.015$) between the timing task stages ($t(19) = 3.492$, $p = 0.0024$).

The increase in the overestimation rate in the reproduction stage can be seen in the individual regression fits which are obtained by taking the Early SOA ratios (objective duration/reproductions) as the intercept and the late SOA ratios as the slopes (Figure 38). Moreover, there seem to be two groups of individuals with regards the overestimation in the reproduction stage block. The individual slopes against the intercept in the late SOA condition seem to show that some participants in the reproduction stage have no increase in the late SOA (even an underestimation for some individuals). See two sub-populations of reproduction block in the Figure 26 which are shown by two boxes).

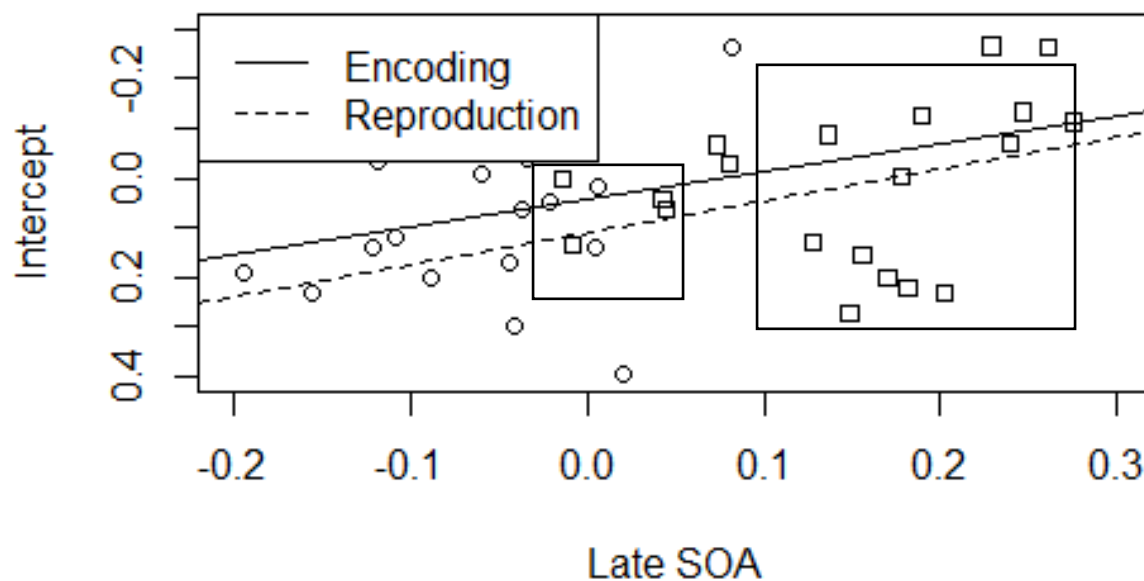


Figure 38. The changes of late SOA estimates in comparison to early SOA estimates in the encoding and reproduction stages. Boxes are for illustration purposes to show two sub-populations. (Square points: Reproduction, Circle: Encoding).

4.4. Discussion

The findings in this chapter will be discussed under several different titles in this section. These titles are the congruency effect, overall task effect, temporal location effect, bi-directional effects and temporal location effect in different blocks.

4.4.1. Congruency Effect

This experiment added to our understandings of the workings of interval timing on top of the contributions which were obtained from the previous chapter. In this chapter, response inhibition (congruency effect), comparison process of timing and response activation overlap are investigated. The first of these three subjects, namely the response inhibition effect, is related to the last level of the internal clock model, namely the decision level. The introduction of a demanding concurrent task in terms of response selection/activation either during the encoding stage of timing – where there is no decision requirement for timing – or during the reproduction stage of timing – in which there is a decision need for the temporal task – resulted in a difference in timing accuracy in these two stages of the reproduction task. Although we could not find a disruptive effect of congruency of the Stroop task while encoding the interval – similar to the finding of the previous chapter with the Simon task – this effect was significant if the congruency manipulation of concurrent task was done while the participants were reproducing the interval. We interpret this result in terms of an overlap between response inhibition of the Stroop task required in the difficult condition, namely the incongruent trials, and the response inhibition requirement of timing in the reproduction stage. Incongruent trials of the Stroop task require an inhibition of the automatic tendency to respond to the spatial position of the stimulus. Similarly, in the time reproduction task, participants have to inhibit a motor response while waiting for the correct moment to end their timing. Greenhouse et al. (2015) state that this preparatory inhibition can be related to task-relevant muscles (e.g., Duque et al., 2010) or can be a rather more general motor inhibition (e.g., Badry et al., 2009). Since the motor response of the Stroop task in our case requires speech muscles but the motor response of timing requires hand muscles, our finding for a disruptive effect due to the overlap between these two tasks – despite requiring different kinds of motor effectors – support the view of a more general kind of inhibition in terms of response preparation. The inhibition requirement of incongruent trials of the Stroop task interferes with the inhibition requirement of timing task– independent from its place within an interval (SOA). The effect should be independent from the temporal location of the concurrent task indeed because there is a continuing need for a response inhibition for the timing task wherever the Stroop task is presented during an interval. However, the response inhibition requirement for the timing task in the reproduction stage does not affect the timing performance by causing an additional disruption which changes as a function of the temporal location of the concurrent task. Otherwise, there would be a stable overestimation of empty intervals in our study (as compared to just reproducing empty intervals but not expecting the occurrence of a possible concurrent task). The effect should be independent from the period which come before the overlap. Indeed, we did

not find an interaction effect of congruency and SOA on timing in the third experiment which supports this hypothesis.

Ogden et al. (2014) provided evidence that the performance of interval reproductions is correlated with working memory tasks including updating, access and switching. However, they did not consider a relation between inhibition and reproduction. On the other hand, our results suggest otherwise since we have shown that there is a congruency effect in the reproduction stage of the reproduction task. Because, as we hypothesized before, the inhibition requirement of the reproduction task does not lead to a disruption in timing when there is no concurrent task within the interval (empty trial). Ogden et al. (2014) did not present a correlation between inhibition and reproduction because they used an individual differences method. In this method, a comparison of individuals who has different working memory capacities is made and timing in these groups are presented. In other words, working memory related effects on timing is presented indirectly. Brown et al. (2013) found bi-directional effects between the Stroop task and production of intervals. However, as regards bi-directional effects between timing and inhibition tasks in terms of random generation in a dual-task, there are different findings regarding this effect. Although Brown (2006) showed interference of RNG (Random Number Generation), Ogden et al. (2011b) could not find any effect of RLG (Random Letter Generation) on timing. Ogden et al. (2014) suggest that the findings of bi-directional effects between Stroop and timing in the Brown et al. (2013) study regarding the degree of attention and interference can be interpreted such that inhibition demands can lead to an interference only when the demands are high. The findings in Brown (2013) were obtained by performing a Stroop task while producing a 5-seconds intervals which means that there can be more than one congruency condition in a single production. Thus, since the findings with regards to the inhibition requirements are based on the comparison of single and dual task conditions, this result is subject to the confusion of congruency and the overall task effect. Similarly, Ogden et al. (2011) who used a production task of 2-seconds intervals did not find a bi-direction effect. Their RLG task was not affected by timing. In this type of comparison – namely single and dual task comparisons – it is difficult to control the inhibition levels in a single production of an interval. Therefore, we claim that this method is more prone to controversial findings due to the possible confounding of inhibition requirements and overall task interference. In the present study, we suggest that the congruency effect which is found in the reproduction stage is subject to the central bottleneck type of interference (i.e. Ruthruff & Pashler, 2010). This is due to the higher memory decay in the incongruent trial reproductions because the conflict resolution in these trials is more demanding in terms of attentional and/or working memory resources compared to the rather automatic response activation in the congruent condition. In other words, this is

the consequence of the more dramatic memory decay as it is predicted by the attentional time-sharing account. Higher decay rate in the incongruent condition causes a loss of accumulated signals more profoundly due to the disruption of maintenance of the currently accumulating representation of the temporal duration in working memory. We suggest that a hypothetically higher amount of attentional resource allocation in the incongruent condition for better performance in timing cannot eliminate this effect because it is rather more like a bottleneck effect.

Besides congruency effect, we have presented that the appearance of a Stroop stimulus and its task-related performance gives rise to another effect – as it has already been suggested in the previous chapter – namely an overall concurrent task effect which affects both stages of the reproduction task – encoding and reproduction.

4.4.2. Overall Concurrent Task Effect

As for the encoding stage, although we did not find a congruency effect on timing we observed a task effect which leads to an underestimation of intervals. This effect is the consequence of Stroop task performance requirement which is compared to the empty trials in our experiment. This effect is argued to be different in nature in comparison to the congruency effect. The concurrent task effect is suggested to be the outcome of an interference in the updating mechanism related to the temporal information which is different from the effect of the inhibition requirement related to congruency. Both congruency and overall task effect is expected to cause a loss of accumulated signals in the internal clock. We suggest that they refer to interference in different levels of the internal clock, respectively. The congruency effect is a result of inhibition requirement of an incongruent trial of the concurrent Stroop task leading to elongated processing as compared to a congruent trial. The inhibition requirement of the Stroop task then overlaps with the inhibition of the timing task on the decision level where a premature response ending the timing task is inhibited as long as the comparison process has not been completed. On the other hand, we claim that the disruption of timing by the concurrent task is the result of an interference with the updating mechanism and thus influences the interaction between the accumulation and working memory parts of the model, in other words between the clock level and the memory level. Online maintenance of temporal information (i.e., Brown and Frieck, 2000; Ogden et al., 2011) is proposed to be related to the updating mechanism in working memory (Ogden et al. 2014). In line with this idea, we have obtained underestimated reproductions in the encoding stage block in the dual-task condition compared to the empty interval timing. Since there is no necessity for a comparison of the memory of the most recent interval and the current temporal information – like a comparison which requires a reference in

LTM –, the task interference is expected to affect the interface between the accumulator on the clock level and the working memory, but does not lead to an interference in the memory translation, namely the value conversion from working memory to the long-term memory, in the context of SET. There is no such memory comparison because this experiment is designed to involve the reproduction of the most recent interval within the current temporal context. In other words, the online maintenance of temporal information is disrupted due to the general requirements of a concurrent task causing an underestimation in timing performance. A similar interference of task requirements with updating is also expected in the reproduction stage which should give rise to an overestimation because of the compensation for the lost signals during processing of the concurrent task. However, our results did show an overestimation in the single task condition already. We interpret this result as a confounding factor of our method in which we present the single task condition, i.e., empty trials randomly mixed with the dual task conditions, i.e., trials filled with a concurrent task. It is likely that participants tended to wait for ending their estimations more than necessary for the potential appearance of a concurrent task. This additional waiting adds to the general task effect. In other words, in the encoding stage they only expect the concurrent task within the limits of the interval itself since they are only experiencing the time to be reproduced later. On the other hand, in the subsequent reproduction stage, they have the control over ending the interval. This confounding factor is the result of the within-subjects design where we are mixing single and dual-task trials along with different types of trials in terms of inhibition (congruent and incongruent trials). By using this method, we have the chance to demonstrate that the inhibition requirements of the concurrent task have an effect independent from the overall task effect. Although we could not show the overall task effect in the reproduction stage in this experiment (due to the confounding factor in the empty trials in the reproduction block), we provided evidence for task effects in the encoding stage in three different experiments (Exp-1-2 in the previous chapter and Exp-3 in this chapter). We think the task effect should be replicable because the same maintenance requirements should be at work while keeping track of time in the reproduction stage too.

As a last point, we have provided evidence for the disruption due to the overall task requirements is subject to the bi-directional effects. In other words, if participants pay more attention to the preparation of the concurrent task, then there should be less available resources for timing (resulting in a temporal location effect and faster Stroop RTs). Similarly, if participants do not prepare for the approaching concurrent task, this would lead to a better (not worse at least) performance in timing (i.e. in the late SOA condition of the encoding block). We propose that the dependence of the bi-directional effects on the attentional demands is restricted to the general task demands as opposed to the inhibition requirements.

4.4.3. Temporal Location Effect-SOA

As regards with the temporal location effect, we obtained a similar pattern of underestimation in the encoding stage across all SOAs (except the middle-late SOA comparison). In addition to that, in this chapter, we also observed a temporal location effect in the reproduction stage – but in the reverse direction. However, we did not find a significant difference between middle and late SOA conditions in the encoding stage block. We can explain the absence of a SOA effect in the encoding stage between middle and late SOAs by the presence of a RT increase in the Stroop task in the late SOA condition in this stage (see Figure 36). This decrease in performance in the concurrent task (Stroop task) can be an indication of a more accurate performance in the primary task (timing task). This issue relates to the discussion mentioned previously about the bi-directional effects of inhibition between the concurrent and the timing task. The reason of the controversy between the findings of a bi-directional influence (i.e. Brown et al. 2013; Brown 2006) and of no bi-directional influence (Ogden et al., 2011) can be the result of the uncontrolled overall task effect and the inhibition requirements of the task. Since we have three different temporal locations (SOAs) in our study we have an appropriate experimental structure for a comparison of bi-directional influences between timing and the concurrent task. We have observed a performance gain in the concurrent task in both previous experiments and in this experiment in general which means the RTs of the Stroop task goes down from early to late SOA conditions. However, we see that Stroop task RTs are higher in the late SOA compared to the middle SOA in the encoding block. We interpreted these high RTs as an indication of the experience of an unexpected event. This interpretation is in line with our hypothesis that the expectancy-related effects on timing in a dual-task design are the consequence of the preparation requirements for the concurrent task. In other words, at the late SOA in the encoding stage the expectation level is arguably low which means that the attentional orientation is not diverted to another domain such as the preparation for the Stroop task, therefore there is no less amounts of attentional resources for timing. In other words, there is no less attention for timing at the end of the interval than in the middle of the interval. Indeed, our results confirmed this line of thinking since we have found no change in the inaccuracy of middle and late SOA reproductions. We suggest that this is an indication of the bi-directional effect between timing performance and Stroop performance. Moreover, since each temporal location includes both types of Stroop stimuli (not just incongruent trials), we cannot attribute the bi-directional effect to the inhibition requirements of the Stroop task, and therefore propose attentional sharing between the timing and the concurrent task. We think that it is the bi-directional effect that explains our findings because the loss of performance gain leads to no further inaccuracy of timing in the late SOA which might otherwise be expected because of the

temporal location manipulation. In short, we suggest that the bi-directional effects between timing and a concurrent task is dependent upon the attentional time-sharing which is a result of an interference in the switch part of the clock level of the internal clock model. As Ogden et al. (2014) propose this effect is probably observable in relation to the attentional demands, but our results suggest that it is not the inhibition requirements which depend on the attentional demands, but the overall task effect causes an interference to a low or higher degree in relation to the attentional resources available for timing.

In contrast to the overall task effect, we have found that the congruency effect was not dependent upon the temporal location of the concurrent task (see Figure 32) which suggests that this effect is not related to the available attentional resources since we expect that there should be lower attentional resources for timing in the later SOA conditions. As we hypothesized before, the effect of the inhibition requirement on timing is rather more appropriate to be considered as a bottleneck effect. As it is discussed in the congruency effect section, this bottleneck causes a further memory decay in the reproduced durations due to the completion of the Stroop task is more demanding in the incongruent condition than in the congruent condition.

4.4.4. Bi-directional Effects

In the previous chapter, we have shown that although there is no congruency effect, there was a task effect of the concurrent task in both experiments. However, previous findings (Duzcu & Hohenberger, 2014) showed that a dual-task which includes a Simon task in the encoding stage causes a dramatic underestimation in the reproduction stage compared to a simple choice reaction (SCR) task which includes only congruent trials in which there is no need for response selection. Thus, our findings of no difference between congruent and incongruent Stroop trials in the encoding stage of the present three experiments, and the light of the results from Duzcu & Hohenberger (2014) which present an effect between the Simon and the SCR task together suggest an overall task effect on timing. Therefore, we interpret these results – including the overall worse performance in Duzcu & Hohenberger (2014) – by a general cognitive load effect. Similar but different to Ogden et al. (2014)'s suggestion on the relation of the inhibition requirement effect and attention, we propose that the actual dependence occurs between attention and task requirements. If there is attentional need for a more demanding task (i.e. Simon task) in general, the cognitive load might change along with the overall sustained attention thus leading to underestimation in relation to the available attentional resources. Notice that controversial findings as regards with the inhibition requirement (i.e. Ogden et al. 2011; Brown et al. 2013) were reported in

studies using a continuous production method in which the participants perform the inhibitory concurrent task. We suggest that this method is more like performing timing in one extended block (the consecutive productions are less likely to be processed as separate trials as it is in our experiment) which is open to effects of changes in sustained attention. Since there are no single trials (without a concurrent task) to compare the inhibition effects with, the controversial results can be attributed to the overall task effects which may change as a function of the level of sustained attention. In short, the bi-directional influence between the timing and the concurrent task is dependent upon the attentional resource change through the manipulation of expectancy/preparation.

Although these reciprocal performance changes in the encoding stage block can be explained by an attentional sharing between the two tasks, we still have to explain the questions of why there is no further timing inaccuracy in the timing task after the middle SOA and why there is a Stroop RT increase after middle SOA. First of all, notice that the average middle SOA in this experiment (1250 msec) was similar to the average of the late SOA of the previous two experiments (1500 msec). In a similar sense to the results of the previous chapter which show us a decrease from the early (500 msec) to the late SOA (1500 msec) condition, there was a decrease in this experiment as well from the early (500 msec) to the middle SOA (1250 msec) condition. However, after this point in the encoding stage of this experiment, we have observed no further underestimation in the late SOA (2000 msec) condition. Since the empty trials are mixed with SOA condition trials, participants might have confused late SOA trials with empty trials. If this is true they encountered an unexpected Stroop stimulus in the late SOA which is evident by the higher Stroop RTs. Since the late SOA stimulus comes later than the midpoint of the overall interval length (1500 msec), this might cause a surprise at the unexpected appearance of the Stroop stimulus which may have led to higher RTs on the one hand, and on the other hand, since the current trial can be anticipated as an empty trial after the midpoint, this would lead to an absence of the underestimation in the late SOA compared to the middle SOA condition. The confusion of late SOA trials with empty trials may also have been arisen because the total number of empty trials is higher than the total number of late SOA trials. In the encoding stage block, the Stroop RT performance decrease (i.e. slower RTs) – more attentional allocation towards timing – eliminates the inaccuracy in timing due to the limited attentional resources is now used for the timing. Other alternative for this relatively compensated timing performance in the late SOA is possibility that the participants might have added some duration to compensate – similar to a numerical addition – in this temporal location. This is possible if we assume that the inner clock is reset in the late SOA disruption – in contrast to the middle SOA – and the participants have a knowledge of elapsed time after Stroop task performance. However,

this alternative is less likely if we consider the Stroop RT increase in the late SOA. A sharing of resources explains the results better.

As regards with the reproduction stage block, the situation is reverse if we look at the early and late SOA conditions for both Stroop task and timing task performance. Because in this case there is a gain in the Stroop RT from early SOA to late SOA (better performance which means lower RTs) but the inaccuracy in timing in the late SOA was much higher than in the early SOA condition. The total expectancy effect in the reproduction stage which is observed comparing the early SOA to the late SOA corresponds to a performance gain (lower RTs) in the Stroop task. In other words, resource sharing is in favour of the Stroop task and this causes an extended overestimation in timing in the late SOA. In the next section, the reason of this variation as regards with the stages of the reproduction task will be discussed.

4.4.5. Temporal Location Effect- SOA + Block

We observed that the assumed change from the middle SOA to the late SOA in the encoding stage is diminished because of the loss of the Stroop RT gain due to a less amount of attentional resource allocation for Stroop task – which is accompanied by a higher RTs – in the late SOA. This situation suggests a diminished expectancy of the concurrent task after the middle SOA. This elimination of expectancy would lead to a vanishing of the expectancy effect on timing – fewer attentional shifts – which is consistent with the absence of the difference in timing between middle and late SOA conditions.

As for the reproduction stage, there is a significant Stroop RT gain (lower RTs) but this time we observe that there is further overestimation in the late SOA compared to the middle SOA. Our results show that the change in timing inaccuracy between early and middle SOA for both stages did not yield a significant difference. In other words, the extent of the expectancy effect is found to be similar in the two stages of the reproduction task if we consider the early and middle SOA conditions. This finding is in line with our hypothesis that the threshold comparison on the decision level of the reproduction stage does not require additional attentional resources. In this respect, we propose that this finding is more in line with a rather implicit nature of timing. If the comparison process which is theorized in SET as an attention consuming process, we would expect to observe a rather more extended expectancy effect in the reproduction stage because of this possibly central process demanding attentional resources. However, our results suggested that there was no shift in the rate of accumulation in the two stages of the reproduction task as regards with early and middle SOA. On the other

hand, a coincidence detection (Matell & Meck, 2004; Buhusi & Meck, 2005) might be a better account since it is applicable to both stages of the reproduction task because it works relatively automatic. In this account, the comparison of the experienced duration with the reference duration is based on coincidence of the captured oscillation patterns for the particular intervals. Thus, the distinction between the reference duration (in the encoding stage) and the compared duration (in the reproduction stage) is less problematic since both stages include the same type of coincidence detection process which captures the offset of the duration.

However, the comparison of early and late SOA conditions in both stages of the reproduction task revealed a more extended overestimation rate in the reproduction stage but underestimation in the encoding stage. The reason why there is no expectancy decrease after the middle SOA in the reproduction stage (which is evident by a modest Stroop RT decrease in comparison to the middle SOA) as opposed to the encoding stage (which is evident by a Stroop RT increase) might be the extra attentional requirement for the response-related process in the reproduction stage since two tasks are competing for the response activation. Since the response preparation for timing is necessary along with the expectancy of the concurrent task, the monitoring requirement of the dual-task in the reproduction stage would prevent the expectancy to decrease in this stage which in turn causes further timing inaccuracy in the late SOA compared to the middle SOA. This finding is also compatible with the hypothesis that there is a further overlap in the late SOA condition of the reproduction stage, namely an overlap for the response activation. The response activation which is independent from the response inhibition is claimed to be the reason for the overlap in favour of the Stroop task (i.e. allocating more attention to Stroop performance in late SOAs of the reproduction block which gives rise to lower RTs) which leads to an extended timing inaccuracy in the late SOA condition in the reproduction stage. In other words, the bi-directional effect works in favour of the Stroop task giving rise to an overestimation in timing. This fact leads to a more extended timing in the reproduction stage in comparison to the encoding stage in terms of the expectancy effect. This is because the resource sharing in the late SOA condition of the encoding stage works in favour of the timing task (no further inaccuracy – relatively better performance) instead of the Stroop task (higher RTs – relatively worse performance).

Another issue to discuss while comparing the SOA effects of the two stages of the timing task is whether any previously discussed finding could be affected due to the absence of a motor response in the encoding stage. Our interpretation of the nature of the comparison requirement as a non-demanding process – which we obtained from the results comparing the early and the middle SOA conditions – might be challenged by the

very fact that there was no motor response in the encoding stage. The analysis was based on the relative mean difference of the SOA conditions in each stage, thus the calculated difference in the reproduction stage was not including a motor response related difference between the early and the middle SOA since both of these SOA conditions were including a motor response which eliminates this confounding factor. However, if a motor response contracts the experienced time, considering there was one motor response less in the encoding stage since there was no timing related motor activity, this might lead to a relatively expanded experience of the interval in the middle SOA condition in comparison to the early SOA in the encoding stage. This factor might eliminate a possible extra effect due to the demanding nature of the comparison process in the reproduction stage. Therefore, a further study should be conducted to consider a potential motor response related difference between the two stages of the timing task. Moreover, in a further study, adding a self-initiated motor response to the empty trials should be a further precaution equalizing all the conditions in the empty trials and the trials with the concurrent task. In this way, we would have more support for the absence of the effect due to the mere expectation because a self-initiated motor response in the other conditions might cause a time contraction.

4.4.6. Expectation or an Interval Onset-Offset Related Switch Account

In the previous chapter, Exp-1 supported a multiplicative expectation effect for the three different interval lengths. This finding was discussed within a framework which includes both expectation related attentional sharing and a working memory decay mechanism. However, Exp-2 supported only the expectation related attentional sharing account but did not arbitrate between working memory decay or a switch related offset registration failure. Both accounts could explain the findings. In this chapter, unlike in the previous chapter, we had a chance to compare the SOA effects (both early-middle SOA and early-late SOA comparisons) in the reproduction stage as well. If we look at the early-middle SOA effects in each interval, we observed 240, 258 and 526 msec effects from the shortest to the longest interval, respectively. An onset related pacemaker acceleration account cannot explain the huge difference between 240-258 msec and 526 msec which corresponds to the difference between short-middle intervals and the longest intervals since the total duration length difference between the shortest interval and the longest interval was only 1000 msec ($= 4000 - 3000$) which only corresponds to one third of the shortest interval. In the longest interval, a linear pacemaker acceleration should cause an additional SOA effect corresponding to one third of the SOA effect in the shortest interval. Note that a non-linear pacemaker that has a lower frequency at the later parts of an interval would predict even fewer pulse losses in the longer intervals. Thus, the prediction of the pacemaker acceleration in the longest interval should be around the

340 msec ($250 + (250/3)$ msec). However, we have found that the SOA effect was around 526 msec which was way above this prediction. Moreover, we cannot explain this augmented SOA effect in the longest interval by assuming an extra interval offset registration failure because these effects were found in the early-middle SOA comparisons. The middle SOAs were 1000, 1250 and 1500 msec for each interval (3000, 3500 and 4000) and the distance from the end of the interval was quite long which should be enough for the participants to complete their concurrent task without any offset registration related timing failure. However, the results from the early-middle SOA comparisons of the intervals can be explained by expectation and working memory decay if we consider a function which increases its effect multiplicatively from the shortest to the longest interval. Moreover, the SOA effect pattern for each interval in the early-late SOA effects (311, 564, 813 msec) also resembles a multiplicative function although we did not fit one statistically. The SOA effect pattern in the encoding stage of this experiment was rather less clear since we observed that the SOA effects in the longest interval were diminished for both early-middle SOA and early-late SOA comparisons as compared to the middle interval. However, this diminishing was more pronounced in the early-late SOA comparison which might be explained by a possible change at the expectation level in the longest intervals. We have observed no further timing disruption in the overall late SOA condition on top of the middle SOA condition and it is possible that this finding which is also associated with the relatively better performance of the concurrent task in the late SOA condition in general can be attributed to the diminished expectation level in the longest interval after a point within an interval in the encoding stage.

CHAPTER 5

The Electrophysiological Markers of Expectation and Decision Processes in Timing

Expectation – which were investigated through the behavioral measurements in the previous experiments – will be the focus of this study as well, however this time, our concern is about the neural markers of this phenomena. The onset event potentials will be our focus since the efficient registration of the interval onset might be useful for a prediction of the responses in relation to the effective registration of the duration length. By this way, it might be possible to use them as a measurement of efficient working memory registration for a response prediction. Moreover, slow potentials which are generally observed between the two temporally separated signals will be investigated in terms of expectation. In addition to the possible expectation related changes in the slow potentials during an interval, we aim to study the event potentials at the end of the interval as a possible expectation marker. The offset event potentials which might be a marker of expectation would be used to predict the subjective responses.

5.1. N1-P2 and CNV Potentials in a Temporal Bisection Task

We will consider two peaks, namely the N1 and P2 peaks, separately for an investigation of timing task responses. Rufener et al. (2014) suggested that N1 and P2 peaks seem to have different source of generations, thus they stated that it is not necessary for these two peaks to occur at the same time in a task performance. In other words, the variability in the peak amplitudes of N1 and P2 peaks along with the performance change should not change in a way of strict dependence. However, this does not mean that the concurrent increases or decreases of these two peak amplitudes are not worth to consider as in the form of N1-P2 complex.

We want to follow the approach of taking these two peaks as separate but related markers. For instance, it is suggested that reduced N1 peaks are associated with higher distraction (i.e. Ponjavic-Conte et al., 2013) which is compatible with the finding that shows an increased N1 peak as a marker of attended stimuli (i.e. Ponjavic-Conte et al., 2012).

5.1.1. The registration of the Interval Beginning and N1 and P2 potentials

As regards to the time interval onset, we expect that higher N1 peaks can be an indication of an attentional orientation towards the onset of interval. Thus, we hypothesize that the higher N1 peaks might be a very early step of a successful registration of a time-stamp in the working memory. Following this approach, as a part of the attempt to predict the accuracy of the task performance, we decided to consider the N1 peak within the context of accurate responses. Thus, we expect higher N1 peaks – as it is a marker of an attentional orientation – in the accurate responses. However, there is no predefined accuracy mapping in a temporal bisection task because there are two standard intervals and the comparison intervals have duration length between these two standards. Thus, there is a middle point somewhere between them which does not belong to any of the standards. We expect that the temporal location of the point of subjective equality (PSE) would be an approximate internal representation for the average of two standards. Therefore, we hypothesize that we should observe high N1 amplitudes in the short responses for the interval lengths shorter than the PSE – which can be assumed to be the accurate response – and similarly the long responses for the intervals longer than the PSE must be associated with higher N1 amplitudes.

As for the P2 peak, Garcia-Larrea et al. (1992) suggested that it is a candidate to be a marker of the stronger inhibition process – high P2 amplitudes – against interference (Rufener et al., 2014). Senderecka et al. (2012) presented that successful inhibition in a stop-signal task was associated with high fronto-central P2 peaks. However, Rufener et al. (2014) presented that P2 peaks were enhanced in the speech task, namely the discrimination of the words and the pseudo words – which needs less inhibition – compared to the non-speech task – in which the background noise was distinguished as short or long – which includes distractors as noise between the words and pseudo words. In other words, higher P2 peaks were associated with less inhibition condition. But, in this study, although the additional distractors were included within in the non-speech task, the performances which were required in both tasks were different. Thus, the requirement of an inhibition for the speech task might be higher due to the relevancy of word discrimination was high although the participants were instructed to listen carefully all the stimulus. In short, the inhibition of general distraction to perform better in a speech task might be already high which was associated with high P2 amplitudes in this study. In line with the potential relevance of P2 peak and the inhibition of distractions, Brandeis et al. (1998) claims that P2 is an indication of an early orientation which influence later processing. Moreover, the comparison of ADHD group and the healthy controls showed that parietocentral P2 peaks were lower in the patient group in the successful stop-signals and this might be an indication of poor attentional resource

allocation (Senderecka et al., 2012). However, once again, there are controversial findings about ADHD and P2 peak which states a relation in a reverse direction (Dimoska et al., 2003; Johnstone & Clarke, 2009; Johnstone et al., 2001; Oades et al., 1996; Satterfield et al., 1994; Smith et al., 2003) as opposed to the Senderecka et al. (2012) study. Thus, we think that the presence of the controversial findings can be explained by considering the difficulty of the task and the performance in that task in terms of accuracy. For instance, Cranford et al. (2004) found that P2 potential decreases in parallel with an increase in the discrimination task difficulty. On the contrary, Kim et al. (2008) showed that P2 amplitude increases with the task difficulty. There is a controversy with regards to the role of P2 peak related to the task difficulty. These previous findings suggest that P2 amplitudes change in relation to the stimulus classification – although there is no agreement in how the discrimination difficulty modulate it – and it is sensitive to the working memory demands. In brief, we hypothesize that the difficult tasks might lead to the higher P2 peaks since they require more selective attention (i.e. Beteleva & Petrenko, 2006; Mueller et al., 2008). In other words, if the healthy participants could not manage to elicit attentional allocation for the approaching steps of the task – which is to be determined by the P2 peak amplitude – for a particularly difficult trial, the outcome of the process is most likely to be associated with the inaccurate responses. On the other hand, as for the easy trials for instance, the link between the accuracy and P2 peak might be blurred since the relatively less amount of attentional orientation might be sufficient to perform. In the onset of the temporal bisection task, since the difficulty of the interval discrimination is not yet determined, we propose that accuracy of the task response will be associated with P2 dependent variation, not with the difficulty of the task. Therefore, we expect high P2 peaks – which is a potential indication of higher attentional allocation – will be associated with the accurate responses. Higher P2 amplitudes might be taken as a better registration of the onset of the interval in the working memory which in turn expected to correspond better discrimination of the intervals as short or long in a bisection task.

5.1.2. Expectation and Contingent Negative Variation (CNV)

Animal studies suggest that some cells – which have activity peaks that are proportional to the interval length – can be addressed as the time-accumulator cells since the activity amplitude might be the neuronal representation of the durations (i.e. Merchant et al. 2013). However, in contrast to the animal studies which present clear ramping activities as the internal representations of time intervals, there exist controversial findings on the topic in human timing literature. For instance, the differentiation of the motor related and the timing specific climbing activity is one of the problems which human timing studies face in the subject field. Nevertheless, there are findings that relate the ongoing

timing with the accumulation of the particular type of activity. For instance, in Wittmann (2013), the relation of the bodily sensations and time perception is indicated as an example of the duration representation which is implemented with a ramping activity in the insular cortex. In human EEG timing studies, CNV (Contingent Negative Variation) – which is a slow negative potential – is proposed as the neural representation of the accumulation process (Wittmann, 2013). Moreover, CNV is claimed to be the signature of subjective timing in the time perception studies which takes the pacemaker-accumulator framework as a model. Although it is proposed that climbing neural activity such as CNV corresponds to the accumulation process of the pacemaker-accumulator models of timing (e.g., Macar et al., 1999; 2004), Kononowicz & Van Rijn (2014) pointed out the controversies about the role of this slow potential (i.e., Ng et al., 2011, Kononowicz & Van Rijn, 2014). The expectation and the response preparation processes are the other candidates which may be related with CNV (Wittmann, 2013). In a temporal generalization task – in which there is one standard interval– Ng et al. (2011) found that CNV increased until a point where the decision between short or long responses were made but after that plateau it started to diminish. This study suggests that CNV is likely to be related with the response preparation processes than the timing itself.

Kononowicz & Van Rijn (2014) proposed that if the peak of the climbing neural activity corresponds to the reference interval as in the study of Ng et al. (2011)'s study, the only way that grants CNV is related with the subjective time intervals is that the decision on short/long responses has been made around that point as it is proposed in Macar & Vidal (2003) study. Similarly, Pfeuty et al. (2003) found that CNV ramping ended around the reference interval in the left and medial frontal sites. But the right frontal activity continued until the end of the stimulus for the longer intervals. It is found that the different standard intervals have the same peak amplitude and thus they have different slopes (Pfeuty et al., 2005). The authors claimed that this finding supports the hypothesis that CNV in humans represents the duration length and it is compatible with the pacemaker-accumulator models of time. However, the setting of a standard interval to the same threshold (peak value) with the training does not guarantee the representation of an interval length to be set to the peak value in the comparison intervals. In other words, especially for the durations longer than the standards, there is no need for CNV peak value to represent anything related to the interval length. For instance, the finding that CNV measured in the supplementary premotor area (SMA) – which is claimed to correspond to the timing itself (e.g., Macar et al., 1999) – could not be replicated by another study (Kononowicz & Van Rijn, 2011) and a habituation effect is suggested to explain these controversial findings.

We formed our hypothesis based on a relation of CNV with expectation and response preparation. Since expectation and response preparation are closely related phenomena, we wanted to decrease the relevance of the motor response related to the timing task. For this purpose, the time between the end of the interval and the motor response was delayed. Therefore, in this situation, we can observe the relation of CNV and expectation in a clearer way. The slow potential (CNV) should keep increasing until the threshold point because of the expectation of a point for a decision, even if not for a response preparation, thus this increment would indirectly mirror the interval length until that point. Our hypothesis is that, if we decrease the speeded response requirements by delaying the motor response, the requirement for expecting the end of the interval would also decrease. Thus, we would observe a stable period of slow potential and a probable decrease after the critical threshold point similar to the findings of Ng et al. (2011).

5.1.3. Expectation, Decision and Offset N1 and P2 Peaks

Kononowicz & Van Rijn (2014) suggested that timing related processes do not end in the standard interval as the CNV climbing activity hypothesis suggest, but the interval offset ERP components (N1P2) would reflect the relation of interval length (including the longer CIs) with the standard intervals. They hypothesized that if the decision is made around the standard interval, there should not be any difference in the offset ERP amplitudes which changes as a function of the interval lengths after the standard interval point. In other words, the interval timing related process for the decision of the response would vanish until the end of the interval in case the decision is made around the standard interval. They called this hypothesis climbing neural activity hypothesis (see Figure 39) since it was suggested that a stable period of CNV is representative of the end of the expectation where the decision is already made (i.e. Ng et al., 2011). However, if timing continues after the standard interval, we should observe a change in the amplitudes of the offset ERPs and this change might be a representative of the intervals. Thus, they proposed a V-shaped pattern around the standard interval in which the most far away intervals from the standard interval would have higher N1P2 amplitude. This hypothesis was addressed as the comparison hypothesis and it was based on the odd-ball studies (Figure 39). According to this hypothesis, Brannon et al. (2008) suggested a comparison which is based on the distance of the intervals to the standard interval in the middle. As the last hypothesis with regards to the offset ERPs which was considered in Kononowicz & Van Rijn (2014), the expectancy account was presented to show a linear decrease from the shortest to the longest interval in terms of N1P2 amplitudes (see Figure 39).

Kononowicz & Van Rijn, (2014) provided results which indicate that N1P2 amplitude at the comparison interval (CI) offset changes in proportional to the distance from the standard interval. These results support the comparison hypothesis and N1P2 complex was also found to explain timing related variance better than the CNV activity (Kononowicz & Van Rijn, 2014). The comparison hypothesis was supported in a temporal generalization study in which participants were trained with one standard interval (SI). In other words, the offset N1P2 predicts a representative change in proportion to the distance to this standard interval.

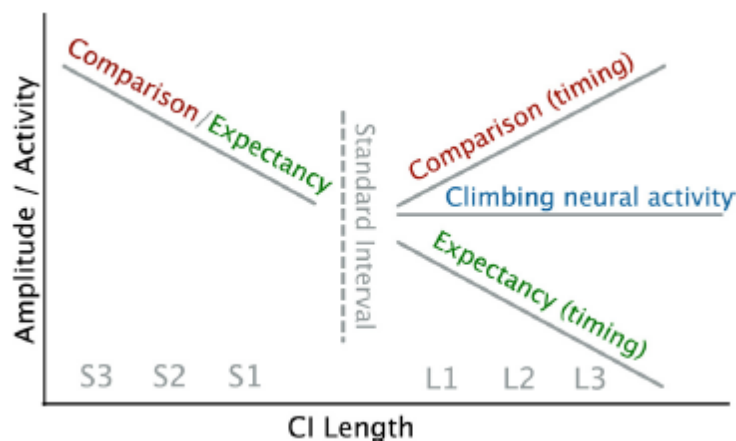


Figure 39. Three alternative hypotheses on offset ERP amplitudes (Kononowicz & Van Rijn, 2014)

In the present experiment, the same hypothesis was tested using a slightly different temporal task, namely a temporal bisection task. In this task, two reference intervals were given to the participants in the training part of the experiment and the participants were asked to respond to the CIs by giving responses about if they think CI is more similar to the short or to the long standard interval. Thus, in this experiment, there was no one middle point given as the only standard interval, but instead there were two reference intervals. In a bisection task, we can expect a point of subjective equality (PSE) which corresponds to an inner reference point for the decisions (i.e., Allan, 1999, 2002a; Allan & Gerhardt, 2001). Firstly, as one of the aim of this experiment with regards to the offset N1P2 is to test whether the N1P2 amplitudes change as a function of distance to the PSE.

Secondly, for the offset ERPs, we aim to consider the account which is based on the expectancy in a more detailed way. Considering the overlap of the two accounts, namely the comparison and expectancy accounts, in their predictions with respect to the intervals that are shorter than the standard interval, we can interpret the hypotheses by taking the presence or the absence of the unexpected events at the end of the intervals

into consideration. For instance, according to the expectancy hypothesis, the shortest interval offset is an unexpected event which shares the same prediction with the comparison hypothesis in terms of amplitudes. However, the situation might be different in the intervals that are longer than the standard interval as regards to the expectancy levels in contrast to the proposed prediction of the expectancy hypothesis (see Figure 39). If a decision is already decided after the standard threshold or the PSE, we would not expect a meaningful change of amplitudes for different responses, namely the short and long responses in a bisection task, at the interval offset. In this experiment, we propose to investigate the roles of N1 and P2 peaks separately since N1 is proposed to be more related to the unexpected event detection (e.g., Chennu et al., 2013; Annic et al., 2014) although P2 peak is rather associated with one of the very first steps of the working memory functions such as stimulus feature detection. Finnigan et al. (2011) stated that N1 is an indicator of an “attentional orientation” (i.e., Luck et al., 1990; Natale et al., 2006). As a compatible finding with its relation to the “unexpected events”, it was also found that the attentional orientation is involuntary (Alho et al., 1997). These findings bring an appropriate base for interpreting the observation of N1 peak as a very early automatic detection marker which can be modulated by attention (i.e., Hermann & Knight, 2001). Accordingly, the auditory N1 potential was found to be more negative for increased attention “towards” the stimulus in various studies (e.g., Coch et al., 2005; Ritter et al., 1988; Mangun, 1995). Thus, we hypothesize that N1 peak amplitude would be higher when the participants subjectively perceive the end of the interval as an unexpected event. Thus, the greater N1 peaks would be an indication of the short responses since we hypothesize that an unexpected end of an interval is an instance of the comparison between the standard (or the PSE) and the current temporal context and this unexpected event marker indicates that the interval does not pass the threshold yet. Because, expecting an event to happen intrinsically implies that the threshold is already passed (i.e. thus it is an expected event) and this would more likely to lead a long response since . In other words, Therefore, the comparison of the subjective response and N1 peaks for a particular interval length will reveal whether the hypothesized role of N1 within a timing context can be helpful to predict subjectivity of timing responses. However, if the decision of the response is made around the PSE, the offset N1 peak would not be a marker of subjective responses and this means that we should not expect a N1 amplitude difference for the short and the long responses in the intervals that are longer than the PSE.

As for the P2 peak, Key et al., (2005) states that the P2 potential is determined at various cognitive tasks such as selective attention (i.e. Beteleva & Petrenko, 2006; Mueller et al., 2008), stimulus changes (i.e., Naatanen, 1990), stimulus feature detection (i.e., Luck & Hillyard, 1994) and the short-term memory (i.e., Golob & Starr, 2000; Starr & Barrett,

1987). The working memory (i.e., Lefebvre et al., 2005; Taylor et al., 1990; Wolach & Pratt, 2001) and the stimulus classification (i.e., Garcia-Larrea et al., 1992) stand out as P2 peak's potential functional roles. Cranford et al. (2004) found that P2 potential decreases in parallel with an increase when the discrimination is difficult. On the contrary, Kim et al. (2008) showed that P2 amplitudes increase with the task difficulty. There is a controversy with regards to the role of P2 peak related to the task difficulty. These previous findings suggest that P2 amplitude changes in relation to the stimulus classification – although there is no agreement in how P2 peak is modulated by the discrimination difficulty – which is responsive to the working memory demands. We want to stress the role of P2 on the selective attention and the stimulus feature detection to emphasize a potentially different nature of this marker in comparison to the N1 peak. Although N1 peak seems to be related to an early automatic detection with its relation to the stimulus dependent attentional orientation, the P2 peak is mostly studied in the context of rather more cognitive aspects of a discrimination task such as feature detection. In addition to that, we should consider the higher P2 amplitude in the voluntary actions or non-actions in which an action is suppressed (i.e. Kühn et al., 2009) along with the higher P2 peak's role on the attentional allocation for the later processing (Brandeis et al., 1998). Thus, we hypothesize that the P2 peak amplitude can be a marker for the discrimination related demands where there is a relatively high difficulty with respect to the relevant response. Related to this point, we do expect any P2 peak amplitude variation which changes as a function of accuracy or response in situations where there is a difficulty in terms of discrimination. In short, the offset P2 peak related change in the subjective responses can be an indication of augmented voluntary effort to discriminate relatively uncertain intervals which are equally subject to be short or long responses.

5.1.4. Methods

In this section, the experimental flow of the experiment, information about EEG data collection and other details of the methodology will be presented.

5.1.4.1. Participants

Twenty-six (12 males) students with a mean age of 21.4 years ($SD = 2.4$) volunteered for the experiment. The data of four participants were not included in the analysis because of the excessive artifacts.

5.1.4.2. Procedure

The two standard intervals (1782 and 2662 sec) were presented in the two training blocks which were preceding the first experimental block and the third experimental block respectively. There were four blocks of experiment to let the participants have a short pause between the blocks during the experiment. The onset and the offset of the intervals were given with two tone bursts (50 msec, 440 Hz) using speakers that were placed at the two sides of the monitor. After the second tone, a feedback was presented which states that the length of the interval was 'short' or 'long'. In the experimental blocks, 5 comparison intervals (1782, 1980, 2200, 2420, 2662 msec) were used for the task in which the participants must decide whether the presented interval was more similar to the short or long standard interval and the participants were asked to press one of the predefined keys (s = short and l = long) when they see a "?" on the screen. The question mark appeared after an interval sampled from a uniform distribution between 1 to 2.5 sec to eliminate the motor response effects on the EEG data (Figure 40).

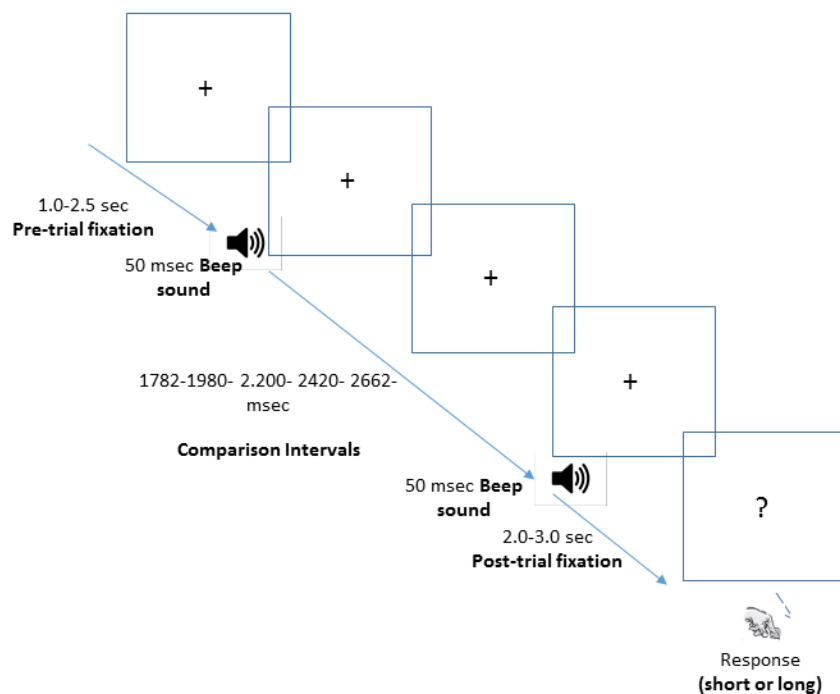


Figure 40. Experimental Flow of the Temporal Bisection Task in Exp-4

CIs (comparison intervals) were chosen in a way which was based on the middle CI (2200 msec) and each of them were % 10 shorter or longer than the closest interval that have

been used. Each block included 12 trials per duration, and 60 trials in total. Inter-trial interval was also sampled from a uniform distribution from 2 to 3 sec. A fixation cross was presented all the time during the experiment except when the participants had to press a key corresponding their decision.

5.1.4.3. EEG acquisition

The electroencephalographic activity was recorded using a 32-channel Portilab (TMSEC International B.V.) system with a sampling rate of 250 Hz. FCz channel is used for all the analysis related with CNV and N1P2 components. Vertical and horizontal EOG activity and both mastoids were measured. For all the channels, impedances were kept below 10. However, for FCz channel the impedance level is kept under 5. The pre-processing steps were done using Brain Vision Analyzer 2.0 by referencing the signal to the mastoids. The data were filtered with a Butterworth filter with a 0.01 Hz low cutoff and 100 Hz high cutoff. The trials with excessive ocular and movement artifacts were excluded from the further analysis. The horizontal eye movements and blinks were corrected with the Gratton & Coles Method.

The N1P2 component was calculated by summing the absolute amplitudes of N1 and the P2 peaks. The time windows for the N1 and P2 peak detection were 70-160 msec and 140-320 msec, respectively. The baseline correction was conducted using the average voltage 100 msec preceding the onset or offset of the duration depending upon the analysis to be conducted.

5.1.5. Results

This section includes several different analyses on both behavioural and neurophysiological data including the determination of the point of subjective equality (PSE), CNV analysis, the onset and the offset N1-P2 peak analysis.

5.1.5.1. The Point of Subjective Equality (PSE)

The point of subjective equality can be defined as the equal probability ($\text{prob} = 0.5$) of the judging the comparison intervals (CIs) as short or long compared to the standard intervals (SI). In our data, the proportion of responding as long in the middle CI (2200 msec) was 0.45. The binomial modelling (i.e., Kingdom & Prins, 2009; Knoblauch & Maloney, 2012; Lu & Doshier, 2013; Gold & Ding, 2013) is frequently used in the classification tasks (Linares & Joan, 2015).

We fitted our data by taking two response options as the binary response variables and the stimulus level as the explanatory variable to determine the PSE using quickpsy package in R (Linares & Joan, 2015). The function – a type of Weibull function – gave the PSE as 2282 msec (Figure 41).

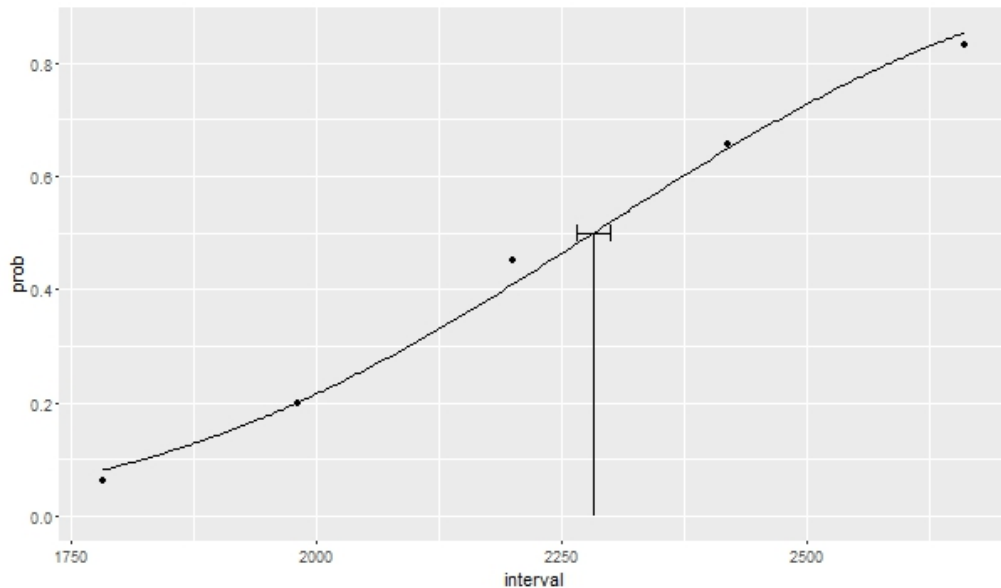


Figure 41. Long Response Proportions for each interval. The proportions are fitted using quickpsy package in R (Linares & Joan, 2015).

To find the slope of the psychometric fit, we used a logistic function of the general linear model (glm) for binomial data. In this case, the PSE was determined at 2283 msec and for the threshold value 0.5, the slope was 0.0012. Higher noise levels – indicating less sharp discrimination – are associated with lower slopes (e.g. Ernst & Banks, 2002). We have obtained relatively shallow slope which indicates that the inflection point of the psychometric function does not present a steep increment. We can interpret this as an indicator of the difficulty of the discrimination task at the middle interval since the proportion of short responses in this interval did not suggest a clear separation of the two groups, namely the intervals before and after the threshold 0.5.

5.1.5.2. CNV Analysis

To test whether there was a change in the increase of the slow potential after the PSE, we conducted a linear mixed effect model including an objective duration term with two levels (shorter/longer than the PSE, namely LeftPSE and RightPSE) and a subjective duration term with two levels (short/long responses). The dependent variable for

LeftPSE group was the difference of the mean amplitude of CNV in the 200 msec period just before the offset of the interval and the mean amplitude of CNV in the range of covering 500 msec after the onset of interval until 200 msec before the offset of the interval. By this way, we had an opportunity to capture the change in the negativity just before the end of the interval. A similar calculation was conducted for the RightPSE group; however, the ranges were different for these two intervals which were longer than the PSE. For the fourth interval, namely the 2420 msec duration, the mean amplitude until the PSE (2282 msec) was subtracted from the mean amplitude for the duration between 2282 msec and the end of the interval. Similarly, for the fifth interval (2662 msec), the CNV change was calculated by the difference of amplitude until the PSE and the amplitude of period after the PSE until the end of the interval.

Table 17. The linear Mixed Effect Model for CNV Analysis

Fixed effects:			
	Estimate	Std. Error	t value
(Intercept)	-0.53375	0.298	-1.790
short: LEFT	0.01343	0.283	0.047
Long: LEFT	-0.11068	0.378	-0.292
short: RIGHT	-0.96863	0.442	-2.188

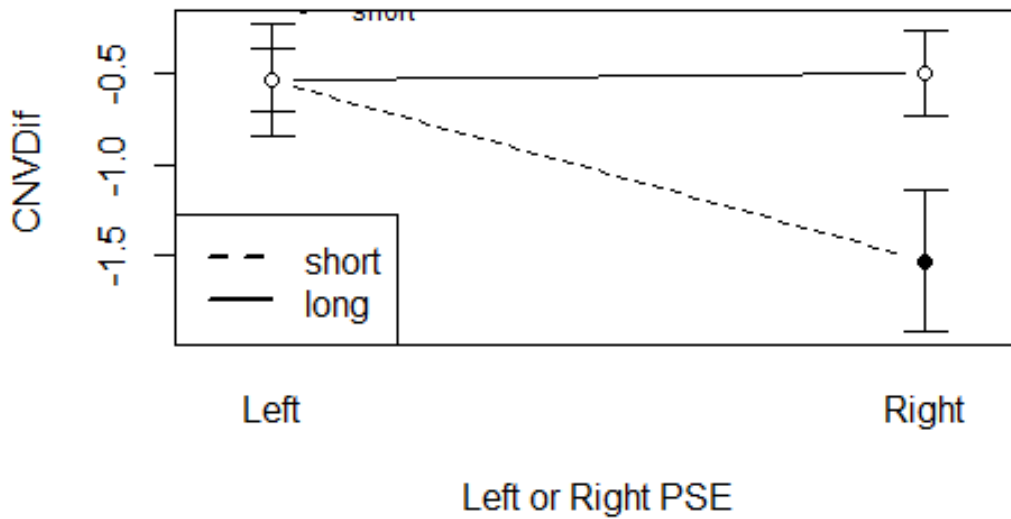


Figure 42. Mean CNV Change for the short and the long responses before and after the PSE

The model (Table 17) revealed that the intercept which corresponds to the long responses in the RightPSE group ($\beta = -0.53$, $p = .073$) did not show a significant effect.

The short responses in the Left PSE group was not found to be significantly different than the intercept ($\beta = 0.01$, $p > .05$). There was no difference between the PSE groups in terms of long responses ($\beta = -0.11$, $p > .05$). However, we did observe that the short responses in the Right PSE group were more negative than the long responses in the Right PSE group ($\beta = -0.96$, $p < .05$) (Figure 42 and Figure 43).

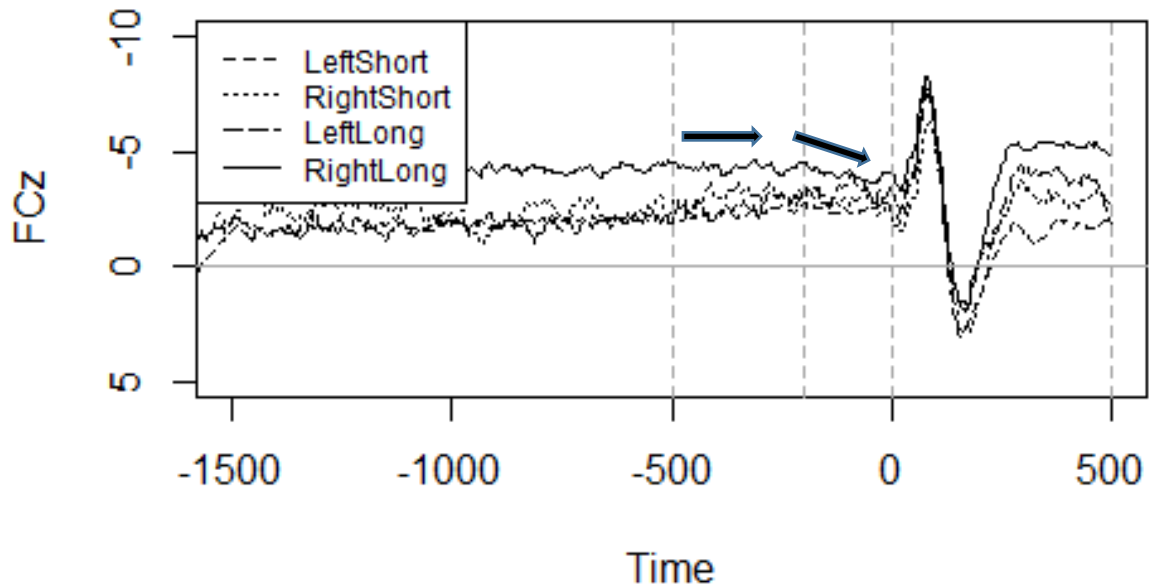


Figure 43. CNVs for the PSE and Response Groups

5.1.5.3. Onset N1P2 Analysis

We have built a linear mixed effect model which had the onset N1P2 amplitudes as the dependent variable, response (short/long) and PSE group (Left or Long) as the independent variables together with the interaction of these two terms. We compared the full model with the reduced model which lacks the interaction term and it was shown that this reduction caused a reduction of significant amount of explained variance ($\Delta AIC = 21$; $\chi^2 = 12$, $p < .001$).

Table 18. The best fitting model for the onset N1P2 amplitude and post-hoc test results

Fixed effects:			
	Estimate	Std. Error	t value
(Intercept)	25.0303	1.226	20.409
long	2.1503	0.547	3.931
Left	1.9062	0.514	3.705
long: Left	-3.3324	0.694	-4.801

Table 18. (cont.)

PSE = Right:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	2.150288	0.5471	3856.35	3.931	0.0001
PSE = Left:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-1.182081	0.4371	3855.47	-2.704	0.0069

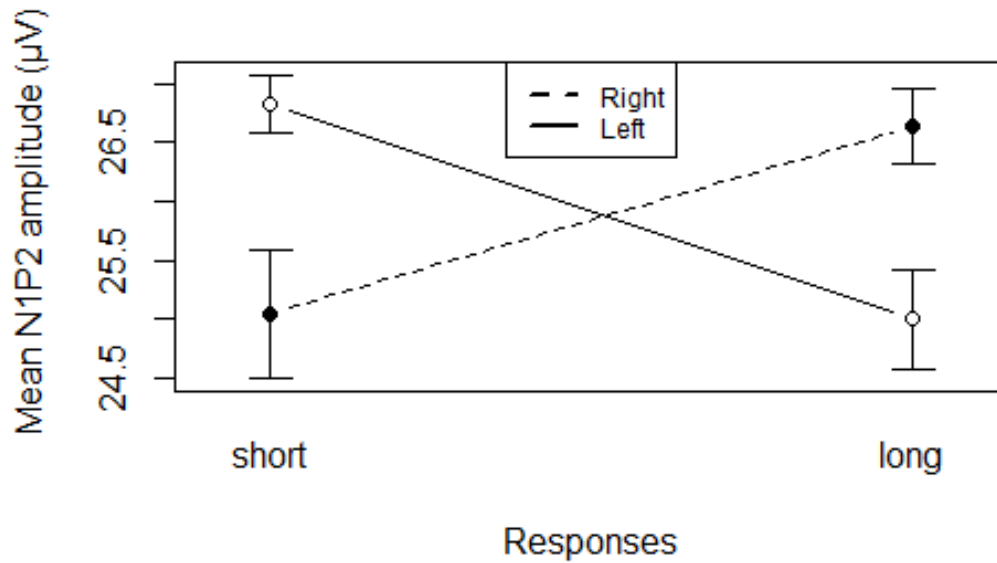


Figure 44. Onset N1P2 amplitudes for short or long responses in two groups of intervals in terms of PSE

The full model results (Table 18) showed that the intercept – which corresponds to the short responses at the Right PSE group – was significant ($\beta = 25.03$, $p < .001$). Moreover, the N1P2 amplitudes for the long responses at the Right PSE group was found to be higher than the short responses at the Right PSE ($\beta = 2.15$, $p < .001$) (Figure 44).

Moreover, there was an interaction for this difference between the short and long responses in terms of the block ($\beta = -3.33, p < .001$). Thus, we performed a post-hoc test to be able to show the difference in terms of PSE block.

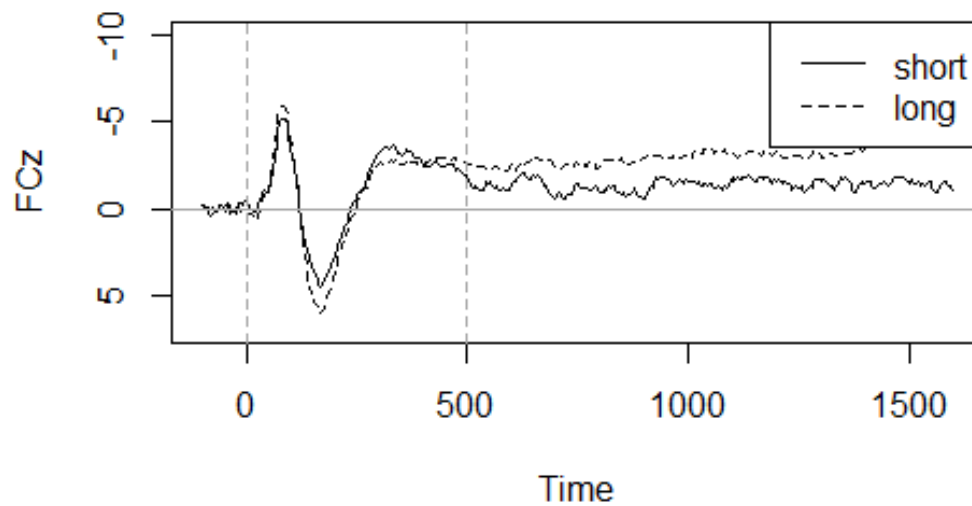


Figure 45. Onset N1P2 for Short and Long Responses in the Right PSE Group

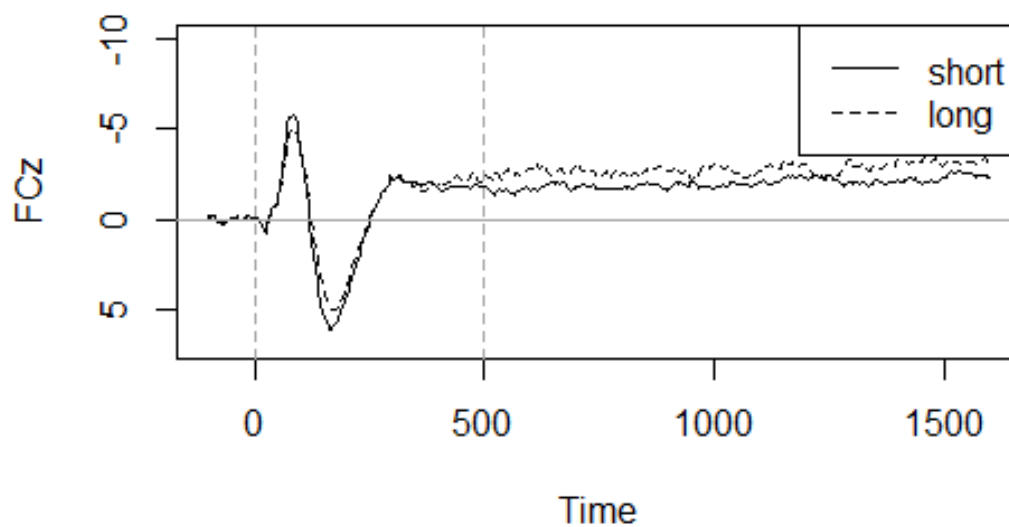


Figure 46. Onset N1P2 for Short and Long Responses in the Left PSE Group

It was shown that the amplitudes for the long responses at the Left PSE group was found to be smaller than the ones for the short responses ($\beta = -1.18, p < .01$) (see Figure 45 and

Figure 46). The accuracy and the onset N1P2 complex is shown in the Figure 47.

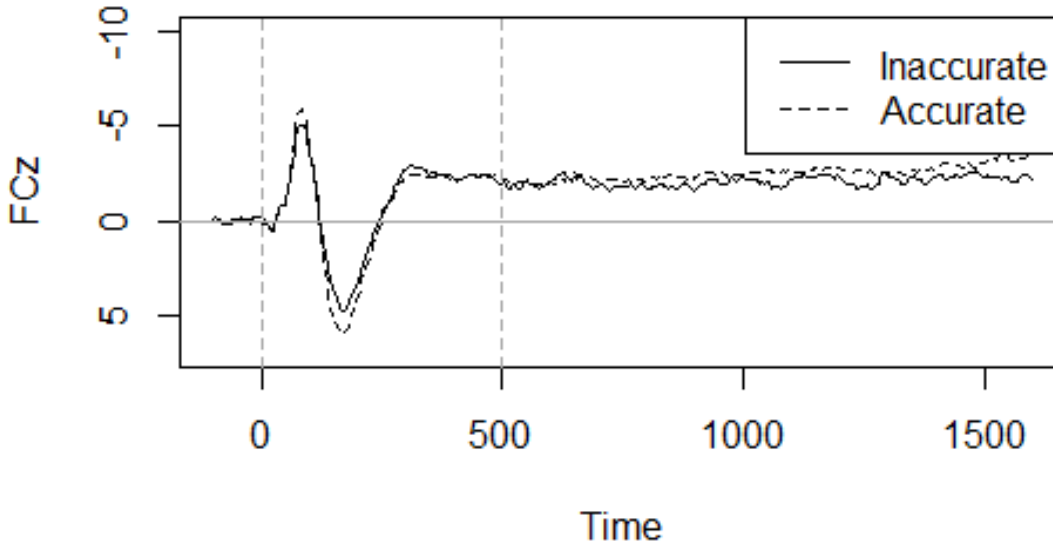


Figure 47. Onset N1P2 for Accuracy in terms of the group PSE and responses

5.1.5.4. Offset N1P2 Analysis for PSE Groups

The first analysis for the offset N1P2 was built upon the same design that includes the PSE group (shorter or longer than the PSE) and subjective responses (short or long) as the independent variables along with the interaction terms of them, and the N1P2 amplitudes as the dependent variable. First, we removed the interaction term to compare it with the full model and this reduction resulted a significant change in the model variance ($\Delta AIC = 5$; $\chi^2 = 4$, $p < .001$). The full model (Table 19) revealed that the intercept which corresponds to the short responses at the Right PSE group was significant ($\beta = 24.7$, $p < .001$).

Table 19. The best fitting model and post-hoc tests for the offset N1P2

Fixed effects:			
	Estimate	Std. Error	t value
(Intercept)	24.5780	1.1818	20.797
long	-0.0671	0.5248	-0.128
Left	1.1036	0.4935	2.236
long: Left	-1.8002	0.6659	-2.703

Table 19. (cont.)					
PSE = Right:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-0.06709946	0.524	3856.30	-0.128	0.8983
PSE = Left:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-1.86730044	0.419	3855.44	-4.453	<.0001

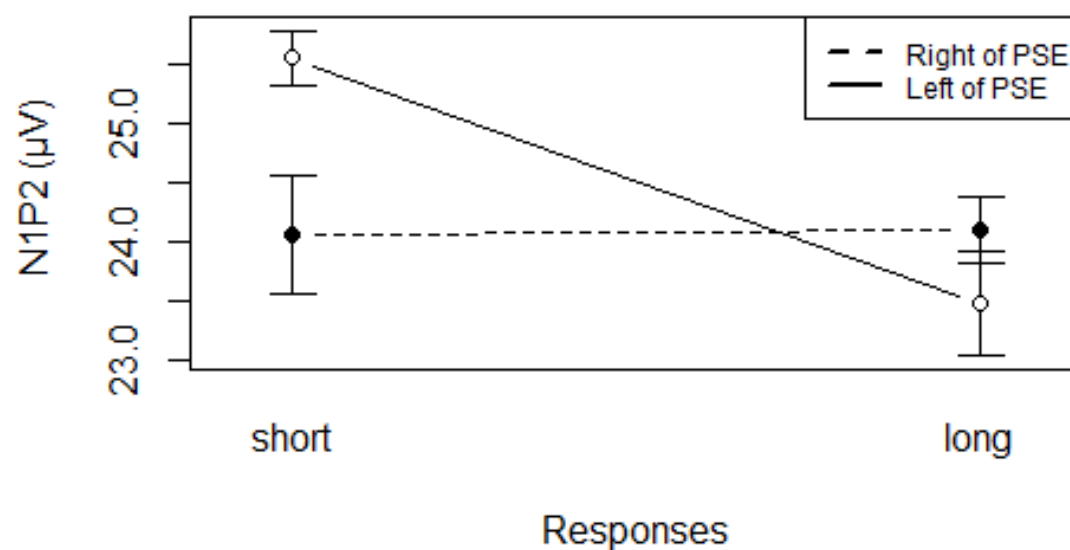


Figure 48. Mean Offset N1P2 amplitudes for the responses in the two groups of PSE

The model does not give a significant difference between short and long responses at Right PSE group ($\beta = -0.07$, $p > .05$) (Figure 48 and Figure 49).

Since there was a significant interaction of Left PSE group in terms of short and long response N1P2 amplitudes suggests ($\beta = -1.8, p < .01$), we conducted a post-hoc test to see the effect of response in the Left PSE group.

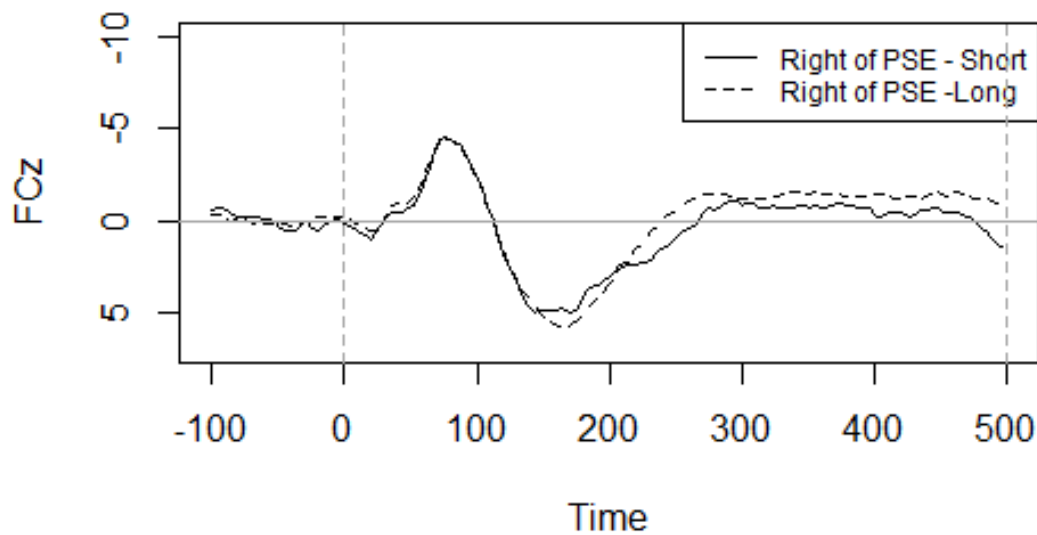


Figure 49. Offset N1P2 potential for short or long responses in the Right PSE group

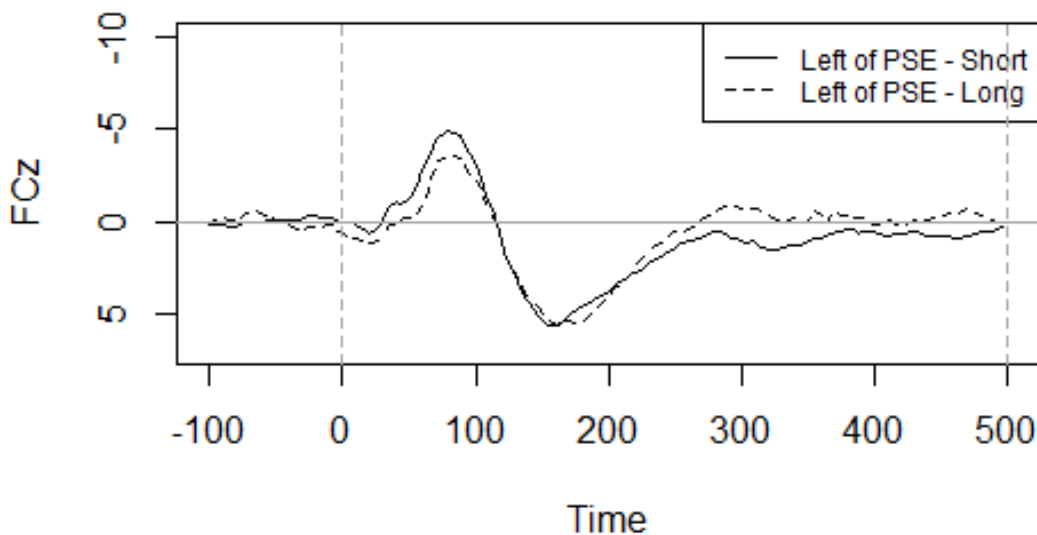


Figure 50. Offset N1P2 potential for short or long responses in the Left PSE group

The post-hoc test showed that the long response N1P2 amplitudes were lower than the short response N1P2 amplitudes in the Left PSE group ($\beta = -1.87, p < .001$) (Figure 48 and

Figure 50).

5.1.5.5. Offset N1P2 Analysis for Distance to the PSE

The full model and the reduced model which lacks interaction was compared for observing whether CIs were affected by the subjective responses as short or long and whether the distance from the middle duration was a factor which affected the measured N1P2 amplitudes. The distance term was defined to have three levels (0, 1, and 2) as the predictor – 0 as the middle duration – and N1P2 amplitudes as the dependent variable with a random intercept per participant. The comparisons were based on the AIC and they revealed that the model with the interaction was better than the reduced model ($\Delta AIC = 7$; $\chi^2 = 11.2$, $p < .001$). The complete model which includes the interaction term showed that the effects of the intercept ($\beta = 25.8$, $p < .001$) – which corresponds to the short responses at the middle interval – was significant. The comparison of the short and long responses in the middle interval was significant ($\beta = -2.72$, $p < .001$). The distance variable for either level was not significant in terms of short responses ($\beta = -0.68$, $p > .05$) and ($\beta = -0.19$, $p > .05$). Since we observed an interaction of the first level of distance and the long responses ($\beta = 2.49$, $p < .001$), we decided to conduct a post-hoc test for this interaction, we saw that the N1P2 amplitudes were higher in the first level of the distance for the long responses ($\beta = 1.81$, $p < .01$), on the other hand, the distance effect for the second level for the long responses was rather close to the significance level ($\beta = 1.12$, $p = .0087$) (Table 20) (Figure 51).

Table 20. The linear mixed effect model for the distance analysis

Fixed effects:					
	Estimate	Std.Error	t value		
(Intercept)	25.8543	1.16	22.122		
distance1	-0.6861	0.49	-1.380		
distance2	-0.1948	0.50	-0.383		
long	-2.7265	0.60	-4.473		
distance1: long	2.4973	0.75	3.318		
distance2: long	1.3163	0.75	1.736		
Response = short:					
contrast	estimate	SE	df	t.ratio	p.value
1 - 0	-0.6861233	0.497	3850.40	-1.380	0.2899
2 - 0	-0.1947885	0.508	3850.70	-0.383	0.8847
Response = long:					
contrast	estimate	SE	df	t.ratio	p.value
1 - 0	1.8111911	0.563	3851.08	3.213	0.0026
2 - 0	1.1214719	0.562	3850.77	1.993	0.0866

We decided to conduct another analysis to investigate whether the response effect in the N1P2 amplitude was dependent upon the individual intervals rather than the distance to the middle duration. Thus, this model was built to include the terms of subjective responses (short/long) and the intervals (5 levels). The results of the complete model – the intercept which corresponds to the middle interval short responses ($\beta = 25.8, p < .001$) – and the post-hoc tests (Table 21) showed that N1P2 amplitude changes depending on the response only in the middle interval ($\beta = -2.72, p < .001$) (see Figure 51).

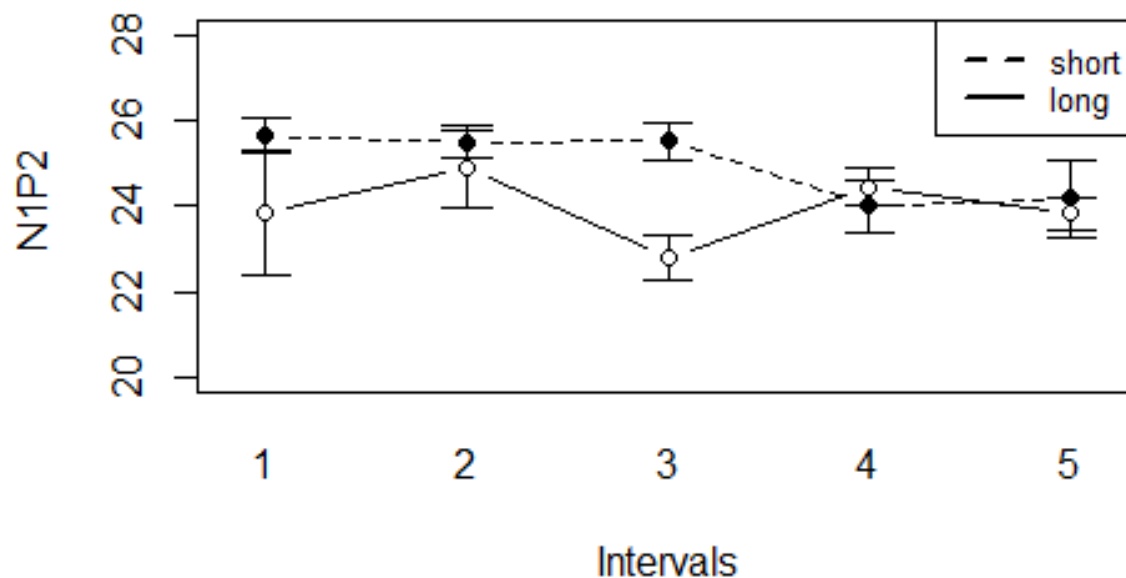


Figure 51. Mean Offset N1P2 amplitudes for each interval and response

Table 21. The linear mixed effect model for the intervals and subjective response analysis

Fixed effects:			
	Estimate	Std.Error	t value
(Intercept)	25.8458	1.168	22.121
interval1	0.0570	0.525	0.109
interval2	-0.5106	0.529	-0.965
interval4	-1.1276	0.677	-1.665
interval5	-1.5603	0.883	-1.767
long	-2.7063	0.609	-4.440
interval1: long	0.5096	1.464	0.348
interval2: long	2.7955	0.973	2.872
interval4: long	2.7751	0.903	3.072
interval5: long	2.7182	1.050	2.587
interval = 3:			

Table 21. (cont.)					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-2.70628162	0.609	3848.21	-4.440	<.0001
interval = 1:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-2.19669212	1.334	3848.48	-1.646	0.0998
interval = 2:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	0.08919953	0.765	3848.29	0.116	0.9073
interval = 4:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	0.06884372	0.674	3848.57	0.102	0.9187
interval = 5:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	0.01191797	0.865	3850.01	0.014	0.9890

These results suggest that N1P2 complex seems to be useful for predicting behavioral responses only in a particular interval. The observation that the offset N1P2 difference in the Left PSE group was suggested to be mostly caused by the difference in the N1 peak difference but not P2 peak in the previous analysis (see Figure 50), thus we decided to conduct another analysis which was based on the amplitudes of N1 and P2 peaks separately in line with the indications in the literature that they are the markers of potentially separate processes in timing related phenomena.

5.1.5.6. Offset N1 Analysis for PSE Groups

The full model included the two PSE groups and the two responses as the independent variables along with the interaction of these two terms and N1 amplitude as the dependent variable. The removal of the interaction term caused a significant change in the variation explanation ($\Delta AIC = 6$; $\chi^2 = 4$, $p < .01$). The complete model revealed that the intercept (which corresponds to the short responses in the Right PSE group) effect was significant ($\beta = 10.2$, $p < .001$) (Table 22).

Table 22. Offset N1 analysis for the PSE Groups and subjective responses

Fixed effects:			
	Estimate	Std.Error	t value
(Intercept)	10.1966	0.583	17.481

Table 22 (cont.)					
long	0.5480	0.396		1.383	
Left	0.7258	0.372		1.948	
long: Left	-1.4194	0.502		-2.823	
PSE = Right:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	0.5479538	0.396	3863.28	1.383	0.1667
PSE = Left:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-0.8714843	0.316	3861.27	-2.753	0.0059
Response = short:					
contrast	estimate	SE	df	t.ratio	p.value
Left - Right	0.7257522	0.372	3859.18	1.948	0.0515
Response = long:					
contrast	estimate	SE	df	t.ratio	p.value
Left - Right	-0.6936859	0.337	3857.35	-2.053	0.0402

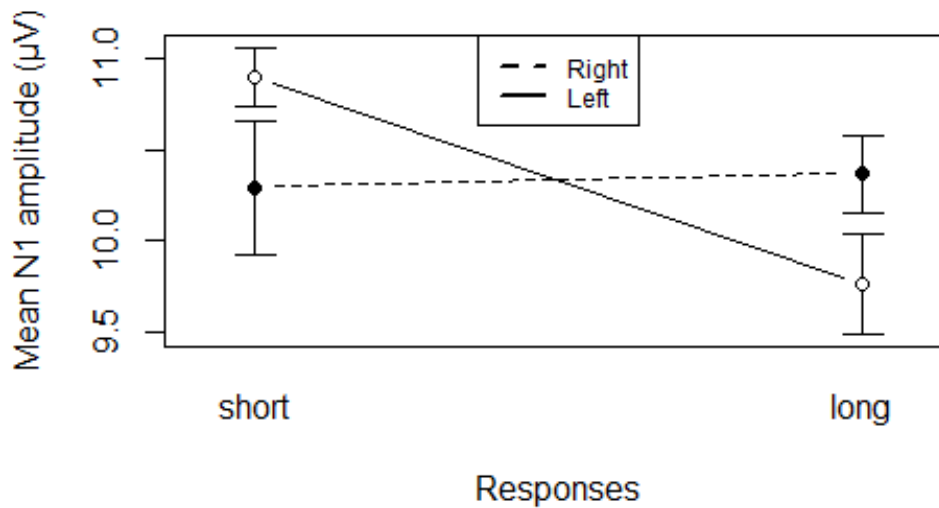


Figure 52. Mean Onset N1 peak amplitudes for the responses in each PSE Group

There was no indication for a difference in N1 amplitudes between the short and the long response in the Right PSE group ($\beta = 0.55$, $p > .05$). However, the presence of the

interaction with regards to the Left PSE group in terms of the short and the long response difference ($\beta = -1.42, p < .01$) suggests that the long response N1 amplitudes were lower than the short response amplitudes in the Left PSE.

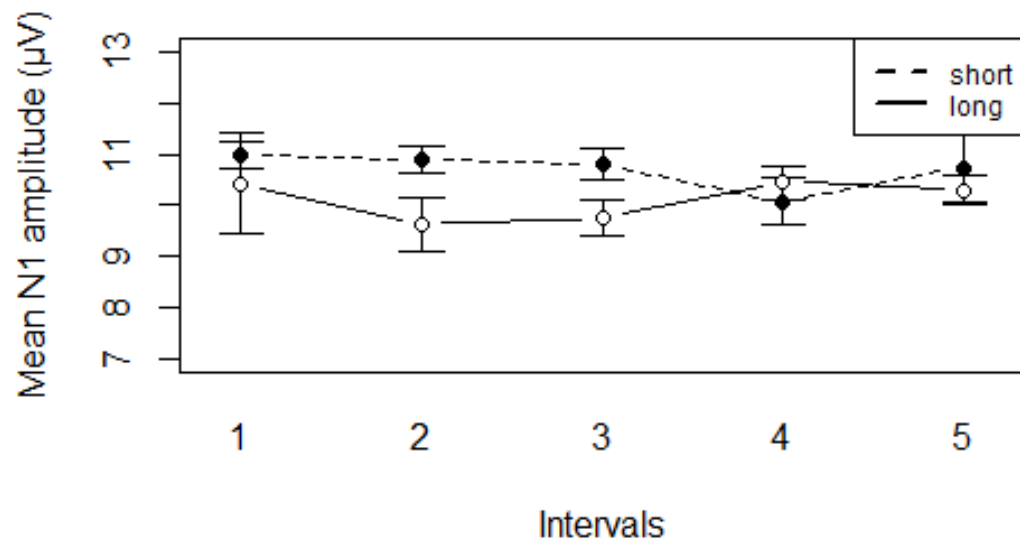


Figure 53. Mean Offset N1 amplitudes for each interval

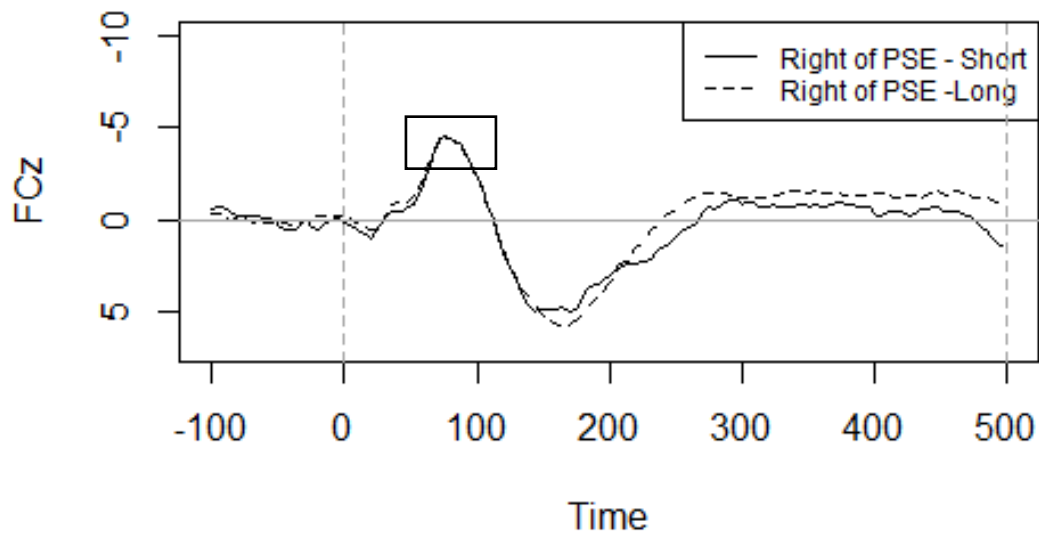


Figure 54. Offset N1 peaks for the responses in the Right PSE group

Indeed, the post-hoc tests revealed that the long response had lower peaks than the short responses in the Left PSE group ($\beta = -0.87, p < .01$) (Figure 52 and Figure 53).

Moreover, a second post-hoc test showed that the short response N1 peaks were marginally higher in the Left PSE than the Right PSE group ($\beta = 0.72, p = .052$), and the long response N1 peaks were found to be lower in the Left PSE than in the Right PSE ($\beta = -0.69, p < .05$) (Figure 54 and Figure 55).

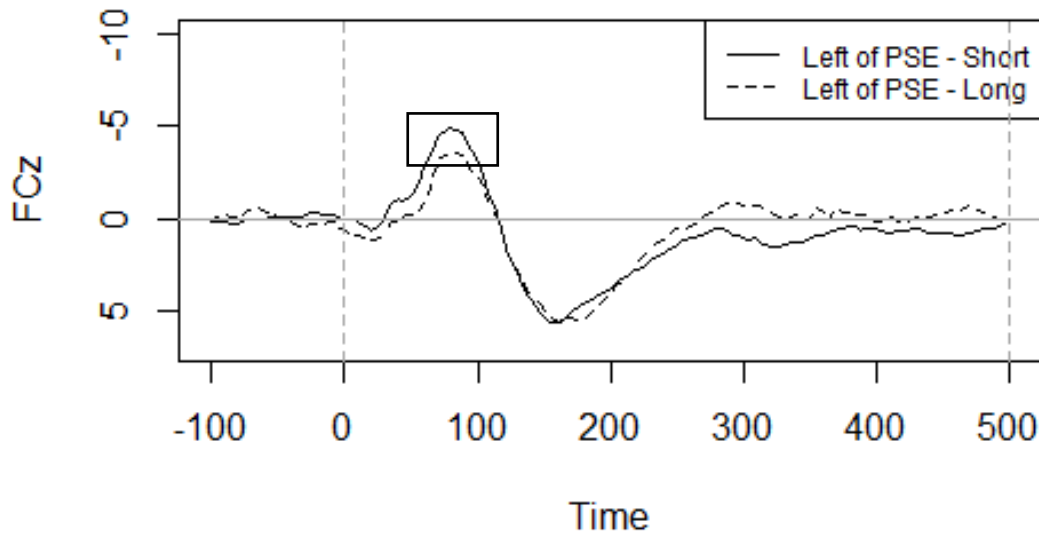


Figure 55. Offset N1 peaks for the responses in the Left PSE group

5.1.5.7. Offset P2 Analysis for PSE Groups

The model included the two PSE groups and the two responses as the independent variables along with the interaction of these two terms and P2 amplitude as the dependent variable. The intercept effect – which corresponds to the long responses in the Left PSE Group – was found to be significant ($\beta = 13.75, p < .001$) and the results indicated that the short responses in the Left PSE group had higher P2 peaks than the long responses in the Left PSE group ($\beta = 1.00, p < .01$) (Table 23). However, we have found no difference between the short and the long responses in the Right PSE group ($\beta = -0.62, p > .05$) (Figure 56).

However, since the P2 difference was suggested to differ not accordingly the PSE groups but change in a particular interval (Figure 56), namely the middle interval, we decided to conduct further analysis which was based on the intervals and the responses.

Table 23. The Best fitting model for the Offset P2 peaks

Fixed effects:					
	Estimate	Std. Error	t value		
(Intercept)	13.7494905	0.805	17.080		
short: Right	0.6227488	0.538	1.155		
long: Right	-0.0006883	0.414	-0.002		
short: Left	1.0061713	0.387	2.594		
PSE = Right:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-0.6234371	0.485	3859.71	-1.284	0.1993
PSE = Left:					
contrast	estimate	SE	df	t.ratio	p.value
long – short	-1.0061713	0.387	3858.24	-2.593	0.0095

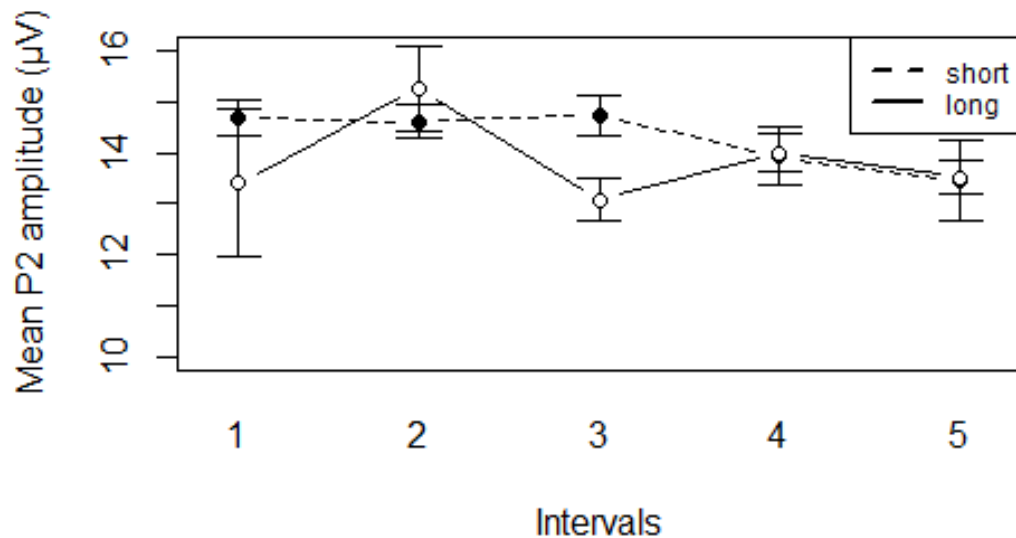


Figure 56. Mean P2 amplitudes for the short and the long responses in each interval

The model results (Table 24) indicated that the intercept – short responses in the middle interval – effect was significant ($\beta = 15.05$, $p < .001$), and the long responses in the middle

interval were founded to have smaller P2 peaks compared to the short responses in the middle interval ($\beta = -1.98, p < .001$) (Figure 57).

Table 24. Interval and Response analysis for P2 peak

Fixed effects:					
	Estimate	Std. Error	t value		
(Intercept)	15.0512	0.82	18.266		
interval1	-0.2852	0.48	-0.587		
interval2	-0.5138	0.48	-1.050		
interval4	-0.5000	0.62	-0.798		
interval5	-1.0470	0.81	-1.281		
long	-1.9775	0.56	-3.506		
interval1: long	0.9803	1.35	0.723		
interval2: long	2.7590	0.90	3.063		
interval4: long	1.3301	0.83	1.591		
interval5: long	1.6009	0.97	1.647		
interval = 3:					
contrast	estimate	SE	df	t.ratio	p.value
long – short	-1.9774678	0.564	3850.07	-3.506	0.0005
interval = 1:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-0.9971213	1.234	3850.55	-0.808	0.4194
interval = 2:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	0.7815157	0.708	3850.20	1.103	0.2702
interval = 4:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-0.6474100	0.624	3850.71	-1.037	0.2997
interval = 5:					
contrast	estimate	SE	df	t.ratio	p.value
long - short	-0.3765364	0.801	3853.20	-0.470	0.6383

The post-hoc tests showed that there was no difference between the short and the long response P2 amplitudes in the other intervals.

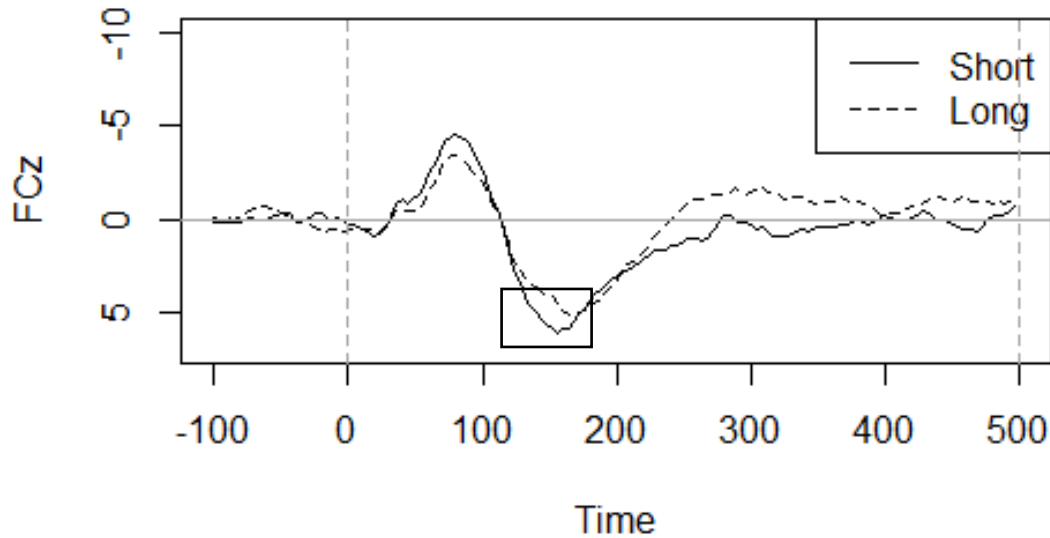


Figure 57. P2 peak difference for the short and the long responses in the middle interval

5.1.6. Discussion

Several different topics such as the relation of expectation and CNV, interval onset registration and N1P2, the relation of offset N1 and P2 peaks to expectation and discrimination will be discussed under different titles of this section.

5.1.6.1. Expectation and CNV

Our results with regards to the relation between expectation and CNV indicated a change in the course of the slow potential around the point of subjective equality as it was suggested in the Ng et al. (2011)'s study. However, this change in the CNV course was found to be dependent upon the subjective responses – that is distinct from the Ng et al. (2011) study – not just related to the interval length. In other words, we did observe a stable period and then a decrease in CNV in the long responses for the long intervals (the intervals longer than the PSE). This slowing down of the ramping activity reflected as a no change (in the analysis) at the end of the interval for the long responses in comparison to the short responses. In other words, we have observed a negativity increase until the end of these intervals in which the participants responded as short. On the other hand, the difference in CNV mean at the end of the intervals for different

responses was not observed for the intervals which were shorter than the PSE (see Figure 43). We can interpret this result by taking the PSE as an internally represented point in the temporal extension of expectation that is determined in terms of the decision about the responses. More interestingly, it is not the objective length of the interval which defines the point because we saw no change in the CNV course when the participants experienced the interval as short even if the intervals were in the same group of intervals, namely longer than the PSE. It seems that the threshold – for deciding a particular interval as being long – was not passed subjectively in these trials (short responses for the long intervals). The reason for these inaccurate responses might be related with a disrupted registration of the interval onset. Indeed, in the long intervals in which the participants responded as short, we have observed an initial decrease of CNV in the onset of these trials (see Figure 45). Moreover, the onset N1P2 analysis already showed that the amplitude of N1P2 – which was hypothesized to be an indicator of the good registration of the interval onset – was low in comparison to the accurate classification of the same length intervals. On the other hand, as for the intervals that were shorter than the PSE, the change in the CNV course seems to be not informative for a purpose of predicting subjective responses. The reason might be the chosen period (200 msec) for the analysis. If the inner threshold point is passed in these trials in a temporal place which is rather closer to the end of the interval, a potential difference in terms of the responses in the short intervals might not be caught in the analysis.

5.1.6.2. The interval Onset Registration and N1P2

We have provided evidence for the relationship of accuracy in timing and the onset N1P2 amplitude in this experiment. Since the hypothesized directions of N1 and P2 peak amplitudes were same – higher peaks are indicators of better attentional orientation and of better inhibition of interference for N1 and P2 respectively – we have based our analysis on the N1P2 amplitude. The better orientation towards an explicit stimulus feature – the presentation of an interval onset in the auditory modality – as it is suggested by augmented N1 peaks and a better inhibition of an inner interference – as a marker of better attentional resource allocation – as it is suggested by increased P2 peaks were found to be associated with the higher accuracy in the responses. Thus, our results support the view that greater P2 peak is related to the stronger inhibition process – as an indication of better protection from an interference – which was found to be evident in the successful trials (i.e. Garcia-Larrea et al., 1992; Senderecka et al., 2012) in contrast to the reverse pattern in which the less inhibition required task have higher P2 peaks (i.e. Rufener et al., 2014). The controversy can be explained by the different task requirements of the speech and non-speech tasks in terms of task performance in the Rufener et al. (2014) study. Speech task might have still more requirement for the

inhibition for the word discrimination than the non-speech task although there are distractors which should be inhibited in the non-speech task. Typically, P2 peak is associated with the difficulty of the task although there are some controversies on this issue. Some findings indicate that the P2 potentials are lower when the discrimination task difficulty is high (i.e. Cranford et al., 2004), on the other hand, other studies showed that P2 peak is higher when the task is difficult (i.e. Kim et al., 2008). As the difficult response demanding which is faced by the participants requires more involvement of the working memory, the difficulty might cause more voluntary effort into the task in hand. The contrasting findings might be resulted from the possibility that P2 changes as a function of the task performances which is related to the accuracy. However, these two studies did not provide such differentiation of the P2 peak in terms of accuracy and thus this might be the reason that they have found different patterns of P2 peak modulation with the difficulty. Since the onset P2 peak cannot be related to the task difficulty yet – i.e. short or long decision for the intervals where the difficulty is high for such a response – we propose that the high P2 peak might correspond to the better activity of the working memory in terms of utilizing attentional resources for later processing of the task relevant stimulus. In this context, the task relevant context is to be attentive to the length of the interval and thus the onset P2 peak is a candidate for being a marker of the low or high distraction for the subsequent necessities of the task. Indeed, low P2 peak amplitudes together with the low N1 peaks were associated with an initial distraction in the course of CNV at least for the inaccurate responses, namely the short responses, in the long intervals (see Figure 45).

5.1.6.3. The offset N1 and P2 Potentials, Expectation and Discrimination

We have hypothesized that the interpretation of the N1 and P2 peaks must differ since the associated roles in the interval offset indicate different predictions in contrast to the onset interval N1P2 complex. For instance, as for the offset N1 peak, the higher amplitudes are proposed to be an indication for the unexpected events since we hypothesize that the attentional orientation – which is involuntary (i.e. Alho et al. 1997) – towards the early stimulus features is in line with the interpretation for the offset N1 peak should be higher for the unexpected events. Indeed, the results showed that N1 peak amplitudes were augmented in the presence of the short responses. This result suggests that N1 peaks were found to be higher when the comparison of the current temporal context with an internal representation of the threshold for a decision did not match. In line with the findings with regards to the suppression of N1 peak with the predictable sounds along with the enhancement of N1 peak with attended sounds (i.e. Paris et al., 2014), we presented that N1 enhancement occurred when the participants cannot predict the end of the interval – when they were not expecting the offset – which

was associated with the short responses. Moreover, Timm et al. (2013) found that N1 suppression is not related to the attentional allocation in self-initiated sounds and they suggested an internal prediction mechanism. Our results are in parallel with this involuntary N1 suppression and enhancement explanation because implicit timing process – along with an automatic decision – were shown to modulate the subjective responses only before the PSE which was a reference point for the internal prediction. After that point, we did not observe a variation in N1 peaks which indicates that it is no more informative in terms of the subjective responses. One of the explanations for this finding is that the decision was already completed around the PSE and this account is different than the previous finding in which the N1P2 was suggested to reflect timing for the intervals which are longer than the standard (i.e. Kononowicz & Van Rijn, 2014). The reason for this controversy between the results with regards to the offset N1P2 might be the fact that the subjective responses were not considered in the previous study.

As for the P2 peak and its relation to the responses, we have presented support for the hypothesis that P2 peak was modulated by the difficulty of the task as it was suggested by the previous studies (Cranford et al., 2004; Kim et al., 2008). Thus, P2 might be indeed related with the attentional boost (i.e. Prandeis et al., 1998) in the face of a voluntary effort (i.e. Kühn et al., 2009) for a better task performance (i.e. Garcia-Larrea et al., 1992; Senderecka et al., 2012). Our results indicated that P2 amplitudes were higher for the short responses only in the middle interval – in which the difficulty was the highest – in an accurate way in terms of the place of the PSE. The lower P2 amplitudes which were associated with the long responses in this interval can be explained by a poor focusing on the discrimination task in terms of the search for an answer. The relation of the P2 peak and the working memory suggests that the low P2 peaks can be seen as an indication of distracted task performance which was also supported by a study which showed that ADHD patients have an attenuated P2 peak in comparison to the healthy participants (i.e. Senderecka et al., 2012). One of the questions is about why we did not observe the variation in the P2 peaks in the other intervals. The suggestion for the same question with regards to the N1 peak is also applicable for P2 peak for the intervals longer than the PSE. The offset ERPs, at least N1P2 complex, does not reflect the subjective responses because of the completed decision process around the PSE, and this line of thinking is valid for the P2 since there is no more necessity for the involvement of the working memory in a higher extend at the offset of the interval. As for the intervals shorter than the PSE except the middle interval, we did not observe a voluntary P2 modulation because the decision is rather automatic that is marked by an expectation related involuntary match or mismatch between the current temporal context and the internal representation of the PSE.

In summary, in this experiment, we have provided support for the hypothesis that states N1 and P2 peaks are electrophysiological markers of independent but related processes. Moreover, these results suggest that N1 is rather more related to an implicit match or mismatch between the temporal information in the context and the internal representation which was built over the experiment. For instance, higher onset N1 peaks can be an indication of an efficient marking in the working memory – which are associated with the accuracy – and similarly the offset N1 peaks can be the efficient registration of the end of the interval – but only for the short intervals in comparison to the PSE – which match with the accurate responses. On the other hand, P2 was found to be modulated by the difficulty in the context which was probably a marker of an effort that was voluntarily provided by the participants when it was needed. In other words, if the N1 augmentation is not sufficient to resolve the response conflict in an automatic way – notice that N1 is higher for the short responses in the middle interval – the accurate response can be given by the participants when the additional attentional boost could be involved for a better performance which was indicated by the higher P2 peaks in the short responses of the middle interval. The accuracy and higher P2 peak amplitudes in the onset of the interval was only observable in the high difficulty condition, namely the middle interval, in the offset of the interval since the decision can be based on a rather automatic matching in the shorter intervals.

5.2. The investigation of Expectation and Discrimination in a tri-section method (Experiment-5)

In this experiment, we have used a new temporal task, namely a tri-section task, to confirm our interpretations in the previous experiment about N1 and P2 peaks.

5.2.1. N1 Peak as a marker of inner threshold for timing related decisions

In the previous experiment, the results suggested that the change in the CNV course after the threshold – namely the PSE – can be a marker of a growing expectation. The decrease in the CNV after a temporal point – which is an inner representation of the highest expectation – can be claimed to be an indication of a diminish in the expectation related processes. Indeed, the offset N1 peak as another marker of expectation – high amplitudes were suggested to be an indication of the unexpected events – does not reflect a modulation of the responses after the point of subjective equality. In other words, N1 peak was found to be an ERP component which helps us to differentiate the subjective responses as short or long in a temporal bisection task.

In this experiment, we have designed a temporal tri-section experiment to test the role

of the N1 peak that was found in a bisection task. In this tri-section task – in which there are three options as short, middle and long responses – we also hypothesize that the N1 peak can predict the subjective responses with respect to the temporal place of the subjective equality point (s). The more crucial question is whether the N1 amplitude is sensitive to the two potential PSEs – namely the PSE1 in between the short and the middle responses and the PSE2 in between the middle and the long responses – or just to the second PSE2 or to an average value of both two PSEs. If there is a particular inner representation for the middle point between the short and the middle standards which is built during the experimental session, we can expect that N1 peak amplitude would be a relevant marker for predicting the short or the middle responses. However, bearing in mind that N1 peak is related to expectation (i.e. Chennu et al., 2013; Annic et al., 2014) and the CNV course – as a marker of growing expectation – can have ramping, stable and declining stages but not a secondary ramping tendency, we hypothesize that N1 peak can only differentiate the responses with respect to only one threshold. In other words, we predict only one threshold in which expectation builds until that point, thus N1 component is more likely to reflect only the differentiation of the long responses from the “shorter” responses, namely the short and the middle responses. We suggest that the most probable temporal point for this hypothesized threshold in this trisection design is the middle standard interval or around the PSE2. To put it another way, we would have an opportunity to test the findings with regards to the N1 peak and its relation to expectation by an introduction of the third response option. The absence of a N1 peak modulation in terms of the short and the middle responses would suggest that expectation develops until a point, thus the prediction of the subjective responses in terms of N1 amplitude is not possible for the short and middle responses.

5.2.2. P2 peak as a potential marker of discrimination difficulty in timing related decisions

In the previous experiment, the bisection task results supported a separate consideration of the offset N1 and P2 peaks since it was found that the responses can be modulated by the N1 peak although there was no any change in the P2 peak amplitude. In contrast to the automatic and involuntary characteristics of N1 component, P2 peak is presented as a component which is rather more open to the working memory related functions (i.e. Lefebvre et al., 2005; Taylor et al., 1990; Wolach & Pratt, 2001) and voluntary effort allocation. Indeed, a modulation of the responses by the offset P2 amplitude in the interval with the highest difficulty was found, and it was argued that this might be an indication of the working memory related attentional burst as a preparation for the subsequent activity/process (i.e. Lenartowicz et al., 2010). The higher P2 peak –for the short responses – was suggested to be for the stimuli which are

“attended” (i.e. Annic et al., 2014), therefore this augmentation gives rise to the accurate responses – which corresponds to the short responses – in terms of the PSE. In this experiment, we propose to put this hypothesis in a test by a design which has potentially more than one temporal locations with high difficulty in terms of the response options. Thus, if the higher P2 peak is a marker for a better evaluation of the interval length with regards to the working memory related processes, we expect higher offset P2 peaks in the accurate responses in terms of the place of the PSEs. In other words, P2 peak related modulation should only be observed in the intervals in which there is a potential difficulty in terms of discrimination. We hypothesize that the interval (s) which are subject to be a target for the P2 related modulation are intervals that are close to the middle standard. The P2 peak hypothesis is related with the previous consideration of N1 and CNV having only one threshold. In other words, since we do not expect a separate inner representation for the differentiation of the short and the middle responses – for instance around the middle point of the short and the middle standards – we can hypothesize that the highest difficulty would be around the middle standard because of its temporal location that is open to both short and long responses. A potential finding for the P2 peak related response manipulation in the more than one intervals would strengthen our interpretation – which is based on a P2 peak modulation as a function of difficulty and accuracy – which was provided in the previous experiment. Moreover, it would be also a considerable finding – upon the results of the previous experiment – if we can have further support for the independence of the response prediction by P2 peak amplitudes from the N1 peak related response prediction.

5.2.3. Methods

In this section, the experimental flow of the experiment, information about EEG data collection and other details of the methodology will be presented.

5.2.3.1 Participants

16 participants with a mean age of 27.3 years volunteered for the experiment. The data of one participant was not included in the analysis since only the half of the data could be collected due to the technical problems.

5.2.3.2. Stimuli and Procedures

Three standard intervals (1440, 2200 and 3220 msec) were presented in the two training blocks preceding the first experimental block and the third experimental block. There were four blocks of the experiment to let the participants have a short pause between

the blocks during the experiment. The onset and the offset of the intervals were given with two tone bursts (50 msec, 440 Hz) using headphones. After the second tone, a feedback presented stating the length of the interval was 'short', 'middle' or 'long'. In the experimental blocks, 9 comparison intervals (1440, 1600, 1782, 1980, 2200, 2420, 2662, 2928, 3220 msec) were used for the task in which the participants must decide whether the presented interval was more similar to the short, the middle or the long standard interval and the participants were asked to press one of the predefined keys (s = short, j = middle and l = long) when they see a "?" on the screen. The question mark appeared after an interval sampled from a uniform distribution between 1 to 2 secs to eliminate potential motor response related confounding factors on the EEG data. CIs (comparison intervals) were chosen based on the middle CI (2200 msec) and each of them were 10% shorter or longer than the closest interval that have been used.

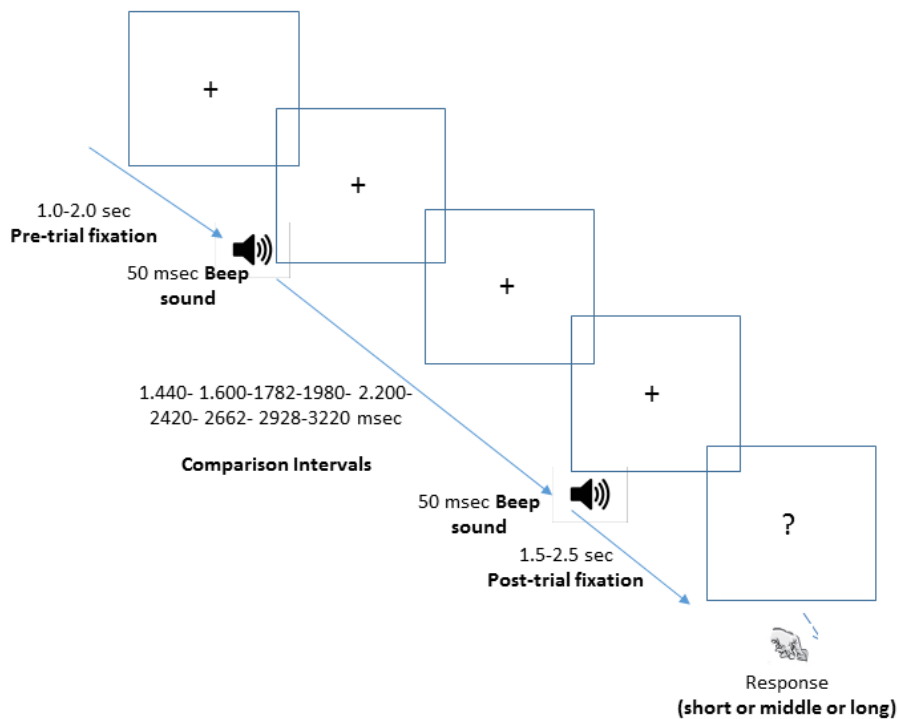


Figure 58. Experimental flow of a trial in a tri-section method (Exp-5)

Each block included 12 trials per duration and 48 trials in total per duration and 432 trials in the whole experiment. Inter-trial interval was also sampled from a uniform distribution from 1.5 to 2.5 sec. A fixation cross was presented all the time during the experiment except when the participants had to press a key corresponding to their decision (Figure 58).

5.2.3.3. EEG acquisition methods

Electroencephalographic activity was recorded using a 32-channel Brain Vision Analyzer system with a sampling rate of 1000 Hz. FCz electrode was used for all the analysis related with CNV and N1P2 components. Vertical and horizontal EOG activity and both mastoids were measured. The impedances were kept below 5. The pre-processing steps were done using Brain Vision Analyzer 2.0 referencing the signal to the mastoids. The data was filtered with a Butterworth filter with a 0.01 Hz low cutoff and 100 Hz high cutoff. The trials with excessive ocular and movement artifacts were excluded from the further analysis. Horizontal eye movements and blinks were corrected with the Gratton & Coles Method.

The N1P2 component was calculated by summing the absolute amplitudes of N1 and the P2 peaks. The time windows for the N1 and P2 peak detection were 70-160 msec and 140-320 msec, respectively. The baseline correction was conducted using the average voltage of the duration of 100 msec which precedes the offset of the duration.

5.2.4. Results

This section includes several different analyses on both behavioural and neurophysiological data including the determination of the point of subjective equality (PSE), CNV analysis, the onset and the offset N1-P2 peak analysis.

5.2.4.1. Point of Subjective Equality (PSE)

The point of subjective equality can be defined as the equal probability ($\text{prob} = 0.5$) of the judging a comparison interval (CIs) as short or long in comparison to the standard intervals (SI). We fitted our data with a binomial modelling by taking the two response options as the binary response variables and the stimulus level as the explanatory variable to determine the PSE using quickpsy package of R (i.e. Linares & Joan, 2015).

The first PSE was determined as 1823 msec and the second PSE was found as 2821 msec (Figure 59).

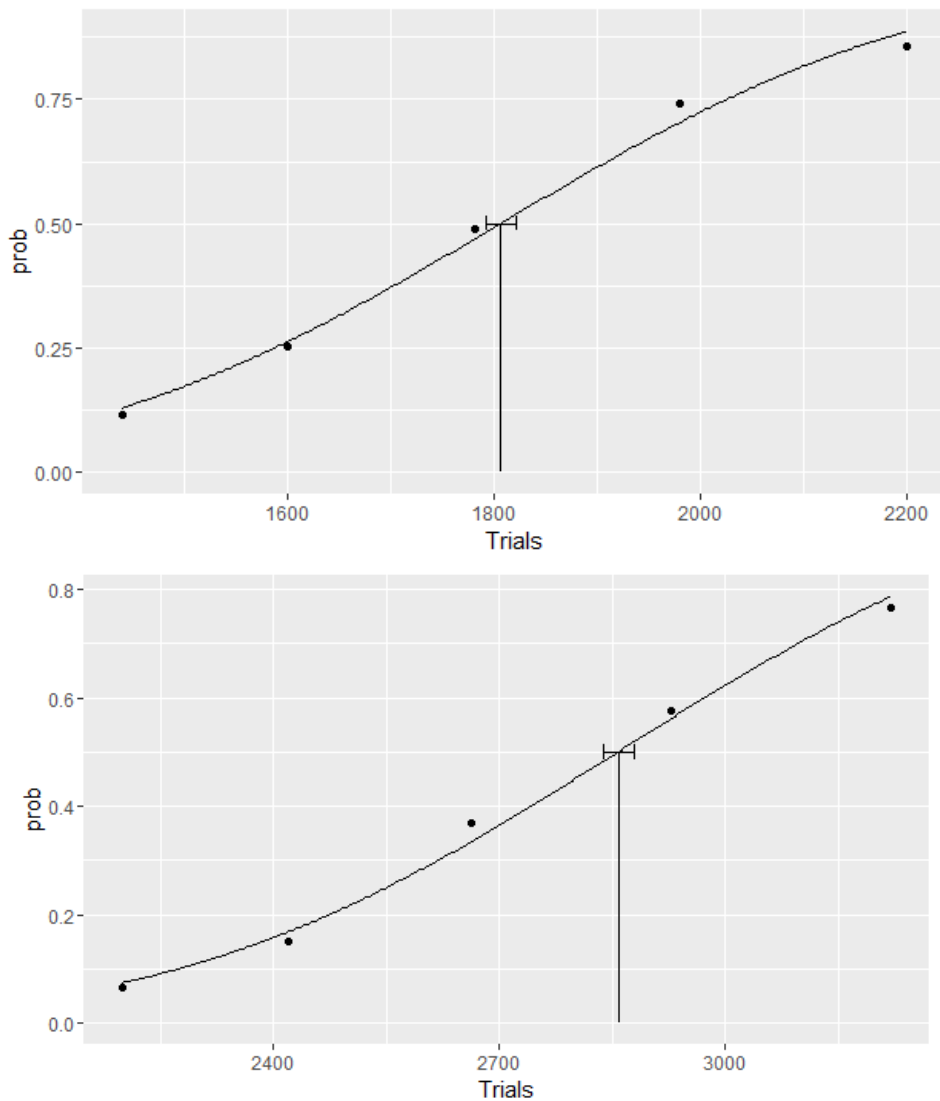


Figure 59. Middle Response Proportions to the Short (PSE-1) (upper panel) and the Middle Response Proportions to the Long Responses (PSE-2) (lower panel)

Both PSEs are shown in Figure 60 to address a right-hand side tail in the tri-section graph.

This result suggests a relatively higher ratio of the middle responses in the objectively longer intervals in comparison to the left side of the graph (see Figure 60).

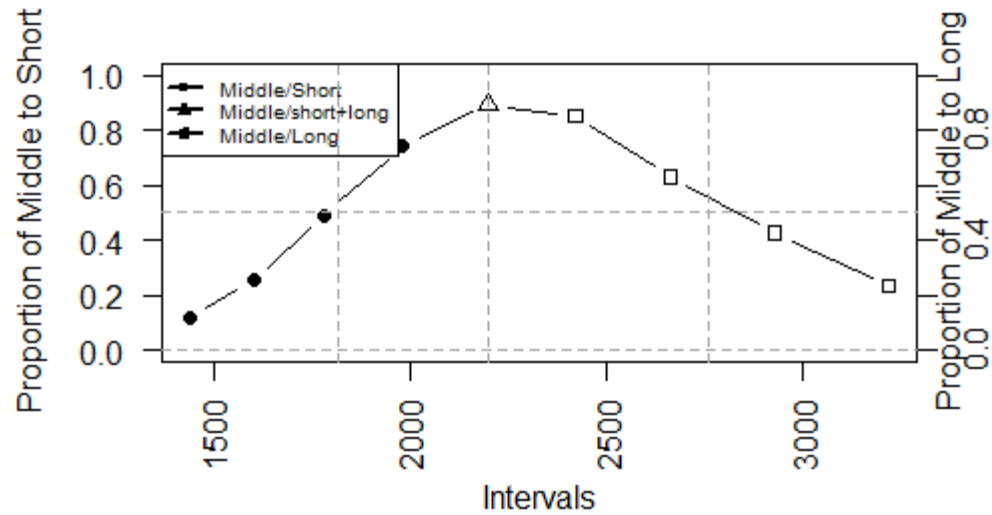


Figure 60. PSE-1 and PSE-2 within the interval scale

5.2.4.2. Offset N1 Peak Analysis

A full model was built that includes the behavioral responses with three levels and four groups of CIs (Group 1: shorter than the middle interval, Group 2: the middle interval, Group 3: the intervals until the PSE2, Group 4: the intervals longer than the PSE2) along with the interaction term to address the role of N1 peak. The reduction of the interaction term did not result in a significant change in the model ($\Delta AIC = 5$; $\chi^2 = 0.95$, $p = .81$). Moreover, we have found a marginal significant effect of the group on the variance explanation ($\Delta AIC = 1$; $\chi^2 = 7.11$, $p = .07$) when we remove the group variable. Thus, we left the model as it is, and the final model, in which the intercept (corresponding to the long responses in the Group 2) showed a significant effect ($\beta = 15.1$, $p < .001$), revealed that the middle responses have higher N1 amplitudes than the long responses ($\beta = 0.92$, $p < .01$). Similarly, the short responses were found to have higher N1 peaks in comparison to the long responses ($\beta = 0.86$, $p < .05$) (Table 25) (Figure 61 and Figure 63).

Table 25. N1 peak analysis for responses and groups

	Estimate	Std.Error	t.value	pvalue
(Intercept)	15.1193872	0.612	24.672	0.0000
short	0.8686883	0.437	1.983	0.0472
middle	0.9213604	0.327	2.814	0.0048
Group1	-0.3418643	0.362	-0.942	0.3457
Group3	-0.7626640	0.376	-2.023	0.0429
Group4	-0.0111484	0.420	-0.026	0.9788

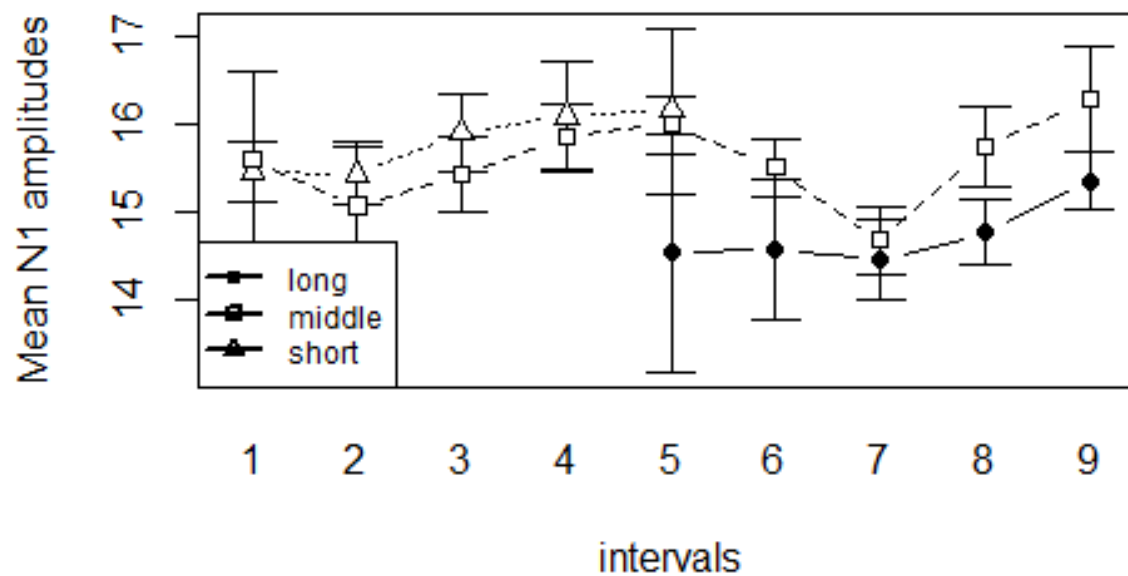


Figure 61. Mean Offset N1 peaks for each interval and response

As for the groups, we did not find a difference between the Group 2 and Group 1 ($\beta = -0.34$, $p = .35$) and Group 4 and Group-1 ($\beta = -.01$, $p = .97$).

However, we have found that the N1 peak amplitudes in Group 3 were significantly lower than the peaks in Group 2 ($\beta = -0.76, p < .05$) (Figure 62 and Figure 64).

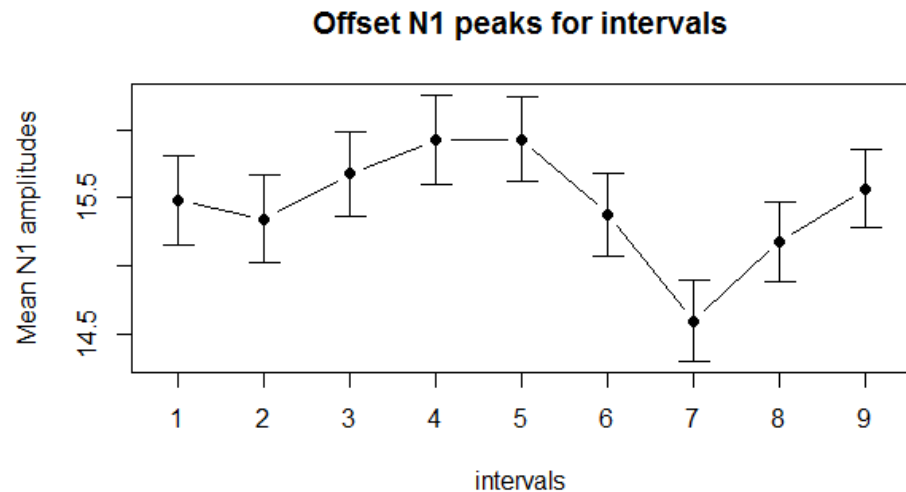


Figure 62. Mean Offset N1 peaks for intervals: Notice that there is amplitude dip in the sixth and the seventh intervals (Group-3) in comparison to the fifth interval (Group-2)

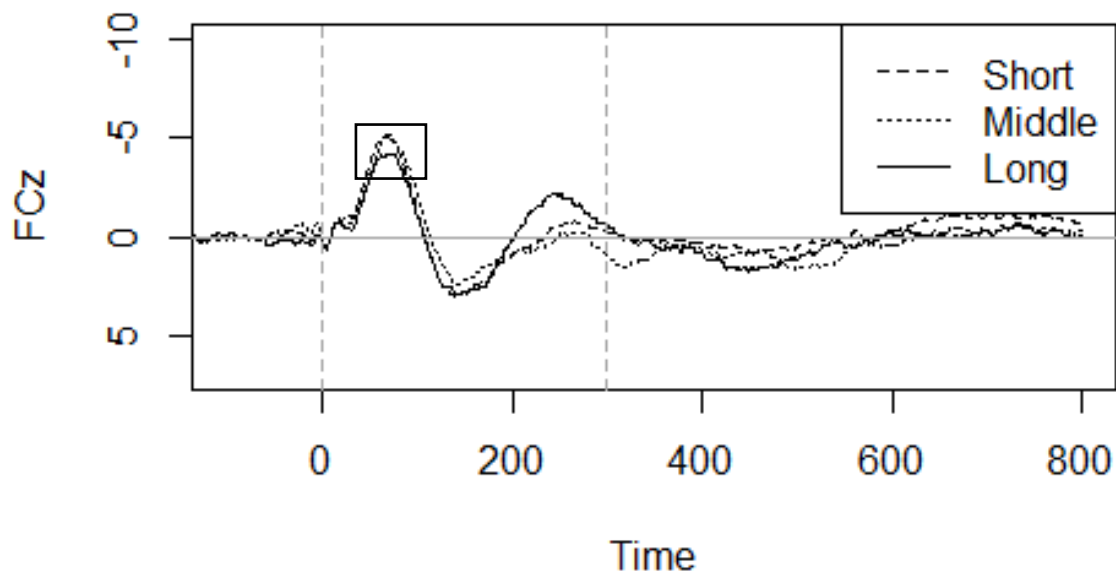


Figure 63. Offset N1 amplitude differences for the subjective responses

In a separate analysis, we have found no trial number effect which indicates no habituation effect during the experimental session.

Moreover, there was no three-way interaction of trial number, the interval length and the subjective responses which indicates no significant trial order effect (See appendix D).

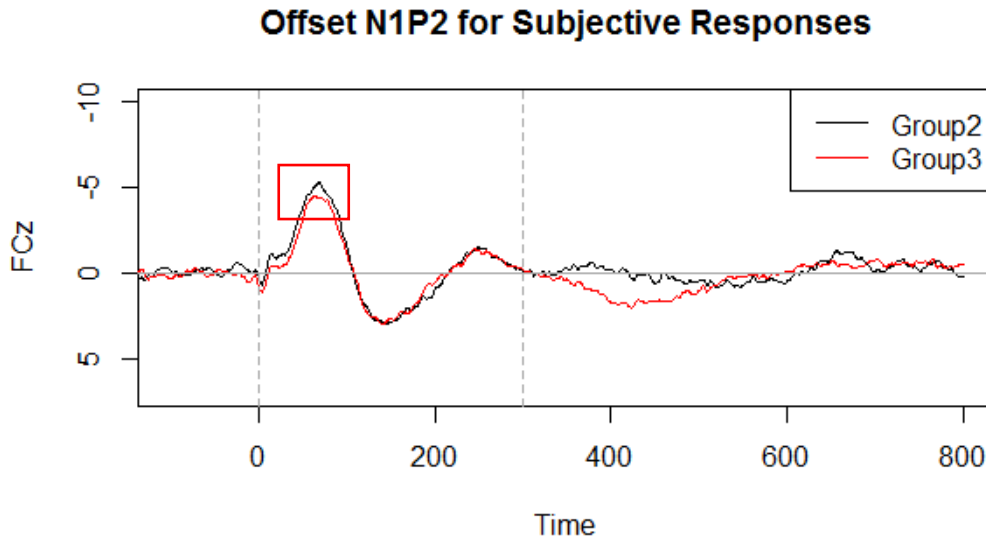


Figure 64. N1 peak difference in terms of different interval groups. Group-2: the middle interval, Group-3: the intervals until the second PSE2 (the 6th and 7th intervals)

5.2.4.3. Offset CNV Analysis

To test whether there is a change in the slow potential after the threshold, we have conducted a linear mixed effect model including groups (Group 1: intervals that are shorter than the PSE1, Group 2: between the PSE1 and the middle standard, Group 3: between the middle standard and the PSE2, Group 4: intervals that are longer than the PSE2) and a subjective response term with three levels (short/middle/long) along with the interaction term. The dependent variable was difference between the last parts and the previous parts of CNV amplitude along the length of the interval. This difference was calculated for the Group-1 and the Group-2 by taking the mean amplitude of CNV in the 200 msec period just before the offset of the interval and the mean amplitude of CNV in the range of covering 400 msec after the onset of interval until 200 msec before the offset of the interval. By this way, we had an opportunity to capture the change in the CNV course just before the end of the interval. A similar calculation was conducted for the other groups; however, the ranges were different for these groups considering the temporal locations which might be subject to a potential CNV course change. For the Group-3, the mean amplitude until the middle standard (2200 msec) was subtracted

from the mean amplitude for the duration between 2200 msec and the end of the interval. Similarly, for the Group-4, the CNV change was calculated by the difference of amplitude until the PSE2 (2821 msec) and the amplitude of the period after the PSE2 until the end of the interval.

A reduction of the interaction term did not result in a significant change in the model ($\Delta AIC = 5$; $\chi^2 = 0.48$, $p = .92$). Moreover, we have found no significant effect of the response on the variance explanation ($\Delta AIC = 0$; $\chi^2 = 3.66$, $p = .15$).

Table 26. The linear Mixed Effect Model for the CNV course change analysis

	Estimate	Std.Error	t.value	pvalue
(Intercept)	0.04391794	0.291	0.1506	0.8802
Group2	0.11631867	0.142	0.8181	0.4132
Group3	0.03007705	0.091	0.3269	0.7436
Group4	0.14213011	0.066	2.1523	0.0313

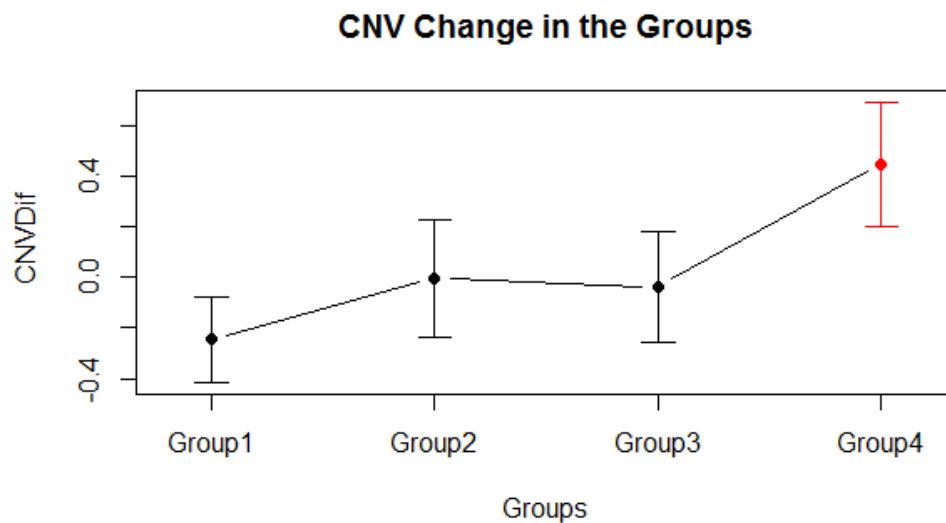


Figure 65. Mean CNV Change in the Groups: Group 1: shorter than PSE1, Group 2: between PSE1 and the middle standard, Group 3: between the middle standard and the PSE2, Group 4: Longer than the PSE2

The final model with a Helmert contrast in which the intercept showed no significant effect ($\beta = 0.04$, $p = 0.88$) revealed that the CNV amplitude change in the Group-4 was higher than the CNV change in the amplitudes of the previous groups ($\beta = 0.14$, $p < .05$).

However, we have found no difference between the Group-3 and the previous groups ($\beta = 0.03$, $p = .74$) and the Group-2 and Group-1 ($\beta = 0.11$, $p = .41$) (Table 26) (Figure 65 and Figure 66).

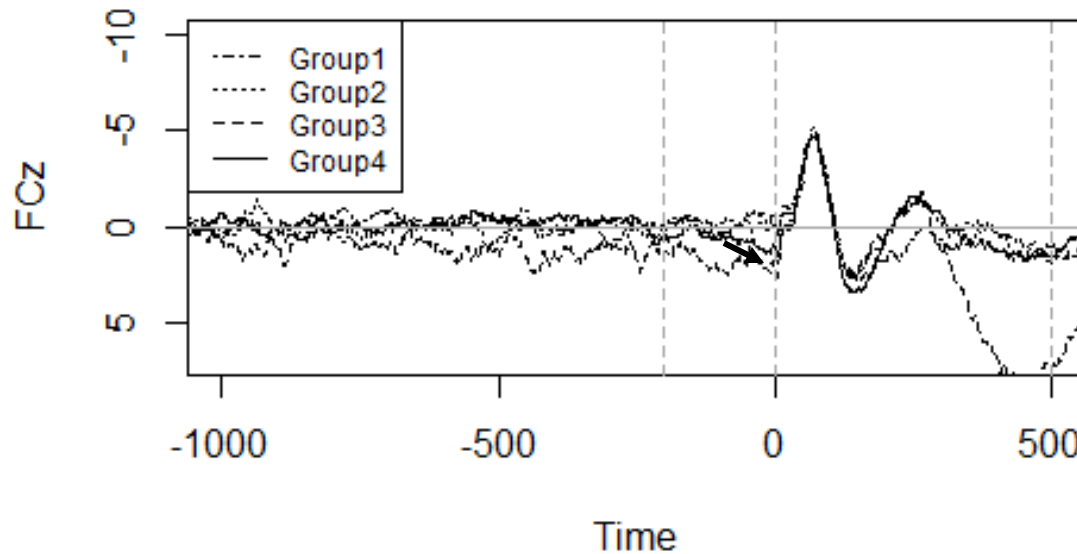


Figure 66. Offset CNV change in different groups of intervals. Notice a dip of the CNV in the Group-4 which is shown by a red arrow

5.2.4.4. Offset P2 Peak Analysis

The two independent variables were included along with their interaction in the model. Interval grouping was determined according to the PSE1, PSE2 and the middle standard. Thus, the first three intervals were taken as the Group-1. The fourth and fifth interval are lumped together into the Group-2, the intervals which remain between the middle standard and the second PSE (i.e. sixth and seventh intervals) were included in the Group-3, and the last group, Group-4, was decided to consist of the last two intervals after the PSE2. The accuracy term was determined in accordance with this grouping in which the short responses in Group-1 along with the middle responses in the Group-2, the middle responses in the Group-3 and the long responses in the Group-4 were accepted as the accurate responses. The results indicated that the intercept – which corresponds to the accurate responses in the Group-1 – had significant effect ($\beta = 17.52$, $p < .001$) and the Group-2 amplitudes were found to be lower than the Group-1 amplitudes for the accurate responses ($\beta = -1.15$, $p < .01$). Similarly, the Group-3 ($\beta = -1.24$, $p < .01$) and the Group-4 ($\beta = -2.26$, $p < .01$) were shown to be low in amplitudes in comparison to the Group-1 (Figure 67). As for the accuracy, we have found no

difference in P2 peak amplitudes between the accurate and the inaccurate responses in the Group-1 ($\beta = -.17, p = 0.73$) (Figure 68).

Table 27. P2 peak analysis for accuracy of responses and Groups

Fixed effects:			
	Estimate	Std. Error	t value
(Intercept)	17.51886	0.837	20.919
Group2	-1.15876	0.413	-2.805
Group3	-1.24078	0.421	-2.942
Group4	-2.26297	0.430	-5.257
Inaccurate	-0.16887	0.496	-0.340
Group2: Inaccurate	-1.50944	0.840	-1.795
Group3: Inaccurate	-1.13440	0.806	-1.407
Group4: Inaccurate	-0.02366	0.777	-0.030

Group = Group1:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate - Accurate	-0.1688672	0.496	5771.39	-0.340	0.7340
Group = Group2:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate - Accurate	-1.6783066	0.673	5771.01	-2.492	0.0127
Group = Group3:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate - Accurate	-1.3032642	0.637	5769.05	-2.044	0.0410
Group = Group4:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate – Accurate	-0.1925310	0.601	5771.56	-0.320	0.7491

The post-hoc test revealed that the inaccurate response in the Group-2 ($\beta = -1.68, p < .05$) (Figure 69) and in Group-3 ($\beta = -1.30, p < .05$) have lower P2 peaks in comparison to the accurate responses (Figure 70).

However, we did not find any difference in terms of accuracy in the Group-4 ($\beta = -0.19$, $p = .75$) (Table 27) (Figure 72).

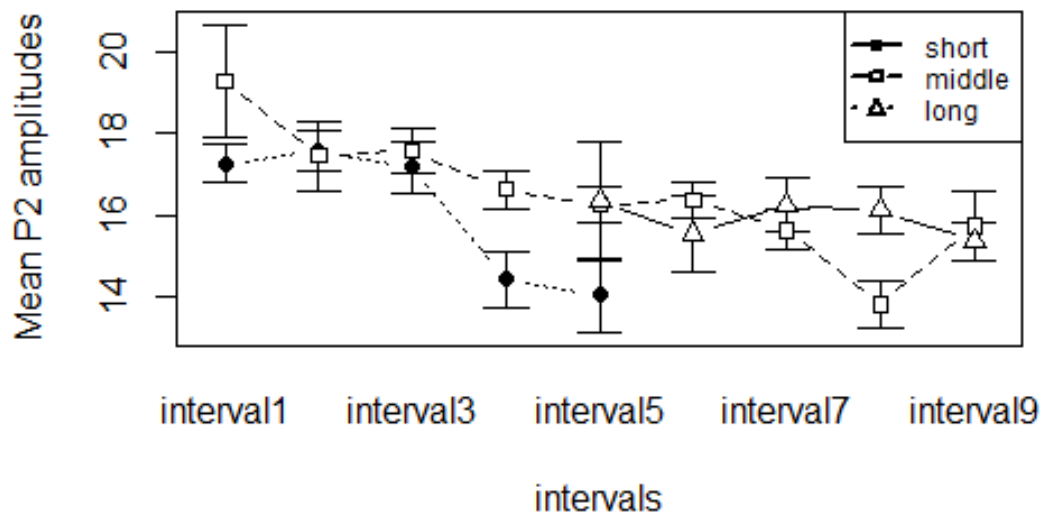


Figure 67. Mean P2 peaks for each interval and responses

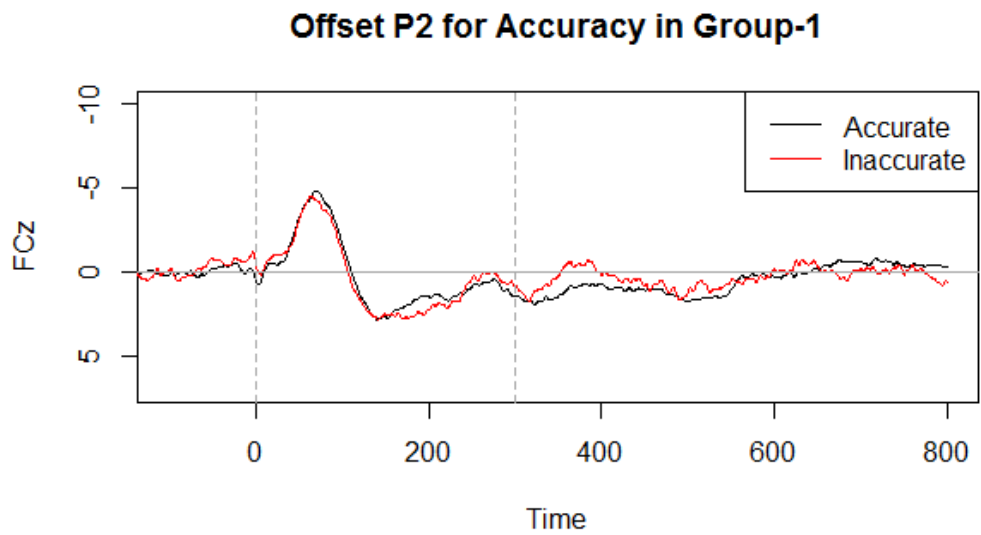


Figure 68. P2 peak comparison in terms of accuracy in the Group-1

In a separate analysis, we have found that the trial order did not affect the P2 amplitudes in terms of the responses which was indicated by the absence of a three-way interaction

between the trial number, the interval length and the response terms (See Appendix D).

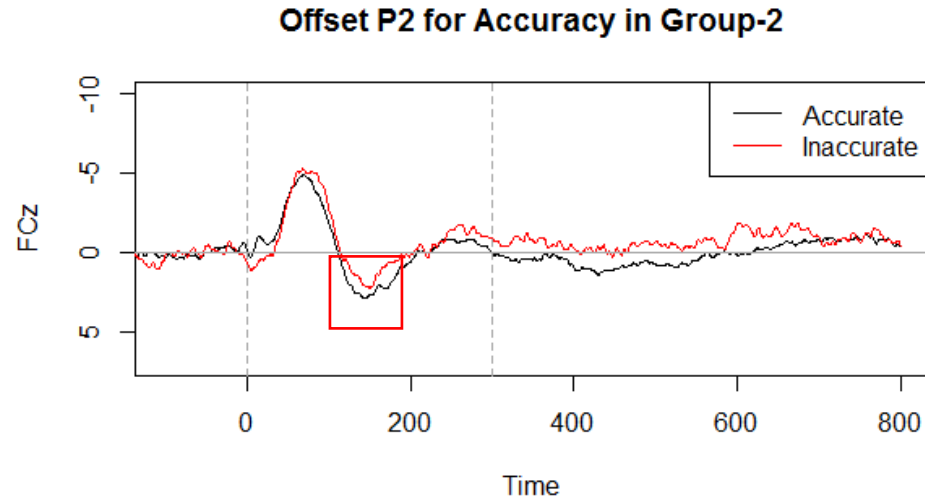


Figure 69. P2 peak comparison in terms of accuracy in the Group-2. Red box: P2 peak

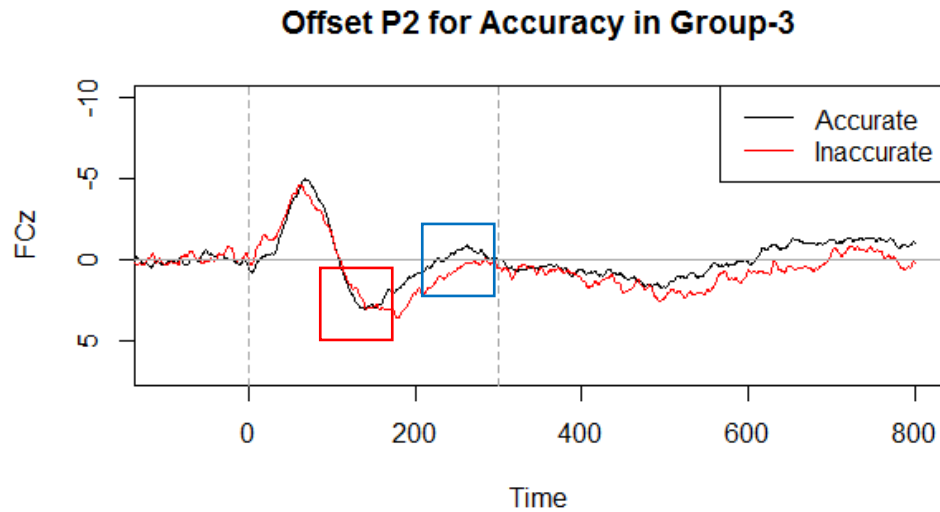


Figure 70. P2 peak comparison in terms of accuracy in the Group-3. Red box: P2 peak and Blue box: N300 peak

Although the results which were based on the individual peaks in a linear mixed effect indicated higher P2 amplitudes for the accurate responses in Group-3, the summed

component does not reflect this image. The reason for this change in the summed ERP component can be explained by a modulation in the subsequent peak. For instance, an amplitude increase in the following peak (peak-3) can cause a diminished amplitude and latency in the preceding one (peak-2) in the summed ERPs (Figure 71). In other words, the increased N300 peak for the accurate responses in the Group-3 might be responsible for the decreased amplitude in the P2 peak of accurate responses which was reflected as no difference in the summed component despite the fact that the results indicated higher P2 peaks in the accurate responses.

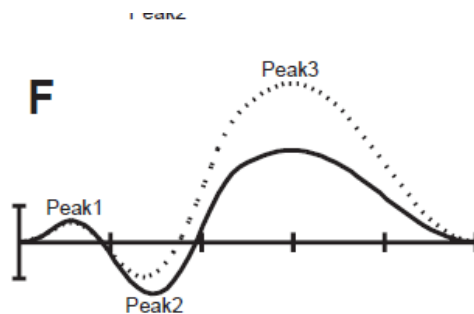


Figure 71. The effect of the subsequent peak increase (Peak-3) on the latency and amplitude of the relevant peak (Peak-2) (Luck, 2005, page 18)

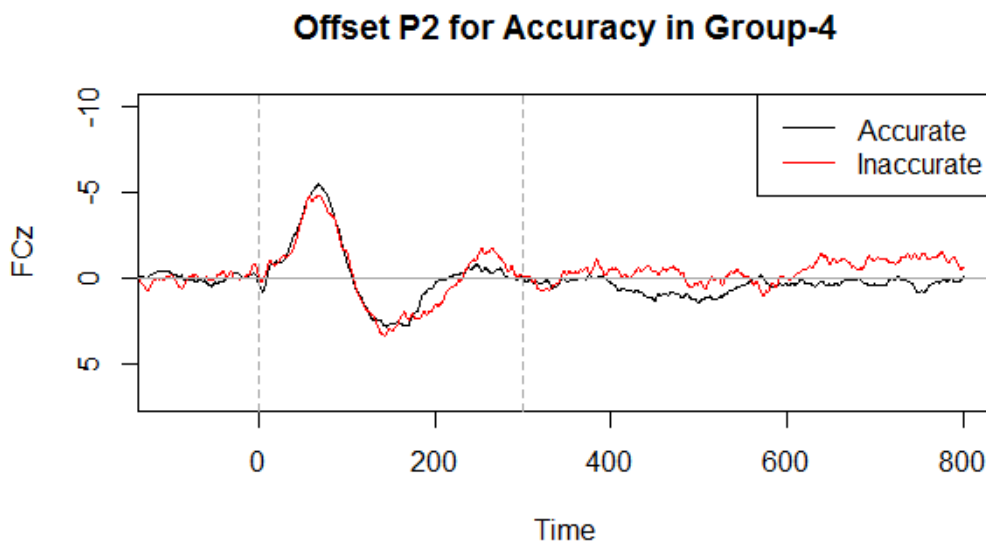


Figure 72. P2 peak comparison in terms of accuracy in the Group-4

In a similar sense to the effect of N300 peak on the P2 in the summed ERPs, we can see an effect of the preceding peak, namely the N1 peak, on the P2 peak in the summed

component (Figure 73). Although the results indicated that there was no significant difference in the P2 amplitudes between the accurate and inaccurate responses in the interval-8 – both as a part of the Group-4 and in a separate analysis that involves the intervals instead of the groups (see Appendix-E) – the summed ERP component reflected a diminished P2 peak for the inaccurate responses.

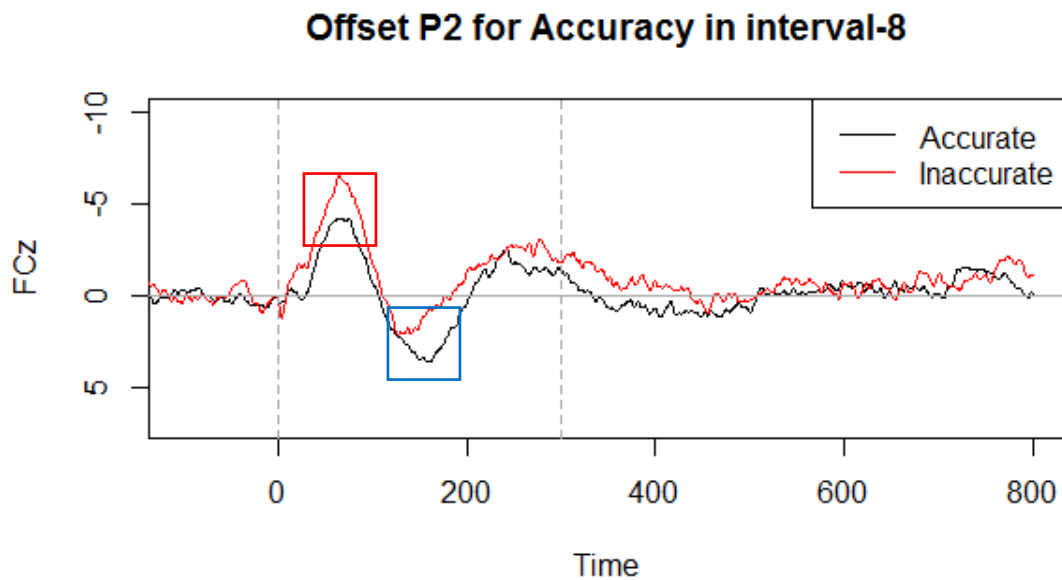


Figure 73. P2 peak comparison in terms of accuracy in the interval-8. Red Box: N1 peak and Blue Box: P2 peak

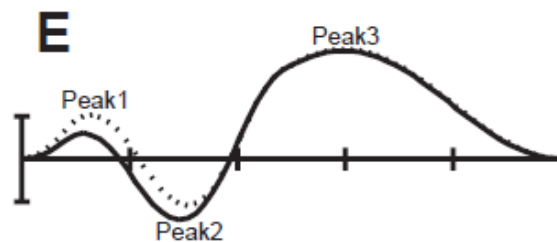


Figure 74. The effect of the preceding peak increase (Peak-1) on the latency and amplitude of the relevant peak (Peak-2) (Luck, 2005, page 18)

We suggest that this is the result of the N1 peak increase in the interval-8 for the inaccurate responses. Indeed, it is suggested to consider the effect of the preceding peak (N1 as peak-1) on the relevant peak (P2 as peak-2) while interpreting the summed components (i.e. Luck, 2005) (Figure 74).

5.2.4.5. Onset N1P2 Peak Analysis

We have built a linear mixed effect model which had the onset N1P2 amplitudes as the dependent variable, four groups of CIs (Group 1: intervals shorter than the middle interval, Group 2: the middle interval, Group 3: the intervals until the PSE2, Group 4: intervals longer than the PSE2) and the accuracy (Accurate responses: short responses in the Group-1, the middle responses in the Group-2, the middle responses in the Group-3 and the long responses in the Group-4) as the independent variables together with the interaction of these two terms.

Table 28. The best fitting model for the onset N1P2 amplitude and post-hoc test results (Exp-5)

Fixed effects:			
	Estimate	Std. Error	t value
(Intercept)	32.679433	1.242	26.299
Inaccurate	0.855153	0.612	1.395
Group2	0.526753	0.501	1.051
Group3	0.279558	0.514	0.543
Group4	0.038789	0.529	0.073
Inaccurate: Group2	-0.670668	1.035	-0.647
Inaccurate: Group3	-1.389851	0.982	-1.415
Inaccurate: Group4	-0.002096	0.957	-0.002

Group = Group1:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate - Accurate	0.8551532	0.612	5712.31	1.395	0.1630
Group = Group2:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate - Accurate	0.1844847	0.829	5711.69	0.222	0.8241
Group = Group3:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate - Accurate	-0.5346979	0.771	5710.83	-0.693	0.4881
Group = Group4:					
contrast	estimate	SE	df	t.ratio	p.value
Inaccurate - Accurate	0.8530575	0.739	5712.60	1.154	0.2487

The full model and the results (Table 28) showed that the intercept – which corresponds to the accurate responses in the Group-1– was significant ($\beta = 32.68, p < .001$). We have found no difference in terms of accuracy in any groups of comparison interval.

5.2.5. Discussion

Several different topics such as the relation of expectation and CNV, the relation of offset N1 and unexpected events, P2 peaks and discrimination difficulty will be discussed under different titles of this section.

5.2.5.1. N1 peak and Unexpected Events

The results in this experiment confirmed our interpretation about the offset N1 peak and its relation to the unexpected events. More importantly, we have provided evidence for a single threshold which represents a temporal location and expectation grows until that point. In other words, it was found that N1 peak amplitude – which was suggested as an involuntary attentional orientation in the literature – can predict shorter or longer responses according to the relevant threshold. Since our results that were based on the N1 peak did not help us to differentiate the responses before the threshold point – namely the short and the middle responses – we propose to interpret this finding as a support for the relation of the N1 peak related process to the implicit timing/expectation until the threshold point. In other words, the change in the N1 peak amplitude did not provide us a basis for a prediction of the short and the middle response. Both the short and the middle responses for the particular intervals, namely the intervals until the middle standard, were given as rather unexpected events in terms of the threshold for giving long responses. Moreover, after the middle interval we have observed an attenuation of N1 peak amplitude (see Figure 62) in the group which includes the two intervals next to the middle interval. The reason of this decrease in the N1 amplitude – which is a marker of the unexpected events – can be explained by the very fact that the interval offsets after the middle standard were expected sufficiently, thus we have observed low amplitudes in this group. In addition to that, it is worth to notice that the response related offset ERP modulation changes from the N1 peak to the P2 peak in the Group-3 (see Figure 67). Considering that the P2 peak is rather more related with a voluntary effort allocation, this finding supports the interpretation of N1 peak – as a marker of an automatic indicator of the responses – the modulation vanishes by giving place to a more working memory related process to retrieve the required response in these trials.

The findings which indicate an N1 peak amplitude regulation additionally indicated a visually observable amplitude difference of the N300 component in the same conditions (see Figure 63). The N300 component was previously associated with object congruency and semantic content of the classification and categorization (e.g. Maguire et al., 2013; Hamm et al., 2002). The Enhanced N300 component can be an indication of an incongruency and can be related to the detection of an unexpected event (Tipples et al., 2013). In our results, we have observed that the longer responses had relatively greater N300 components in comparison to the short/middle responses. Interestingly, Tipples et al. (2013) suggested that higher negativity of this component is an indication of a violation of an expectation. Considering the relation of this component to semantic information, we can interpret this augmented N300 component as a potential marker which indicates the participants' higher order cognitive reaction towards the situation that the threshold has been passed in the longer intervals. The bisection experiment also provided a similar picture (see Figure 55): in the conditions in which there is an N1 peak regulation, there was a difference in the N300 component as well in these conditions. However, it is questionable whether this N300 related amplitude regulation can be isolated from an N1 peak regulation (e.g. Right PSE group; see Figure 54). Therefore, N1 and N300 should be analyzed together to cover the predictions for both sides: before the PSE and after the PSE in a further study.

5.2.5.2. CNV Course Change and PSE2

The results provided support for a similar interpretation as in the bisection task in terms of the change in the CNV course. In the previous experiment, we have found a progressing increase in the CNV negativity when the participants responded as short although the change in the negativity of the slow potential for the long responses did not occur in the same extend. Crucially, this difference was observed for the intervals longer than the single PSE in the bisection experiment. This was because the observed change in the CNV course in the long responses (see Figure 66). We have interpreted this change as an evidence for the diminished expectation after the threshold in which the decision related process for the response was already completed. Similarly, the findings from this experiment have provided that the group which includes intervals longer than the PSE2 (Group-4) showed a change from the negativity towards a positivity in the CNV course in comparison to the previous groups. This is interpreted as a further support for the existence of a CNV course change after a threshold which was formed throughout the experiment. We have taken this change of CNV course particularly after the PSE2 as an observation which fits to the offset N1 peak decrease in the Group-3. The previous section has indicated a N1 peak difference between the middle standard and the Group-3. In other words, a decrease in the N1 peak in Group-3 – the higher N1 peaks are

associated with unexpected events – can be interpreted as a marker of quite expected events in this group since it is the closest group to the threshold (PSE2) in terms of the interval length. Thus, we have observed a change in the CNV course after this highly expected temporal point which was validated by the diminished negativity (higher positivity) in the Group-4. As for last point to discuss, we need to point out the fact that negativity in the slow potential was not in the same extend with the previous experiment. Although, the baseline corrections for both experiments were done by considering the duration before the onset of the interval, we did not observe enough negativity between the onset and the offset of the interval in the trisection experiment. The reason might be the relatively extended duration scale in the trisection experiment which might explain the absence of no steady ramping in this experiment. Because, there was different parts of an interval along the experience of it since the participants needed to consider the three response options. This fluctuation in terms of response possibilities might be responsible for this absence of a stable negativity in this experiment. However, although we did not find a ramping negativity, we have provided support for the CNV course change after the threshold despite the course change occurred towards positivity instead of diminished/steady negativity.

5.2.5.3. P2 peak and Discrimination

P2 peak was suggested to be as an early indicator of an attentional burst which is related to a preparation for the subsequent activity/process (i.e. Lenartowicz et al., 2010). Indeed, we have observed higher amplitudes of the offset P2 peak when the participants responded accurately in terms of the location of the PSEs. In other words, higher P2 peaks correspond to the middle responses in the Group-2 (see Figure 69) and Group-3 (see Figure 70). In the Group-2, we have already discussed that N1 peak amplitude was not found to be useful for predicting the short and the middle responses. Although we have observed same magnitude of N1 peaks in this group, the results have provided that the enhanced P2 amplitudes corresponds to the middle responses in contrast to the diminished peaks for the short responses. The requirement for an evaluation in the face of an uncertain response – since the discrimination was not subject to an automatic detection, and thus it was difficult– forces a selection which was rather more open to a top-down attentional modulation (i.e. Ortega et al., 2008) which in turn gave rise to a frontal lobe positivity (i.e. Potts, 2004) as revealing itself by a higher P2 peak amplitudes. Similarly, in the Group-3, the results indicated that the higher P2 peaks correspond to the middle responses – accurate – instead of the long responses which was accepted as inaccurate responses for this group. For the reason for why we did not observe the peak difference in the P2 component in the summed ERP, we have argued that this was a subsequent peak effect (see Peak-3 in Figure 71) which corresponds to an increase in

N300 peak amplitude, which in turn caused a diminished P2 peak of the accurate responses in the summed component. In contrast to the Group-2 and the Group-3, we did not find a P2 peak modulation with respect to the accuracy in the Group-1 and Group-4. Similar to the neighbor peak effect on the relevant component for the Group-3, we can see the effect of N1 peak on the summed component of the P2 peak in terms of accuracy in the interval-8. However, this time, the effect caused a misleading shape of the difference in the P2 peak in the interval-8 despite the fact that the results indicated otherwise (see Figure 73). This was exemplified in the Figure 74 by showing that the amplitude difference in the preceding peak can lead to a change in the shape of the summed subsequent peak. In summary, the consideration of the two components, namely the N1 and the P2 peaks, was valuable and appropriate for better interpretations when we can isolate one component from each other. In our experiment, this was achieved in the Group-2 in which we observed similar N1 peaks but different P2 peaks and in the Group-3 in which again similar N1 peaks having statistically different P2 peaks except the point that another (N300 peak) had an effect on the summed P2 peak.

5.2.5.4. Onset N1P2 and Accuracy

In this experiment, we could not find a relation of the onset N1P2 complex and accuracy in contrast to the finding that was provided in the bisection task. We interpret this result by a potential tendency of the participants towards responding as middle when the response was not as apparent as they are in the short or the long responses which was shown by the offset P2 related regulation in these intervals. In other words, the accuracy related manipulation might not be that evident in the presence of three response options. Although, the accuracy related manipulation was rather more clear in a bisection task since there was no backup response option, it might be less likely to find an onset ERP prediction in terms of accuracy when there is an extra option in the trisection task.

CHAPTER 6

GENERAL DISCUSSION

A summary of all findings of this thesis will be presented first to provide a reminder for all the experiments before discussing these findings in terms of their significance in the field. The first two experiments gave us a chance to investigate the concurrent task effects and temporal location effects on timing at the encoding stage of a reproduction task. We have found that a requirement to perform a second task – during the experience of an interval to be timed – causes a disruption in timing. As it is expected, this disruption was manifested as an underestimation in the reproduction of the intervals. In other words, the intervals that include no concurrent task are not underestimated. Although there was an overall task effect on timing which is resulted from the performance requirement of the concurrent task, we have shown that the nature of this concurrent task disruption does not change as a function of the difficulty of the concurrent task. For instance, performing a concurrent task that requires a more demanding process, namely the incongruent Simon stimulus, did not result in more profound underestimation in comparison to the relatively easier trials of the Simon task. Besides the presence of an overall task effect and the absence of a congruency effect on the encoding requirements of timing, the results have indicated that performing Simon task towards the end of an interval causes more underestimation than the situation where the Simon task is placed earlier within an interval. This temporal location effect was found in both experiments in a similar extend. The purpose of the difference between the Exp-1 and Exp-2, namely the difference in the incongruent trial frequency within the total number of the trials that include a concurrent task, was to further investigate whether the Simon task demands in the incongruent trials can affect encoding of an interval in a more attention demanding design of these trials. Since we decreased the number of incongruent trials within the session in Exp-2, the appearance of infrequent and difficult Simon trials would cause more dramatic disruption within the flow of a trial in an incongruent condition. Along with the rare occurrence of incongruent trials, the percentage of the relatively easier trials of Simon task, namely the congruent trials, are increased. This frequency manipulation is expected to affect the extend of the Simon effect. Indeed, we have shown that the Simon effect in Exp-2 increased 3-4 times in comparison to the Exp-1. However, although the processing demand of the Simon task increased as it is indicated by a more profound Simon effect, this does not reflect to the timing performance because we have found no congruency effect all the same.

Besides the experimental findings such as overall task effect, the temporal location effect, the absence of timing disruption in the empty trials and the absence of the congruency effect, we have provided theoretical implications of these findings in the Chapter-3. Discussions about the relations of our findings and the relevant accounts within the internal clock framework such as attentional time-sharing and attentional switch will be given below under the titles of expectation and interference effects.

Chapter-4 that includes the Exp-3 was about the comparison of the two stages of a reproduction task. The first stage, as it is investigated in the previous chapter, does include an experience of an interval which is then to be timed and this stage can be interrupted by a concurrent task requirement during the encoding of the interval. The second stage of a reproduction task, namely the reproduction stage, can also be manipulated by a concurrent task. In this experiment, with three levels of temporal location (early-middle-late SOA conditions), we have shown that there was a temporal location effect at both stages. As it is expected, this effect was in the direction of underestimation in the encoding stage and in the direction of overestimation in the reproduction stage. Moreover, a comparison which is based on early SOA and middle SOA showed a similar extend of temporal location effect at these stages at least for these levels. A discussion of the implications of this finding about the nature of decision level of an internal clock is provided later in this chapter. In contrast to the finding that shows a similar temporal location effect – early-middle SOA comparison – at both stages of interval timing, we have found that an interval experience is more disrupted (overestimated) at late SOA in the reproduction stage in comparison to the timing disruption (underestimated) in the encoding stage. This finding is discussed in the interference section of this chapter since it is interpreted that there exists a response overlap of timing and Stroop tasks towards to the end of the interval. In addition to the temporal location effect, there was an overall task effect in the encoding stage which is in line with the previous chapter results, however, we could not make a healthy comparison between the empty trials and the trials that contain the Stroop task in the reproduction stage because of a confounding factor in the trials of this stage. The reproductions of the empty trials were found to be higher even from the reproductions which include a concurrent task. A possible confounding factor is discussed in the interference section. Besides the temporal location effect and overall task effects, the most substantial finding of this experiment was the presence of a congruency effect in the reproduction stage in contrast to the absence of this effect in the encoding stage. A relevant discussion to account for this dissociation of the congruency effect with respect to the different stages of a reproduction task is provided within the theoretical background of the attentional-time sharing hypothesis in the interference section of this chapter by addressing the response inhibition requirements of timing and Stroop tasks.

The last two experiments of this thesis were combined in the Chapter-5 to study the neural markers of timing related phenomena such as expectation, and temporal discrimination. In the Exp-4, which includes a bisection task, we have shown that CNV slow potential course change predicts the subjective responses of the participants. In other words, CNV grows up until a point around an inner threshold which is formed by the contribution of both short and long standards, then it goes down (i.e. towards positivity) in the long responses. However, this was only valid in the intervals which were longer than the PSE. CNV analysis at the end of an interval in Exp-5 – which was a tri-section experiment – revealed similar indications about the CNV course change. This time, the slow potential went towards the positivity at the longest interval group without manipulated by the subjective responses. A discussion of the role of CNV and our findings is given in the expectation section. Another neural marker which was studied in this chapter in terms of expectation was N1 peak that was observed at the offset of an interval. We have shown that N1 peak amplitude differs depending on the subjective responses in both bisection and tri-section experiments. In the bisection experiment in which there were two response options, N1 peak amplitude was shown to be higher for the short responses in comparison to the long responses. In the trisection experiment in which there were three response options, N1 peak amplitude was useful to differentiate the long responses – which had lower amplitudes – from the short and the middle responses that had higher amplitudes. However, we have found no evidence for a difference between N1 peak amplitudes of the short and the middle responses in this experiment. Moreover, the results indicated that N1 amplitude decreases even for the middle responses at the intervals which were close to a threshold which separates the middle responses from the long responses. This was showed in a group difference for the N1 peak amplitudes that give rise to a decrease in the overall N1 peak amplitudes near the threshold. A discussion that arises from the question of what is represented by the N1 peak and its relation to expectation will be presented in the expectation section. In addition to the relation between N1 peak and expectation, we have found that the offset P2 peak – which is associated with the working memory related processes – was regulated by the discrimination difficulty and showed greater amplitudes for the accurate responses. In the bisection experiment, the P2 peak was found to have higher amplitudes for the short responses at the middle interval. This finding is also in line with the accuracy with respect to the PSE that the accurate responses were associated with the higher amplitudes. Similarly, in the trisection experiment, P2 peak regulation was observed for the intervals in which there was a high amount of difficulty in the temporal discrimination which was indicated by the fact that the most obvious responses were unlikely in that temporal location. In this experiment, the P2 peak amplitudes were found greater for the middle responses at the middle groups of intervals. In other words, the accurate responses – which were determined by the temporal locations of the PSE– had

higher P2 peak amplitudes. P2 peak related discussions are provided in the temporal discrimination section of this chapter. As for last finding, we have presented that the onset N1P2 complex amplitudes were higher at the correct responses of the bisection task. However, the results did not provide the same finding in terms of a relation between the N1P2 amplitudes and the accuracy in the trisection experiment. Nevertheless, the relation of the N1P2 amplitude and the discrimination of a temporal event at the interval onset is discussed under the temporal discrimination section.

6.1. Expectation and Interval Timing

The temporal location effect in timing can be explained by an attentional resource sharing between the timing task and the expectation of the concurrent task. Our results provided support for the attentional time-sharing account rather than the attentional switch account. In the attentional time-sharing account (i.e. Buhusi & Meck, 2009a), resource sharing depends on the requirements of the two tasks which must be performed at the same time. Thus, the lack of timing resources results with a memory decay of the accumulated temporal information. Buhusi & Meck (2009a) indicated that a distractor/gap causes a memory decay. In our experiments, the concurrent task should be taken as a distractor in this context. Our hypothesis for the temporal location effect is based on the resource sharing between timing of an interval and monitoring an approaching concurrent task within that interval. The response preparation requirement for the concurrent task – which appears in the later parts of an interval – leads to a less available resources for timing when the concurrent task stimulus must be performed. Thus, the lack of the attentional resources makes it difficult to maintain the relevant temporal information which is in turn observed by a higher rate of memory decay in the conditions which have a concurrent task later within an interval. We have favoured this account rather than the attentional switch account since our results can be explained better with a memory decay mechanism. Although the attentional switch account – which is based on the disruption in the pulse accumulation during encoding due to the attentional shifts – can explain the temporal location effect which is based on a comparison between the early SOA and the late SOA, it cannot explain the absence of an underestimation in the empty trials. In this account, the expectation of an approaching concurrent task stimulus directly affects the number of accumulated pulses – prevents the accumulation from the very beginning in the late SOA conditions – which causes an accumulation of the few number of pulses. Therefore, within the predictions of this account, the expectation of an approaching stimulus itself must disrupt timing. However, our result showed that there was no underestimation (the ratio of the reproductions/objective duration was around 1 or little more) in the empty trials even though there was an expectation of the concurrent task until some point within an

interval. These results imply that although timing is dependent upon the attentional demands – as it is realized by the temporal location effect – it seems that this dependence is regulated through the working memory demands which was indicated by the absence of purely attentional influence – as it was realized by the accurate timing in the empty trials – in the situations such as expecting something but not performing any action besides timing. This picture suggests that the attentional influences on timing should be studied by involving working memory related phenomena.

As regards to the details of a typical internal clock model, our results did not provide a support for a switch mechanism – which works through an attentional regulation – between the pacemaker and the accumulator. Although this flickering of the switch apparatus between the two states – namely the closed and opened states which corresponds to the attention for timing and attention for the non-temporal task respectively – implies quick manipulations for the attentional regulations, our results do not suggest this kind of mechanism. For instance, a monitoring requirement of the concurrent task (expectation) makes the concurrent task performance better (i.e. lower RTs in the late SOA conditions), we have interpreted this finding as a resource sharing between the temporal information (elapsing time within an interval) and the preparation for a non-temporal task (i.e. monitoring the concurrent task which approaches) in the attentional switch account. In other words, in this account, attention is conceptualized as an entity which can be divided between temporality and the non-temporal task requirements. In addition to the experimental finding in our study, namely the absence of an underestimation in the empty trials, which do not suggest this kind division between interval timing and the expectation of the non-temporal task, this line of thinking that differentiates the temporality and the non-temporal events (such as concurrent tasks etc.) is also problematic from the theoretical perspective. It is problematic because attention is taken as an independent concept which does not include an intrinsic relation with the most relevant task performance mechanism namely the working memory. Notice that a switch (i.e. Lejeune, 1998) or a gate (i.e. Zakay, 2000) between the pacemaker and the accumulator can be regulated by attention in a typical internal clock model, but the effect of attention works extrinsically on the switch as a meaning of the context (such as a start gun) or on the gate as a voluntary attentional allocation, and the relationship of attention and the working memory is not established within the model. However, the attentional time-sharing account builds this perspective by proposing a resource sharing between the working memory for time and the resources for the task requirements in the context. Thus, the attentional effects on timing is realized as a realization of the working memory component of the model in this account. In addition to its compatibility with our results, we propose that considering attention with its close relation to the working memory mechanism is another plus of this account.

Another implication of our results and the attentional time-sharing account is that timing is disrupted only if there is an explicit event within an interval. For instance, during the encoding of an interval, the occurrence of the concurrent task is another event besides the start and the end of the interval. It is the event – namely the concurrent task that needs attention for its performance – that causes the decay in the working memory. In other words, if there is no intruder event within an interval (the empty trials), the beginning event (i.e. fixation or a sound) and the ending event of the interval – which is experienced in the encoding part of the reproduction task – can be recognized accurately in the reproduction part of the reproduction task without any expectation effect (i.e. the accurate timing in the empty trials without any event). Thus, our result for the temporal location effects in these behavioural studies suggest an event based timing which is based on the events which are to be processed in the working memory rather than an eventless attentional resource sharing between timing and the expectation of a stimulus.

As regards to expectation phenomena, we have provided electrophysiological support as well for the event based account of the expectation effects. Our results revealed that N1 peak – which is a marker of an automatic event detection – at the offset of an interval is regulated as a function of the subjective responses. More precisely, N1 peak showed greater amplitudes for the short responses with respect to a threshold (i.e. the point of subjective equality). As a parallel to the suggestion for the role of N1 peak in the literature (i.e. Chennu et al., 2013; Annic et al., 2014) which points out higher peak amplitudes for the unexpected events, we have interpreted our results, namely the higher amplitudes for the subjectively short durations, as an indication of an unexpected end of an interval. In our electrophysiological studies, the sounds were used as events that determine the beginning and the end of an interval. Thus, hearing a beep sound which informs the end of an interval was an event to be compared to an inner threshold. Thus, the processing of the end of an interval as an unexpected event can be interpreted as an automatic mismatch between the inner threshold and the current interval length. In addition to our behavioral findings which favor an event based timing, this type of interpretation for the N1 peak is in line with the event based timing too, because the mismatch detection occurs fast and automatically – the N1 peak as a very early component of the information processing – in this account.

Providing an EEG component as a marker for the subjective timing responses and this marker as being a relatively automatic component – namely the sensory based attentional orientation in response to the unexpected events – of an information processing sequence have theoretical implications with respect to the timing models. For instance, the detection process actually corresponds to a comparison process between the threshold and the current interval within a typical internal clock model. These results

do not suggest a demanding process for the decision level of the internal clock model in terms of the working memory requirements. Therefore, a coincidence detection model (Matell & Meck, 2000; Van Rijn et al., 2014) suits more to explain our results. In this model, a start and an end event determine a specific interval length which is based on the specific patterns of the oscillations at the time of the occurrence of these events. Thus, recognizing an event as the end of an interval as equal as the previously experienced interval depends on the detection of the particular oscillation pattern. This detection is automatic because it does not require an explicit comparison and it is based on the match or mismatch of the pattern in the context and the threshold. In other words, although the pulse value in the accumulator needs to be compared in every update of the value in a typical consideration of the comparison process, this is not necessary in the event based coincidence detection. Moreover, in contrast to the rule based decision level, the comparison process in the coincidence detection is not a process which requires a retrieval of a reference value from the long-term memory (i.e. threshold/PSE). N1 peak is apparently not related to a retrieval process and it is better to conceptualize a threshold (i.e. the PSE) as a strengthened oscillation pattern which allows an immediate match or mismatch detection at the end of an interval. As a last support, in which our results provide for a coincidence detection type of decision level in timing, we should mention our finding about the non-demanding nature of the comparison process in one of our behavioral findings. The results which were based on the comparison of the two stages of a reproduction task (i.e. the encoding and the reproduction stages) showed that the comparison process in the middle SOA condition of the reproduction stage block did not reveal an extra timing disruption due to an overlap between a potentially demanding comparison process (i.e. a typical threshold comparison which may require a continuous value retrieval during the elapsing time) and the concurrent task. The same extent of the temporal location effect in both stages of the reproduction task – namely the encoding stage which does not require a comparison process and the reproduction stage which requires a comparison – suggests that the comparison process might not be a demanding process. In this account, it is hypothesized that there should be more disruption in timing in the middle SOA of the reproduction stage block because attention was already shared due to the attentional time-sharing (i.e. as it is shown by the temporal location effect) and the lack of attention should be reflected more in timing disruption because there is an extra process (i.e. the comparison process) in this SOA condition. However, this interpretation is not that obvious because it assumes that there is a continuous comparison process throughout the interval. One can argue that the comparison process (even if it is demanding) might be concentrated towards the end of an interval. However, bearing in mind that the comparison process should not be conceived as an explicit comparison but it can be a non-conscious process, it is questionable how a timing mechanism can know that an elapsing time is getting

closer towards the end of an interval without comparing it with a previously learned threshold or standard. Thus, following that we propose that there should be still some sort of comparison process even in the middle SOA and our results indicated that this comparison process was not demanding in terms of the working memory resources (i.e. a retrieval process of the threshold etc.) because we have found no extra disruption in the reproduction stage which requires a comparison.

On the other hand, N1 peak amplitude regulation of the subjective responses was present only for the intervals which were shorter than the PSE in the bisection task. Short and long responses could not be predicted by N1 peak amplitudes for the long intervals. Is this finding against the coincidence detection account? The absence of a subjective response regulation after the threshold indicates only the vanishing of the N1 peak amplitude difference after the PSE. Since the elapsing time passes the point where the inner threshold is built and the experience of the interval is beyond that point, the comparison has already been completed at the end of the interval. This interpretation is also compatible with the coincidence detection because expectation grows until the threshold point. In other words, if expectation does not grow sufficiently at the end of an interval, an immediate reaction due to an unexpected event corresponds to the short responses with the higher amplitudes. On the other hand, if expectation grows sufficiently until the threshold point and a particular interval passes this point, a decision has already been made at the end of the interval and this was indicated by an absence of a subjective response regulation by N1 peaks. The absence of N1 peak regulation at the end of the interval for the long intervals can be explained by the independence of the subjectively long responses in the end of the objectively long intervals because we have proposed that a comparison and thus a decision for a response is completed at offset of the interval. So, what might be the reason for observing short responses after the threshold point? Our result provided evidence for the relation of the onset N1P2 complex and the accuracy with respect to the PSE. Responding as short after the inner threshold probably is related to a problem in the registration of the start of an interval. If the onset event is not registered effectively in a particular interval, the synchronization of the neuronal populations which have same periodicity (i.e. Van Rijn et al., 2011) might not be achieved, thus a participant might not be able to give an appropriate response in response to that particular interval's ending. Thus, if there is no proper registration of the beginning of the interval, N1 peak may not show a sensitivity for the short responses after the threshold in the long intervals.

In addition to the understanding about the N1 peak that was presented above, we have also obtained results which show a relation of expectation and CNV. In the bisection task, CNV course changed towards the end of the interval for the long responses in the

intervals longer than the PSE. More precisely, when the participants decided that the relevant interval was longer than the inner threshold, then CNV started to decrease. This finding supports the view that CNV ramping activity grows until an inner threshold and the course of CNV is a marker of expectation. Similarly, we have observed that CNV course changes direction in the last two intervals (Group-4) of the trisection task which indicates another threshold around the seventh interval of the nine-interval scale of this experiment. More importantly, it was found that N1 peak amplitudes were lower in the Group-3 (the sixth and the seventh intervals) in comparison to the preceding group. This finding is also in line with our interpretation with regards to expectation and CNV/N1 peak couple. The change of CNV course in the last group indicates that expectation was in its highest level around the seventh interval, and then it starts to diminish due to the completion of the decision process around this interval. The lower N1 peak amplitudes in the sixth and the seventh intervals also supports this hypothesis which states that expectation was high around these intervals. Indeed, the relatively lower N1 peak is a marker for the expected events in contrast to the higher N1 amplitudes which are associated with the unexpected events.

6.2. Interference and Interval Timing

Our results revealed that performing a concurrent task have an overall effect – which is independent from its difficulty – on timing in the encoding stage. In other words, the concurrent task (i.e. Simon task or Stroop task) performance requirements causes a loss of accumulated pulses. Moreover, this loss of accumulated pulses occurred within the attentional time-sharing framework and showed the same rate of memory decay for both congruent and incongruent trials in the encoding stage. This finding was discussed by the help of the attentional time-sharing account since its predictions are more appropriate to explain our results. An alternative account, namely the switch account, predicts that flickering in the switch apparatus of a typical internal clock model is regulated by the attentional shifts and thus in the incongruent trials – which requires further attention to solve the stimulus-response conflict (Roelofs, 2003; Coderre et al., 2011; Machado-Pinheiro et al., 2010) – attention is diverted away from timing. According to this hypothesis, solving the conflict in the incongruent trials takes time and this extra process should be shown as the Simon or the Stroop effect. More importantly, this extra time for the conflict resolution must be carried exactly to the timing underestimation in the encoding stage. However, in our experiments we did not find any underestimation in timing of the incongruent trials and even there was a numerical difference it was in the opposite direction since the incongruent trial reproduction ratios were higher than the congruent trial ratios. Therefore, the attentional switch account was not supported by our findings with respect to the predictions about the congruency of the concurrent

task. The attentional time-sharing account does not predict a higher memory decay rate in the incongruent trials because there was no processing overlap between the timing requirements in the encoding stage and of the incongruent trials. In the theoretical understanding of the memory decay accounts, the only difference can arise from the little bit longer (i.e. the Simon/Stroop effect duration) decay duration in the incongruent trials. However, if we consider that the memory decay starts from the beginning of the concurrent task and timing task overlap, the extra memory decay during the extra time due to the Simon/Stroop effect (i.e. 30-60 msec) within the total overlap duration (i.e. 750 msec) cannot add a significant difference between the congruent and the incongruent trials. Thus, the attentional time-sharing account can predict our results with regards to both the presence of an overall task effect and the absence of congruency effect.

In contrast to the findings with respect to the congruency in the encoding stage, we have presented that there was a significant congruency effect in the reproduction stage of the reproduction task. We have proposed that the higher memory decay in the incongruent trials arise from the overlap between the response inhibition requirements of the timing task (i.e. inhibition for not to terminate an estimation prematurely in the reproduction stage) and of the incongruent trials. The overlap rises from the process requirements of the same type in the working memory which probably creates an extra cognitive load in the incongruent trials. This cognitive load makes it difficult to maintain the temporal information in these trials (i.e. higher memory decay) which is in turn leads to a more disrupted timing (i.e. overestimation) in the incongruent trials of the reproduction stage. Notice that the attentional switch account can also explain the significant difference between the congruent and incongruent trials, however as it is discussed above, this account predicts an exact carry over effects between timing and the concurrent task. However, in addition to that it has no explanation for the absence of the congruency effect in the encoding stage, the attentional switch account prediction for the reproduction stage is not compatible with our results. Because we have found that the congruency effect on timing (i.e. durational [in msec] correspondence of the ratio difference) was around 100 msec even though the Stroop effect in the reproduction stage was 44 msec. It is difficult to make this difference coincide with the carry over effect prediction of the attentional switch account. We should also mention a possible alternative explanation regarding the absence of a motor response related to the timing task in the encoding stage to account for the dissociation between the two stages of the reproduction stage. The reason that we could not find a congruency effect in the encoding stage might be related to the absence of a motor response which can explain the congruency effect in the reproduction stage. In other words, if we assume that the incongruent trials of the Stroop task caused more timing disruption due to a motor response requirement of the timing task, then we can consider the possibility that the congruency effect was not solely due to the overlap of the inhibition requirement of

timing and Stroop task, but there might be a motor response related factor in our observation in the reproduction stage. Thus, there is a need for a further study to reveal whether the congruency effect can be affected by introducing a motor response in the encoding stage of the timing task.

As a last instance of an interference effect in one of our experiments (Exp-3), we have stated that there was a response overlap of timing and Stroop task in the late SOA condition of the reproduction stage block. In other words, timing disruption in the late SOA of the reproduction stage block was higher than the late SOA of the encoding stage block. We have interpreted this finding as a response activation overlap of the two tasks because there was an intrinsic necessity to perform the Stroop task first, and then a participant can finish her time estimation in the late SOA of the reproduction stage. Therefore, this sequential response necessity delays the response activation process of the timing task which results in more overestimated reproductions in the late SOA. We prefer to discuss this finding in terms of response overlap rather than a disruption due to an overlap between the comparison process of timing – which might be argued that it is concentrated only towards the end of the interval – and the concurrent task. One reason for that preference is that we think that there must be some sort of comparison process throughout the whole interval (see Section: Expectation and Interval Timing). Thus, if we accept that there is a comparison process throughout the whole interval, we cannot explain the fact that why we did not find this extra timing disruption in the middle SOA condition of the reproduction stage block. In that sense, a sequential responding necessity which arises in the late SOA of the reproduction stage block can explain our results better.

6.3. Discrimination Difficulty and Interval Timing

We have showed that the offset P2 peak was regulated with respect to the subjective responses in a different way than the N1 peak. Although N1 peak amplitude was presented as a marker for expectation in timing, the P2 peak amplitude showed a regulation in terms of difficulty in time discrimination. Moreover, these two peaks have different target intervals which was exemplified by the relation of the P2 peak and the middle intervals. In the bisection task, the P2 peak amplitude was greater for the short responses. Considering the role of P2 peak in an attentional burst for the further information processing, we can only interpret this result by the location of the middle duration with respect to the PSE. In the bisection task, the PSE is found to be at the slightly right of the middle interval and we can interpret the higher peak amplitude for the short responses as a marker of accuracy in accordance with the temporal location of the PSE. In this line of thinking, if the automatic detection mechanism which was

indicated by the N1 peak did not yield an outcome for a response, a further working memory related processing was needed to give an appropriate response. Indeed, P2 is suggested to be related to the working memory functionally (i.e. Lefebvre et al., 2005; Taylor et al., 1990; Wolach & Pratt, 2001). However, there is a controversy about the relation of the P2 peak amplitude and the difficulty and both findings such as higher amplitudes for higher difficulty (i.e. Kim et al., 2008) and lower amplitudes for higher difficulty (i.e. Cranford et al., 2004) were presented. Our results in the bisection task supports the relation of the difficulty and the P2 peak, but it does not present a clear-cut relation between difficulty and P2 peak amplitude because we suggest to interpret the results in terms of response accuracy. Therefore, higher P2 peak amplitudes for short the response can be taken within this accuracy perspective. Indeed, this explanation was verified in our trisection task. P2 peak amplitude regulation in terms of the subjective responses was observed only in the middle intervals. However, in this case there was a third response option, thus the difficulty in terms of a discrimination extends over several intervals depending on the temporal location of the two PSEs between the short and the middle responses and between the middle and the long responses respectively. Our results revealed that the intervals between the two PSEs can be taken as the middle intervals which are subject to be processed as the difficult discriminations. Indeed, in the four intervals which correspond to this middle categorization showed a P2 peak regulation as a function of the subjective responses. Moreover, this regulation was compatible with the findings in terms of accuracy in the bisection task. In other words, the middle responses showed greater amplitudes in comparison to the short or long responses in these intervals which can be accepted as the difficult trials in terms of discrimination. These intervals can be count as difficult even though there was a third response option as well in the training session of the experiment since the number of training trials were very few in comparison to the experimental trial number. Thus, the response tendencies and relative locations of the PSEs were rather determined during the course of the experiment. In other words, the relatively shorter and the longer intervals were subject to be recognized easier than the middle intervals and P2 peaks were higher in the accurate responses (i.e. the middle response) in these relatively difficult trials.

In conclusion, in this thesis, a comparison between the two accounts – namely the attentional switch and the attentional time-sharing – has been made with respect to their predictions for the expectation and the congruency effects in timing. We have provided support for the attentional time-sharing account. Moreover, our findings can contribute to the discussion on the role of attention in timing and to the question that how this role should be integrated into the internal clock models. Our results suggest an attentional perspective in timing which should be understood in a way which is more

closely related to the working memory component of the internal clock models. In that sense, especially our results on expectation and N1 peak favors an event based timing perspective which was reflected by the detection of the oscillation patterns in the pre-frontal cortex which is typically determined to be a brain region for the working memory functions. Moreover, our findings are promising to establish a further relationship of the two electrophysiological markers, namely CNV and N1 peak, with respect to their role to understand expectation phenomena in timing.

6.4. Expectation or an Interval Onset-Offset Related Switch Account

In the previous chapters, an alternative to the expectation based account was discussed. In this alternative, we have discussed whether a possible interval onset registration or an offset registration related timing disruption can explain our findings. For this purpose, we have compared the SOA effects in different intervals to see whether this effect had an additive or a multiplicative nature. The results of Exp-1 supported expectation related attentional time-sharing and working memory decay mechanisms since the pattern for the SOA effects for different interval lengths were in line with what we would expect from a multiplicative function. In Exp-2, although the extent of the longest interval still fitted a multiplicative function in comparison to the shorter intervals, we found that shorter intervals had a similar SOA related difference in msec although these effects were not significant (see Appendix B). This finding does not suggest a significant expectation effect or a significant onset related timing disruption due to a pacemaker related acceleration in the early SOA conditions of these shorter trials. Therefore, timing disruption due to the temporal location (SOA effect – 267 msec) in the longest interval was discussed by comparing the predictions of the expectation based account and a possible offset registration related timing disruption. First of all, we pointed out that a possible offset registration failure (i.e. a premature ending of an interval due to the concurrent task) by the opening of the switch – which means a stop of signal accumulation from pacemaker to accumulator) – may account only for the longest interval but not for the shorter ones although all intervals had the same distance of the concurrent task to the end of the interval. Thus, we proposed that there should be fewer attentional resources in the longest interval at the time of the appearance of the concurrent task which in turn leads to a failure in the continuation of time keeping by a premature opening of the switch. Moreover, for this to be true, we suggested that there should be already an attentional sharing between timing and monitoring of the concurrent task before the appearance of the concurrent task which we called expectation effect. In other words, if there is a sharing – independent of its mechanism – due to expectation, this means that we should observe more disruption in these longest intervals. Our results from Exp-2 favour attentional sharing but they are also consistent

with both working memory maintenance problems (i.e. memory decay) and the premature offset registration (i.e. early stop mode of the switch). In brief, the results of Exp-1 support both expectation related attentional sharing and the working memory decay although Exp-2 only supports expectation related attentional sharing but this sharing is open to be explained by both mechanisms, namely the decay function and the switch failure explanation.

CHAPTER 7

LIMITATIONS AND FUTURE STUDIES

One of the limitations of this study as regards to the design issues is the aforementioned confounding factor in the empty trials of the reproduction stage of the Exp-3. In this condition, since the empty trials were included in the same block with the trials that include a concurrent task, the participants were probably tended to wait longer than their recently experienced interval requires. This is possible because the participants can finish their estimation whenever they want in this block. Therefore, in this interval, they might want to see whether any concurrent task stimulus would be appeared on the screen even though it was time to finish their estimation at some point. This factor was absent in the encoding stage block because the given time was ending in a pre-determined way since the participants were experiencing the interval but they did not need to perform a motor response. We have found really overestimated reproductions in the empty trials of the reproduction stage block due to this confounding factor which was not related to the expectation phenomenon but it was a result of the trials which were under the control of the participants. This situation can be eliminated by introducing a separate block for the empty trials.

In this thesis, we have defended a view which considers expectation and interference effects together in interval timing by favouring the attentional time-sharing account in comparison to the attentional switch account. However, these accounts are based on mostly psychological models in the timing literature, and thus our results and interpretations should not be taken as a rigid stance for favouring decay functions over switch functions of the cognitive system in general. One limitation of this thesis is that we could not investigate the carry over effects in enough detail to be able to decide between the switch based account and the serial bottleneck. Although we interpreted the results of this study for the congruency effects against the serial bottleneck explanations of the attentional switch account, discussions about the computational foundations of the switch based explanations were not a subject of this thesis since our results were related to an internal clock switch on a specific level but not directly related

to some switch based serial processing in a cognitive system. It is highly possible to think of a serial processing framework which can yield outcomes similar to our results. Although the nature of the attentional switch was not a topic of this thesis, and sharing was only assumed without a deliberate stance about how it could be possible (e.g.

attentional time-sharing), timing is a quite appropriate topic to study the details of the serial bottleneck and thus further studies should be conducted for this purpose only.

Moreover, we can enumerate some points arguing against our views when we are discussing the findings. For instance, we assumed a version of Simon/Stroop task which emphasizes the attentional orientation type of explanation to argue against the switch account. However, as mentioned in the general discussion, the absence of a timing task related motor response in the encoding stage might be responsible for the dissociation that we found in the congruency effect. Moreover, the absence of an expectation effect in the empty trials was taken as one of the core findings to support our view favouring the working memory decay, however, although there was more evidence for multiplicative type of expectation effect than additive effects, the findings from different intervals were not fully sufficient to support our view. Therefore, we need more studies to eliminate carefully, if possible, the potential changes of the clock modes at the onset and the offset of the intervals to be able to further support our results.

As for the neurophysiological findings of this study, we have provided evidence for differential associations of the two ERP components, namely N1 and P2. However, we need further studies on how to isolate or combine these components by manipulating various requirements of a timing task. Moreover, a study which combines the reproduction method and the N1 peak can provide new perspectives on the nature of the temporal location effects in the behavioural studies. Furthermore, a future study which combines both N1 and N300 components in time based decisions seems to be a promising way to investigate the categorization of time intervals.

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APPENDICES

APPENDIX A

SOA – Duration Length Analysis (Exp-1)

In the model, three independent variables were included. The dependent variable was the reproduced estimations. One of the independent variables was temporal location which has three levels: Early SOA, late SOA and NoSimon. The second variable was congruency which has two levels: Congruent, incongruent. As last variable in the analysis, interval length is added as factors that includes three levels of different intervals as interval1, interval2 and interval3. Moreover, the model was including the interaction of SOA and duration length effects. The intercept term corresponding to the congruent late SOA condition in the interval-1 was found to be significant ($\beta = 2040.4$, $p < .001$). Since the interaction of interval-3 and SOA was significant ($\beta = 194.4$, $p < .001$), we have conducted post-hoc tests to reveal the SOA effect in each interval separately. The results indicated that the reproductions at the Early SOA condition were not significantly longer than the ones at the Late SOA condition in the interval-1 ($\beta = 73.11$, $p = 0.26$) (Table 29). However, we have found that SOA effect was significant in the interval-2 ($\beta = 110.3$, $p < .05$). Moreover, in the interval-3, this effect was also significant ($\beta = 267.5$, $p < .001$).

Table 29. Linear Mixed Effect Model and Post-hoc tests for the interaction of SOA and duration length (Exp-1)

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	2040.40	111.36	17.90	18.322	4.76e-13 ***
SOAEarly	73.11	50.86	2355.50	1.438	0.15070
SOANoSimon	156.70	51.75	2355.50	3.028	0.00249 **
Interval2	293.75	50.13	2355.60	5.860	5.28e-09 ***
Interval3	545.27	51.95	2355.50	10.496	< 2e-16 ***
incongruent	15.11	28.93	2355.40	0.522	0.60158
SOAEarly:interval2	37.21	70.40	2355.50	0.529	0.59715

Table 29. (cont.)					
SOANoSimon:interval2	57.96	70.49	2355.60	0.822	0.41097
SOAEarly:interval3	194.44	71.86	2355.40	2.706	0.00687 **
SOANoSimon:interval3	155.27	70.33	2355.50	2.208	0.02735 *
Post-hoc Tests					
Length = interval1:					
contrast	estimate	SE	df	t.ratio	p.value
Early - Late	73.112	50.860	2306.11	1.438	0.2632
Length = interval2:					
contrast	estimate	SE	df	t.ratio	p.value
Early - Late	110.322	48.714	2306.27	2.265	0.0450
Length = interval3:					
contrast	estimate	SE	df	t.ratio	p.value
Early - Late	267.54971	50.816	2306.13	5.265	<.0001

APPENDIX B

SOA – Duration Length Analysis (Exp-2)

In the model, three independent variables were included. The dependent variable was the reproduced estimations. One of the independent variables was temporal location which has three levels: Early SOA, late SOA and NoSimon. The second variable was congruency which has two levels: Congruent, incongruent. As last variable in the analysis, interval length is added as factors that includes three levels of different intervals as interval1, interval2 and interval3. Moreover, the model was including the interaction of SOA and duration length effects. The intercept term corresponding to the congruent late SOA condition in the interval-1 was found to be significant ($\beta = 1980.1$, $p < .001$). Since the interaction of interval-3 and SOA was significant ($\beta = 210.6$, $p < .001$), we have conducted post-hoc tests to reveal the SOA effect in each interval separately. The results indicated that the reproductions at the Early SOA condition were not significantly longer than the ones at the Late SOA condition in the interval-1 ($\beta = 50.9$, $p = 0.40$) and in the interval-2 ($\beta = 53.9$, $p = .036$) (Table 30). However, in the interval-3, this effect was significant ($\beta = 261.5$, $p < .001$).

Table 30. Linear Mixed Effect Model and Post-hoc tests for the interaction of SOA and duration length (Exp-2)

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	1980.058	132.909	14.400	14.898	3.72e-10
SOAEarly	50.955	43.628	2339.700	1.168	0.242958
SOANoSimon	201.324	43.867	2339.700	4.589	4.68e-06
interval2	209.059	43.915	2339.700	4.760	2.05e-06
interval3	388.145	44.141	2339.700	8.793	< 2e-16
incongruent	11.922	32.469	2339.700	0.367	0.713522

Table 30. (cont.)

SOANoSimon:interval2	91.963	61.440	2339.700	1.497	0.134586
SOAEarly:interval3	210.601	61.852	2339.700	3.405	0.000673
SOANoSimon:interval3	194.809	61.607	2339.700	3.162	0.001586

Post-hoc Tests

Length = interval1:					
contrast	estimate	SE	df	t.ratio	p.value
Early - Late	50.954	43.628	2348.01	1.168	0.4024
Length = interval2:					
contrast	estimate	SE	df	t.ratio	p.value
Early - Late	53.958	43.715	2348.02	1.234	0.3650
Length = interval3:					
contrast	estimate	SE	df	t.ratio	p.value
Early - Late	261.555	43.84078	2348.00	5.966	<.0001

APPENDIX C

SOA – Duration Length Analysis – Encoding Stage - (Exp-3)

In the model, three independent variables were included. The dependent variable was the reproduced estimations. One of the independent variables was temporal location which has three levels: Early SOA, late SOA and NoSimon. The second variable was congruency which has two levels: Congruent, incongruent. As last variable in the analysis, interval length is added as factors that includes three levels of different intervals as interval1, interval2 and interval3. Moreover, the model was including the interaction of SOA and duration length effects. The intercept term corresponding to the congruent early SOA condition in the interval-1 was found to be significant ($\beta = 3485.4$, $p < .001$). Since the interaction of interval-2 and late SOA ($\beta = -363.2$, $p < .001$) and of interval-3 and late SOA was significant ($\beta = 280.8$, $p < .05$), we have conducted post-hoc tests to reveal the SOA effect in each interval separately. The results indicated that the reproductions at the Middle SOA condition were not significantly shorter than the ones at the Early SOA condition in the interval-1 ($\beta = -156.1$, $p = 0.14$) (Table 31). However, in the interval-2 ($\beta = -313.4$, $p < .001$) and in the interval-3, this effect was significant ($\beta = -271.9$, $p < .001$). As for the Early SOA and late SOA comparison, the results revealed that SOA effect was this effect was not significant in the interval-1 ($\beta = -75.2$, $p = 0.67$). However, we observed that late SOA reproductions were significantly shorter than the early SOA reproductions in the interval-2 ($\beta = -438.5$, $p < .001$) and in the interval-3 ($\beta = -356.1$, $p < .001$).

Table 31. Linear Mixed Effect Model and Post-hoc tests for the interaction of SOA and duration length (Exp-3)- Encoding Stage

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	3485.40	138.48	28.70	25.169	< 2e-16
SOAmiddle	-156.09	81.30	2160.90	-1.920	0.05500
SOAlate	-75.25	83.24	2161.00	-0.904	0.36612
SOANoStroop	-55.61	75.50	2161.00	-0.737	0.46150
Interval2	345.26	81.92	2160.90	4.215	2.60e-05
Interval3	503.53	79.63	2161.00	6.324	3.09e-10
incongruent	43.62	37.39	2160.80	1.167	0.24347
SOAmiddle:interval2	-157.33	112.88	2160.90	-1.394	0.16351

Table 31. (cont.)					
SOAlate:interval2	-363.27	114.61	2160.90	-3.170	0.00155
SOANoStroop:interval2	-59.81	104.09	2161.30	-0.575	0.56563
SOAmiddle:interval3	-115.91	112.02	2160.90	-1.035	0.30094
SOAlate:interval3	-280.85	113.67	2161.00	-2.471	0.01356
SOANoStroop:interval3	76.81	102.73	2161.50	0.748	0.45473
interval = 1:					
contrast	estimate	SE	df	t.ratio	p.value
middle - early	-156.089	81.301	2037.14	-1.920	0.1409
late - early	-75.247	83.242	2037.25	-0.904	0.6737
interval = 2:					
contrast	estimate	SE	df	t.ratio	p. value
middle - early	-313.422	78.390	2037.16	-3.998	0.0002
late - early	-438.514	78.809	2037.19	-5.564	<.0001
interval = 3:					
contrast	estimate	SE	df	t.ratio	p.value
middle - early	-271.994	77.059	2037.15	-3.530	0.0012
late - early	-356.098	77.409	2037.14	-4.600	<.0001

In the model for the duration length analysis in the reproduction stage , three independent variables were included. The dependent variable was the reproduced estimations. One of the independent variables was temporal location which has three levels: Early SOA, late SOA and NoSimon. The second variable was congruency which has two levels: Congruent, incongruent. As last variable in the analysis, interval length is added as factors that includes three levels of different intervals as interval1, interval2 and interval3. Moreover, the model was including the interaction of SOA and duration length effects. The intercept term corresponding to the congruent early SOA condition in the interval-1 was found to be significant ($\beta = 3250.8$, $p < .001$). Since the interaction of interval-2 and late SOA ($\beta = 213.6$, $p < .05$) and of interval-3 and late SOA was significant ($\beta = 443.5$, $p < .001$), we have conducted post-hoc tests to reveal the SOA effect in each interval separately. The results indicated that the reproductions at the Middle SOA condition were significantly longer than the ones at the Early SOA condition in the interval-1 ($\beta = 253.8$, $p < 0.01$) (Table 32), in the interval-2 ($\beta = 256.4$, $p < .001$) and in the interval-3, this effect was significant ($\beta = 494.9$, $p < .001$). As for the Early SOA and late SOA comparison, the results revealed that SOA effect was this effect was also significant in the interval-1 ($\beta = 325.2$, $p < 0.01$), in the interval-2 ($\beta = 538.8$, $p < .001$) and in the interval-3 ($\beta = 768.7$, $p < .001$).

Table 32. Linear Mixed Effect Model and Post-hoc tests for the interaction of SOA and duration length (Exp-3)- Reproduction Stage

Fixed effects:					
	Estimate	Std. Error	df	t value	p-value
(Intercept)	3250.848	109.957	31.6000	29.565	< 2e-16
SOAmiddle	253.852	74.370	1983.40	3.413	0.000655
SOAlate	325.218	73.422	1983.40	4.429	9.96e-06
SOANoStroop	417.040	68.503	1983.60	6.088	1.37e-09
Interval-2	237.538	74.203	1983.50	3.201	0.001390
Interval-3	364.435	72.554	1983.50	5.023	5.55e-07
incongruent	100.209	34.942	1983.20	2.868	0.004177
SOAmiddle:interval-2	2.628	106.135	1983.50	0.025	0.980243
SOAlate:interval-2	213.642	104.479	1983.40	2.045	0.041005
SOANoStroop:interval-2	-0.773	95.234	1983.90	-0.008	0.993518
SOAmiddle:interval-3	241.140	104.331	1983.50	2.311	0.020919
Table 32. (cont.)					
SOAlate:interval-3	443.543	102.923	1983.50	4.309	1.72e-05
SOANoStroop:interval-3	215.660	95.428	1984.00	2.260	0.023934
interval = 1:					
contrast	estimate	SE	df	t.ratio	p.value
middle - early	253.852	74.370	2057.17	3.413	0.0019
late - early	325.218	73.422	2057.23	4.429	<.0001
durF = 0:					
contrast	estimate	SE	df	t.ratio	p.value
middle - early	256.480	75.802	2057.30	3.384	0.0021
late - early	538.860	74.391	2057.23	7.244	<.0001
interval = 2:					
contrast	estimate	SE	df	t.ratio	p.value
middle - early	494.992	73.139	2057.32	6.768	<.0001
late - early	768.761	72.084	2057.25	10.665	<.0001

APPENDIX D

Trial Order Analysis for N1 and P2 peaks

A full model that includes behavioral responses with three levels, interval lengths, trial number (as a continuous variable) and their interactions including a three-way interaction between them as independent variables and N1 peak amplitude as the dependent variable, is conducted. The reduction of the three-way interaction term did not result in a significant change in the model ($\Delta AIC = 4$; $\chi^2 = 2.47$, $p = .48$). Response and interval interaction effect was no significant ($\Delta AIC = 1$; $\chi^2 = 6.9$, $p = .08$). However, the removal of the trial number term had no effect on the N1 peak amplitudes ($\Delta AIC = 1$; $\chi^2 = 4.8$, $p = .18$). Moreover, removal of response and trial interaction did not reveal an effect on the variation ($\Delta AIC = 1$; $\chi^2 = 4.5$, $p = .10$). (Table 33). In the final model, we could not find an additional effect of Trial number on N1 peak amplitudes ($\beta = 0.0003$, $p = .68$) besides previously shown response effect.

Table 33. Trial order analysis for N1 peak

	Estimate	Std.Error	t.value	pvalue
(Intercept)	1.427357e+01	0.702	20.329	0.0000
Trial	3.218662e-04	0.0008	0.4019	0.6877
middle	9.773527e-01	0.3039	3.2156	0.0013
short	1.178054e+00	0.4345	2.7106	0.0067
interval	6.713244e-02	0.0587	1.1429	0.2530

A second model for P2 peak that includes behavioral responses with three levels, interval lengths, trial number and their interactions including a three-way interaction between them as independent variables and P2 peak amplitude as the dependent variable, is conducted. The reduction of the three-way interaction term did not lead to a significant change in the model ($\Delta AIC = 0$; $\chi^2 = 4.0$, $p = .13$). (Table 34). The model revealed no trial number effect ($\beta = 0.0065$, $p = .66$). However, the interaction between trial number and interval length was significant ($\beta = 0.0016$, $p < .05$).

Table 34. Trial order analysis for P2 peak

	Estimate	Std.Error	t.value	pvalue
(Intercept)	16.76775	2.3541	7.122	1.058487e-12
middle	2.28096	2.0439	1.115	2.644319e-01
short	0.98463	2.1567	0.456	6.480005e-01
Trial	-0.00530	0.0054	-0.982	3.258254e-01
interval	-0.39051	0.2674	-1.460	1.442689e-01
middle:Trial	0.00038	0.0031	0.122	9.027356e-01
short:Trial	0.00540	0.0045	1.198	2.305690e-01
middle:interval	-0.26005	0.2456	-1.058	2.897790e-01
short:interval	-0.19318	0.2747	-0.703	4.819178e-01
Trial:interval	0.00158	0.0006	2.556	1.056412e-02

APPENDIX E

INTERVAL-8 ANALYSIS

A model that includes behavioral responses with three levels and interval lengths and their interactions as independent variables and P2 peak amplitude as the dependent variable, was conducted (Table 35). Post-hoc tests revealed that the analysis did not provide a difference between the middle and the long response in the interval-8 ($p = 0.47$).

Table 35. Analysis for a comparison of response amplitudes for each interval

Fixed effects:			
	Estimate	Std. Error	t value
(Intercept)	18.3650	1.3923	13.191
Short	-0.9744	1.2175	-0.800
Long	-9.4500	7.1488	-1.322
interval2	-1.3290	1.3746	-0.967
interval3	-1.0897	1.2677	-0.860
interval4	-1.8218	1.2325	-1.478
interval5	-2.1687	1.2243	-1.771
interval6	-1.9282	1.2247	-1.574
interval7	-2.2922	1.2478	-1.837
interval8	-3.8156	1.2973	-2.941
interval9	-2.3611	1.4072	-1.678
short:interval2	1.6425	1.5046	1.092
Long :interval2	12.8328	12.2987	1.043
short:interval3	1.1591	1.4435	0.803
Long :interval3	7.4725	8.0993	0.923
short:interval4	-0.8376	1.5230	-0.550
Long :interval4	17.9976	7.7195	2.331
Short:interval5	-0.4821	1.6960	-0.284
Long :interval5	7.5960	7.3269	1.037
short:interval6	0.1663	2.0650	0.081

Table 35. (cont.)					
Long :interval6	7.0858	7.2375	0.979		
short:interval7	2.4189	2.6427	0.915		
Long :interval7	8.6813	7.1944	1.207		
short:interval8	3.4617	2.6240	1.319		
Long :interval8	10.3021	7.1938	1.432		
short:interval9	7.9557	3.3518	2.374		
Long :interval9	8.5917	7.2105	1.192		
interval = interval1:					
contrast	estimate	SE	df	z.ratio	p.value
1 - 2	-0.9744081	1.217	NA	-0.800	0.6335
intervalF = interval2:					
contrast	estimate	SE	df	z.ratio	p.value
1 - 2	0.668	0.893	NA	0.748	0.6680
intervalF = interval3:					
contrast	estimate	SE	df	z.ratio	p.value
1 - 2	0.1846	0.782	NA	0.236	0.9487
intervalF = interval4:					
contrast	estimate	SE	df	z.ratio	p.value
1 - 2	-1.8120	0.919	NA	-1.972	0.0908
intervalF = interval5:					
contrast	estimate	SE	df	z.ratio	p.value
1 - 2	-1.4564	1.178	NA	-1.236	0.3638
3 - 2	-1.8539	1.626	NA	-1.140	0.4185
intervalF = interval6:					
contrast	estimate	SE	df	z.ratio	p.value
3 - 2	-2.3641	1.137	NA	-2.078	0.0710
intervalF = interval7:					
contrast	estimate	SE	df	z.ratio	p.value
3 - 2	-0.7687	0.815	NA	-0.943	0.5404
intervalF = interval8:					
contrast	estimate	SE	df	z.ratio	p.value
3 - 2	0.8521	0.812	NA	1.048	0.4739
intervalF = interval9:					
contrast	estimate	SE	df	z.ratio	p.value
3 - 2	-0.8582	0.943	NA	-0.909	0.5621

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Refereed Conference Paper:

Garaas, T. W., Marino, F., Duzcu, H. & Pomplun, M. A design for real-time neural modeling with dendritic computation on the GPU. Proceedings of the 5th International Workshop on Artificial Neural Networks and Intelligent Information Processing (ANNIIP 2009). Milan, Italy.

Posters:

The Simon effect for horizontal and vertical stimulus-response relations: Evidence for similar effect functions in a uni-manual dynamical response paradigm, DuCog II, Dubrovnik Conference on Cognitive Science, Dubrovnik/Croatia, 6-9 May 2010, Halil Duzcu, Özgür Erişen, Annette Hohenberger

ONGOING RESEARCH- PUBLICATION

- 1- Time-Sharing and Attentional Switch Accounts for the Congruency and Expectation Effects in Timing
- 2- N1P2 Complex and CNV as Markers of Expectation in a Bisection Task
- 3- Investigation of threshold and temporal discrimination in a tri-section task: N1 and P2 peaks

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EDUCATION

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