

DOCTORAL DISSERTATION

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**ELECTROPHYSIOLOGICAL CORRELATES
OF THE ATTENTION-DISTRACTION
BALANCE**



2018

¹ADATLAP

a doktori értekezés nyilvánosságra hozatalához

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**ELECTROPHYSIOLOGICAL CORRELATES OF
THE ATTENTION-DISTRACTION BALANCE**

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“Distraction is the only thing that consoles us for miseries and yet it is itself the greatest of our miseries.”

(Blaise Pascal)

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- Horváth, J., Gaál, Zs. A., & Volosin, M. (2017). Sound-offset brain potentials show retained sensory processing, but increased cognitive control in older adults. *Neurobiology of Aging: Age-related Phenomena Neurodegeneration and Neuropathology*, 57, 232-246.
- Volosin, M.**, Gaál Zs. A., & Horváth, J. (2017a). Task-optimal auditory attention set restored as fast in older as in younger adults after distraction. *Biological Psychology*, 126, 71-81.
- Volosin, M.**, Gaál, Zs. A., & Horváth, J. (2017). The duration of distraction during active and passive listening in younger and older adults reflected in N1 amplitudes. Poster presented at *CORTICAL FEEDBACK Spring School*, Jena, Germany.
- Volosin, M.**, Gaál Zs. A., & Horváth, J. (2017b). Age-related processing delay reveals cause of apparent sensory excitability following auditory stimulation. *Scientific Reports*, 7, 10143.
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- Volosin, M.**, Grimm, S., & Horváth, J. (2016). Exploiting temporal predictability: Event-related potential correlates of task-supportive temporal cue processing in auditory distraction. *Brain Research*, 1639, 120-131.
- Volosin, M.**, Grimm, S., & Horváth, J. (2015). Distraction versus task-set change: investigating the functional role of P3a elicited in oddball paradigms. Poster presented at *7th Mismatch Negativity Conference: Error Signals from the Brain*, Leipzig, Germany.
- Volosin, M.**, & Horváth, J. (2014). Knowledge of sequence structure prevents auditory distraction: An ERP study. *International Journal of Psychophysiology*, 92, 93-98.
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Volosin, M., & Horváth, J. (2013). A hallási figyelmi elterelődés idői jellegzetességei. Symposia talk at *A Magyar Pszichológiai Társaság (MPT) XXII. Országos Nagygyűlése: "Kapcsolataink világa"*. Budapest, Hungary.

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Volosin, M., Németh, D., & Janacsek, K. (2012). A kor előrehaladtával járó kognitív hanyatlás vizsgálata a Mini Mental Teszt (MMSE) és a Montreal Kognitív Felmérés (MoCA) segítségével. Poster presented at *A Magyar Pszichológiai Társaság (MPT) XXI. Országos Nagygyűlése: "A tudomány emberi arca"*. Szombathely, Hungary.

Volosin, M. (2012). Az időskori kognitív hanyatlás és a nyelvi tünetek vizsgálata a Mini Mental Teszt és a Montreal Kognitív Felmérés segítségével. Talk presented at *Újabb lehetőségek az afázia diagnosztikájában és terápiájában, a rehabilitáció színterei*. Budapest, Hungary.

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ABSTRACT

Constant and dynamic change characterizes the surrounding world we are living in. In order to interact with our environment in an adaptive way, we need to decide which events to attend to and which ones to ignore. Predictions based on the regularities of the environment make it possible to foresee future events, which allows us to prepare for these events by forming selective attention sets. Rare, unexpectedly occurring sensory events disrupt these attentional sets, capture our attention, in other words, they distract us. It has been suggested that this balance between attention and distraction changes across the lifespan; specifically, the balance seems to be shifted towards distractibility in older adults, but the exact nature of this shift remains ambiguous. The aim of my doctoral dissertation was to investigate how the cognitive system extracts and exploits regularities to achieve the most efficient information processing in the face of distraction, and compared the time needed to recover from a distracted state in younger and older adults. We utilized the method of event-related potentials (ERPs) in all studies to follow-up cognitive processes with a high temporal precision. The first two studies focused on the effects of predictability: ERP results in Study I showed that when information on the presentation time of distracting events was constantly and explicitly provided, distraction was significantly diminished compared to the condition when no predictions could be formed. In Study II, we showed that participants detected and utilized probabilistic regularities in a tone pattern even when they were not informed of the structure of the acoustic stimulation. Study III and Study IV compared the duration of distraction between younger and older adults and revealed that although both age groups recovered from the distracted state by about 650 ms after distracter onset, the processing of fine temporal resolution was deteriorated in older adults. Importantly, however, in a task situation, older adults could compensate for this decline by the recruitment of additional cognitive sources and enhanced attention.

ABSZTRAKT

A világ, amely körülvesz bennünket, folyamatosan és dinamikusan változik. Annak érdekében, hogy képesek legyünk megfelelően interakcióba lépni környezetünkkel, elengedhetetlen annak szelektálása, hogy mely eseményekre figyeljünk és melyeket hagyjuk figyelmen kívül. A környezet szabályosságai alapján képesek vagyunk olyan szelektív figyelmi beállítódásokat kialakítani, amelyek lehetővé teszik a közeljövőben bekövetkező események előrejelzését, valamint az ezekre való felkészülést. A váratlanul bekövetkező ritka szenzoros események azonban a figyelmünk megragadásával megszakítják ezeket a figyelmi beállítódásokat, tehát elterelnek bennünket. A figyelem és az elterelődés ezen egyensúlya az élet folyamán változik, ezáltal az idős személyek általában erősebb elterelődésre való fogékonysággal jellemezhetőek, azonban még nem egészen feltárt, hogy ez milyen okokra vezethető vissza. Így a doktori disszertációm célja egyrészt annak vizsgálata, hogy az emberi információfeldolgozó rendszer miként nyeri ki a környezetből a szabályosságokat és használja fel azokat az elterelődéssel szembeni lehető leghatékonyabb működés érdekében; másrészt az elterelt állapot idői jellemzőit is vizsgáltuk kutatásainkban idős és fiatal felnőttek körében. A kognitív folyamatok lehető legnagyobb idői pontossággal történő feltérképezése érdekében vizsgálatainkban az eseményhez kötött potenciálok (EKP, a későbbiekben event-related potentials – ERPs) módszerét alkalmaztuk. A disszertációban bemutatott első két tanulmány középpontjában a bejósolhatóság hatása állt: az első kísérletben kimutattuk, hogy amennyiben explicit és folyamatosan jelen lévő információval rendelkezünk az elterelő inger megjelenésének idejéről, szignifikánsan csökkent elterelődés tapasztalható ahhoz a feltételhez képest, amikor nincs lehetőség predikciók állítására. A második vizsgálatunk eredményei arra engednek következtetni, hogy egy akusztikus mintázat szabályosságait akkor is képesek vagyunk észlelni és felhasználni, amikor nem vagyunk a szabályszerűségekre vonatkozó tudatos információk birtokában. A harmadik és negyedik tanulmányban az elterelt állapot időtartamát hasonlítottuk össze idős és fiatal felnőttek körében, és bár eredményeink alapján mindkét életkori csoport esetén az elterelő esemény után 650 ms alatt véget ér az elterelődés, az akusztikus ingerek finom idői struktúrájának feldolgozása időskorra sérülést mutat. Fontos azonban kiemelni, hogy feladathelyzetben ez a változás megnövekedett figyelemmel és további kognitív források mozgósításával megfelelően kompenzálható.

INTRODUCTION

Chapter 1: The attention-distraction balance

The concept of attention as a crucial factor in human performance extends back to the beginning of the experimental psychology, more than a century back. According to James, “every one knows what attention is. It is taking the possession by the mind, in a clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called *distraction*, and *Zerstreuung* in German” (James, 1890, p. 403.).

The duality of attention and distraction described by James (1890) can be experienced numerous times in everyday life. Imagine that you are reading a highly interesting book. You are absolutely engaged in this activity and try to ignore all the ambient noises like the sounds of neighbors or the traffic in the street. But suddenly, the fire alarm is starting with loud, salient sounds, capturing your attention, in other words, it is distracting you. Along with distraction, the sound of fire alarm also motivates you to evaluate the situation: does it worth more to continue reading or rather change your behavior and leave the room (as illustrated in Fig. 1.1). Apparently, it is important to being able not only to focus on an ongoing activity but to get distracted as well: distracting events might provide valuable information regarding our subsequent behavior and our survival in general, therefore, suppressing them entirely would not be ecologically adaptive (see e. g. Parmentier, 2014). As it will be presented later in detail, the balance of attention and distraction depends both on voluntarily directed top-down and involuntary bottom-up mechanisms.

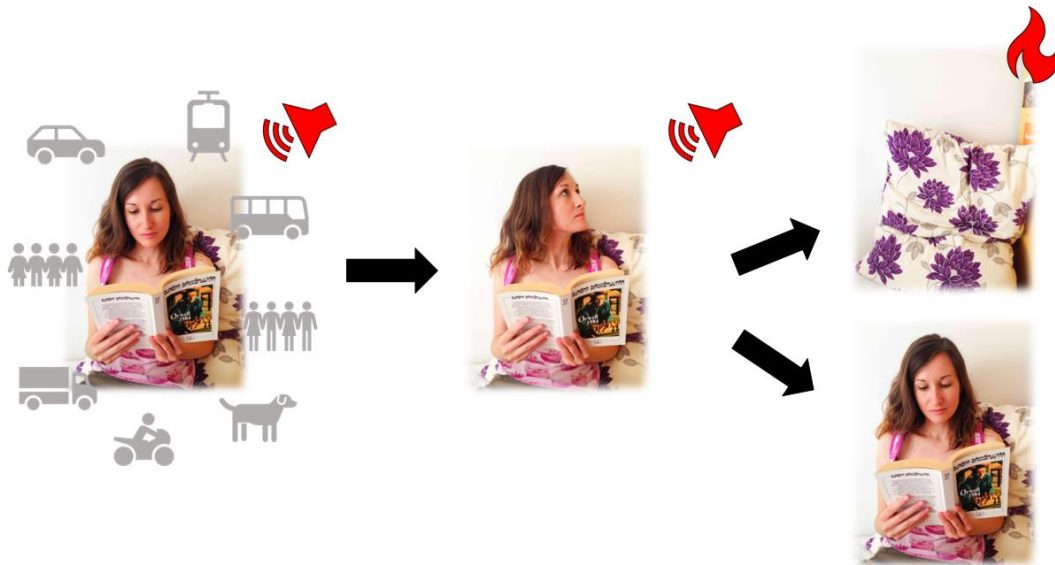


Fig. 1.1. Schematic illustration of an everyday scenario demonstrating the attention-distraction balance. Rare, unexpected acoustic events from the environment capture one's attention, that is, they distract us.

The main topic of the present dissertation is this dynamic balance between attention and distraction. First, I present several possible definitions and theories of attention and distraction, highlighting the distraction paradigm utilized and extended in our studies. Next, I describe several age-related changes in attentional processing reflected in behavior and relate these to structural and functional changes in the brain. After that, I introduce the event-related potential reflections of the processing stages of involuntary attention change and recovery from distraction, and formulate the questions and hypotheses which were investigated in our studies.

1.1 What we talk about when we talk about attention?

As pointed out by James (1890), everyone knows what attention is, however, its concept is remarkably broad, not only in the everyday use of language but in scientific terms as well. Without attention, it would be almost impossible to interact with our physical and social environment and to respond to them. However, the complexity of the external world and the limited capacity of human information processing system does not allow to process everything with an equal efficiency, so we need to select the relevant information. That is, attention is a mechanism for selection in order to choose a

specific source of external stimulation (e.g., a certain modality, or different features of the environment), internal thoughts or action plans, strongly connected to consciousness. Beside selecting the appropriate channel or response, we also need to take voluntary and conscious control over automatic and routine behavior which can be performed without investing too much mental effort or attention. For example, despite being a complex motoric act, riding our bike engages a very small amount of our cognitive capacity and we are able to perform different activities at the same time, like having a conversation or monitoring the traffic around us. This monitoring process is crucial to supervise and control our goal-directed behavior from time to time, to overcome and inhibit automatic actions and to detect errors. Moreover, the concept of attention includes the level of activation, such as being aroused, fatigue or drowsy. The optimal level of activation makes possible to pay attention in general. That is, attention can be defined as a multidimensional construct, in which the optimal level of activation enables to select task-relevant information and to control our mental, emotional and physical actions (Rueda, Posner & Rothbart, 2011; Rueda, Pozuelos & C3mbita, 2015).

Attentional processes can be categorized based on the amount of voluntariness as well, that is, whether driven by external stimuli (bottom-up) or endogenous (top-down) processes like expectations or intentions. Control processes such as error detection and monitoring the environment are considered as endogenous and voluntarily directed mechanisms in general. On the other hand, salient events from the environment such as the unexpected sound of the fire alarm can alert us and orient our attention to the eliciting object or modality in an automatic bottom-up manner, also labeled as distraction. An opposite phenomenon can also happen when we voluntarily choose what we aim to attend to because the event is relevant regarding our activity (for example, we focus on a book or conversation because it is interesting and keeps us alerted as well). The present dissertation focuses mainly on the fluctuations between automatic and controlled processes of alerting and voluntary attention, however, it is important to emphasize that all three aspects (alerting, orienting, control) of attention play important roles in maintaining everyday activities (Petersen & Posner, 2012; Rueda, Pozuelos & C3mbita, 2015).

In the next subsections, I introduce two theories on attention and distraction. First, I describe the theory of attentional network (Posner & Petersen, 1990) which is one of the most influential theories of attention in the recent cca. 30 years. Second, I

focus on the distraction paradigm introduced by Schröger & Wolff (1998b) which provided the theoretical foundation for the studies in the present dissertation.

1.2 Theory of attentional networks

The literature on the cognitive neuroscientific aspects of attention is dominated by the view that attentional functions can be related to three distinct networks: one plays a role in maintaining vigilance and alerting, the second is related to orienting attention, and the third one contributes to executive control (Petersen & Posner, 2012; Posner, 2016; Posner & Petersen, 1990; Rueda, Pozuelos & Cómbita, 2015). The efficiency of these three functions is measurable with the Attention Network Test (ANT) which has visual (Fan, MacCandlis, Sommer, Raz & Posner, 2002) and auditory versions (Roberts, Summerfield & Hall, 2006) and also a variant adapted for children (Rueda, Posner & Rothbart, 2011). The visual ANT combines the flanker task (Eriksen & Eriksen, 1974) with spatial cueing task (Posner, 1980). The target stimulus is an arrow pointing either to the left or to the right and participants' task is to press the corresponding button. Targets are surrounded by task-irrelevant flanker arrows pointing to the same (congruent) or to the opposite (incongruent) direction. The incongruity based on conflict between the direction of the arrow and the response button requires executive control and top-down regulation. Besides, cues preceding each trial indicate when or where the target will be presented, allowing participants to prepare for response (Fan et al., 2002; Posner, 2016).

In the auditory version, sinusoid tones (Zhang, Barry, Moore & Amitay, 2012) or spoken words (Roberts, Summerfield & Hall, 2006) are presented with high or low pitch to the one ear while monoaural or binaural cues precede them informing about the location (left or right ear) or the timing of target tones (Roberts, Summerfield & Hall, 2006). Spatial cues induce the orientation of attention while non-spatial cues lead to alerting in both in vision and hearing (Stewart & Amitay, 2015). The alerting and executive control effects were demonstrated in both modalities reflected by speeded up response times following cues (alerting) and slowing to incongruent cue-target pairs (executive control). However, spatial orienting processes were more robust in the visual modality, that is, when cues indicated the presentation direction of targets, response times decreased in the visual task only (Roberts, Summerfield & Hall, 2006; Stewart & Amitay, 2015).

The widespread use of positron emission tomography (PET) in the '90s and later the other functional brain imaging techniques allowed to identify the contribution of different brain structures more accurately behind the behavioral effects (Petersen & Posner, 2012). The anatomy of the three networks are presented in Figure 1.2.1. The origin of the alerting network was located in the arousal-related areas in the thalamic and brain stem regions in the right hemisphere including locus coeruleus responsible for norepinephrine secretion (Aston-Jones & Cohen, 2005; Sturm & Willmes, 2001). These areas are usually active during cue processing, and cues presented before target events also support participants to prepare for the upcoming task-relevant events resulting in faster response times (Petersen & Posner, 2012).

During attentional orienting, parietal cortical areas show enhanced activation with frontal contribution when selecting visual stimuli (Posner & Petersen, 1990). The later update of the model differentiates the orienting network to two further subnetworks. The dorsal system including parietal areas and a small set of frontal regions (frontal eye fields) is responsible for rapid attentional control related to cue utilization processes. In contrast, the ventral system becomes active after the occurrence of the target is presented and it consists of temporoparietal junction and parietal cortical areas with an enhanced contribution of ventral frontal cortex (Corbetta & Schulman, 2002; Petersen & Posner, 2012). In order to achieve an optimal orienting function, the parallel activity of dorsal and ventral systems is required (Petersen & Posner, 2012). The third part of the attention network model is the executive control which is linked to middle and lateral frontal and anterior cingulate cortex and is responsible for conflict monitoring and relates strongly on voluntarily directed, top-down processes (Zhang et al., 2012). The presence of two executive networks was later suggested by Dosenbach and colleagues (2008): the fronto-parietal system involved in fast, adaptive control and the opercular network playing role in sustained attention (Dosenbach, Fair, Cohen, Schlaggar & Petersen, 2008).

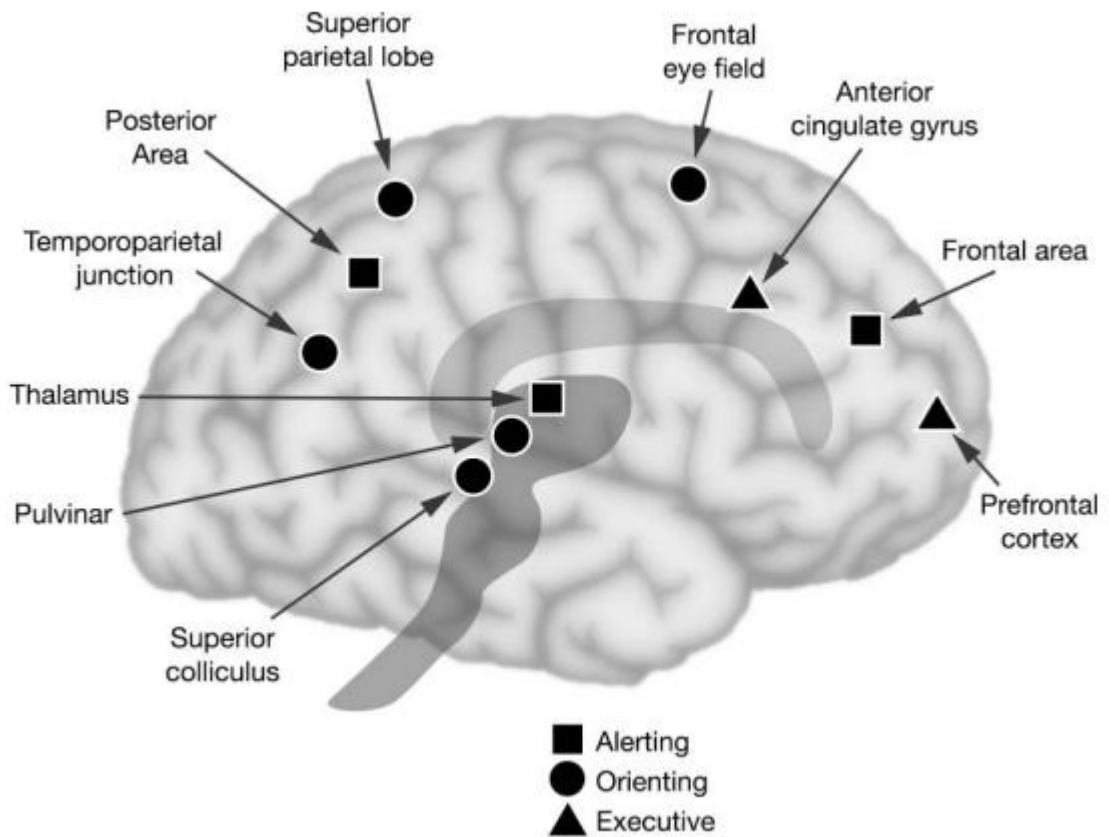


Fig. 1.2.1. The anatomy of alerting, orienting and executive networks based on imaging studies (Posner & Rothbart, 2007; Figure 2., pp. 6.).

Although the framework of attentional systems provides essential information on how different attention-related mechanisms can be distinguished in their anatomical and functional aspects, and how they contribute to task performance, the time course of these processes remains ambiguous. Moreover, visual modality dominates the field of research therefore generalization of results from brain imaging studies to auditory modality is difficult (Alho, Salmi, Koistinen, Salonen & Rinne, 2015). In contrast, the auditory distraction paradigm which I introduce in the next subsection allows to investigate the distinct stages of auditory attention more accurately and gives insight to its temporal aspects as well.

1.3 The distraction paradigm

Sensory events closely preceding task-relevant stimuli are not always in the role of cues: when they occur rarely or unexpectedly, they rather distract us. While the attention network task highlights the role of voluntary orientation of attention, the

distraction task emphasizes processes occurring when attention is captured by task-irrelevant unexpected stimuli. The instructions and the context in the two types of tasks also differ: in contrast to paradigms investigating attention network with explicit instructions to pay attention to cues, in distraction tasks participants are instructed to ignore distracting events. Moreover, while the cues provide task-relevant information by allowing to form expectations about the forthcoming target events, distracters are regarded as task-irrelevant stimuli. Distraction paradigm can be therefore a useful method to follow-up the dynamic balance between the orienting and voluntary attention which is reflected well in the electrophysiological signals, particularly in ERPs. I introduce ERP correlates of distraction and attention in detail in Chapter 3.

A widely utilized paradigm to investigate distraction is the so-called oddball paradigm in which rare (10-20%) sensory events, termed *deviant*, or *novel stimuli* unexpectedly break the regularity built-up by frequently presented stimuli (termed *standards*). In variations of the oddball paradigm, deviance might be delivered on the same or different stimulus and in the same or different modality than task-relevant events. In the auditory-visual version (Escera, Alho, Winkler & Näätänen, 1998) participants typically perform a visual classification task (e.g., 50-50% numeric odd/even discrimination) and each visual stimulus is preceded either by a standard or a pitch-deviant or novel environmental tone. The auditory paradigm was introduced by Schröger and Wolff (1998b) who presented short and long (100 and 200 ms) tones with 50-50% probability. The pitch of the tones changed occasionally (deviants) and participants had to perform a duration discrimination task while ignoring pitch. These two-alternative forced choice tasks enable to attribute behavioral or electrophysiological (see later) differences between deviant and standard trials at least in part to distraction-related processing because the same task has to be performed on both type of trials (Schröger & Wolff, 1998b).

Behavioral distraction effects were clearly observable in both type of paradigms: deviant stimuli lead to increased reaction times in auditory-visual (Alho, Escera, Díaz, Yago & Serra, 1997; Escera, Alho, Winkler & Näätänen, 1998; Escera, Yago & Alho, 2001; Yago, Corral, Escera, 2001) and auditory (Berti, Roeber & Schröger, 2004; Berti & Schröger, 2001; Horváth, Czigler, Birkás, Winkler & Gervai, 2009; Horváth, Winkler & Bendixen, 2008; Roeber, Berti & Schröger, 2003; Roeber, Berti, Widmann & Schröger, 2005; Roeber, Widmann & Schröger, 2003; Schröger & Wolff, 1998a, 1998b;

Wetzel, Widmann, Berti & Schröger, 2006) arrangement as well. Distracters were also accompanied with decreased accuracy compared to standards in most of the cases (except: Berti & Schröger, 2001; Horváth et al., 2009; Schröger & Wolff, 1998a; Yago, Corral & Escera, 2001).

1.3.1 The role of predictability in distraction

The vast majority of the early studies on auditory distraction implicitly assumes that deviance or rarity is sufficient to induce behavioral distraction-effects (e. g. Escera et al., 1998). This view has been challenged by numerous subsequent studies using auditory-visual oddball tasks and found either abolished distraction or even reversed effects (Parmentier, Elsley & Ljungberg, 2010; SanMiguel, Linden & Escera, 2010; Wetzel, Widmann & Schröger, 2012; for a review see Parmentier, 2014) and consistently emphasized the importance the temporal structure of the tasks. That is, when target events always follow distracters with a certain temporal separation, distracters can be regarded rather as unspecific warning signals than task-irrelevant events (Li, Parmentier & Zhang, 2013; Parmentier, 2014). For example, Parmentier, Elsley and Ljungberg (2010) varied the predictive value of distracters regarding the presentation of the target in a digit-classification task: in the informative condition, target always appeared after a constant temporal interval, while in the uninformative condition, only 50% of the sounds were followed by a target with a varied temporal separation, and in the informative deviant condition only deviants carried information about the upcoming target. They found that distraction effect abolished when distracters were uninformative, otherwise it was present in case of informative conditions. In a similar paradigm, when participants had to make decision on pictures (cloth or animal), preceding deviant or novel sounds elicited distraction effect only when they provided information on the upcoming target (Wetzel, Schröger & Widmann, 2013). Moreover, when only the rare novels were informative, they even resulted in facilitation (Wetzel, Widmann & Schröger, 2012).

The constant temporal separation between task-irrelevant and task-relevant events can be observed in pure auditory tasks as well, however, not so evidently as in auditory-visual tasks. In auditory duration-discrimination tasks, target events correspond to the offsets of short tones because decision can be made at these time points (tones either stop or continue). In order to perform the task successfully, participants also need to attend to the onset of the tones (e. g. Li, Parmentier & Zhang,

2013; Parmentier, 2014). Therefore, unexpected pitch-deviant tone onsets capture participants' attention and lead to distraction. In the auditory modality, only one study varied systematically the informative value of tone onsets. Li, Parmentier and Zhang (2013) presented buzzing tones binaurally moving from the center either to the right or to the left with 50-50% probability. In the event information condition, all tones included movements, but the onset did not predict its exact timing while in the temporal information condition, movement always occurred at 200 ms following tone onset but only in the half of the trials. In the uninformative condition, only the 50% of sounds included movements at variable times relative to sound onsets. Finally, in the fourth condition, tone onsets predicted both the occurrence and timing of movement. They found comparable results to auditory-visual studies: distraction occurred only when tone onsets were informative regarding the presence of movement (that is, movement was present at all trials), irrespectively of its timing (Li, Parmentier & Zhang, 2013).

Although the studies presented above suggest that participants can implicitly exploit the informative value of otherwise task-irrelevant events, a different set of studies demonstrated that cues presented before tones indicating whether it will be a standard or deviant prevented participants from distraction. In these studies, participants performed a duration discrimination task and visual cues preceding them in 340-900 ms indicated whether the following tone will be a standard or deviant but did not convey any information on the task-relevant dimension (duration). The consistent finding was that deviance-related reaction-time delay and distraction-related ERP-effects (see later) abolished when cues predicted the type (deviant or standard) of the forthcoming tone either fully (Horváth, Sussman, Winkler & Schröger, 2011; Sussman, Winkler & Schröger, 2003; Wetzels, Widmann & Schröger, 2007) or even with reliability of 80% (Horváth & Bendixen, 2012). Because in the everyday life situations – in contrast to the laboratory settings – almost no sound can be fully predicted, it is especially important to take into account some degree of variability when utilizing paradigms and models containing predictability (Winkler & Schröger, 2015).

In summary, behavioral results from auditory distraction paradigms suggest that deviance or rarity is not enough to induce distraction; rather those events capture attention which might be potentially useful or informative regarding the ongoing and future behavior. For example, when the occurrence of a task-irrelevant or deviant stimulus can be utilized to predict the presentation time of a task-relevant one, the

human cognitive system starts to treat them as potential alerting cues. In order to be able to exploit such regularities, a dynamic balance is necessary between voluntarily controlled top-down and the alerting bottom-up processes. This balance, however, shifts during lifetime, suggesting an enhanced distractibility in older adults. Chapter 2 introduces shortly the cognitive and anatomical changes during healthy aging and describes the main theories explaining these processes.

Chapter 2. Age-related changes in attention and distraction

2.1 Cognitive changes associated with aging

Given that societies of today are aging significantly, and age-related cognitive deficits are more and more widespread, it is crucial to understand the process of healthy aging and its impact on cognitive functions. Aging is often associated with decline not only at perceptual level but in higher cognitive functions as well, interacting with each other in a complex way. For example, older adults often struggle with peripheral hearing loss especially to high frequencies which is primarily caused by inner ear damage (presbycusis; Gates & Mills, 2005). While audiogram is a widely used diagnostic tool to detect peripheral hearing loss, it is insensitive to declines at the level of central auditory system. A typical symptom for such central auditory system damage is that older adults often report difficulties in listening to and following conversations, especially in noise (Eckert, 2011; Humes & Young, 2016; Pichora-Fuller, 2003a), even when their audiogram falls in the normal range.

There are several, not mutually exclusive potential explanations for this complex phenomenon: first, it is possible that aging affects both lower perceptual and higher cognitive processes as a general factor (“common cause hypothesis”), second, declined cognition might lead to poor performance in perceptual tests (“cognitive load on perception hypothesis”), third, an impoverished perceptual input possibly affects performance in cognitive tasks (“degradation hypothesis”) and fourth, over longer exposure to impoverished perceptual input can also result in cognitive decline (“sensory deprivation hypothesis”) (Pichora-Fuller, 2003b; Roberts & Allen, 2016). The decline of two fundamental cognitive factors contributing both to difficulties in everyday situations and to poor performance on test batteries are remembering and attention (Roberts & Allen, 2016). When explaining how cognitive processing changes in general with aging, two widely used approaches should be mentioned and described in detail. According these theories, aging is accompanied by a general slowing of cognitive processing (Salthouse, 1996) and the deterioration of inhibitory functions resulting in impaired ability to filter out irrelevant information (Hasher, Lustig & Zacks, 2007).

2.1.1 Theory of general slowing

The idea of the slowing processing speed assumes that older age is associated with a decreased speed on motor, decision making or perceptual tasks and that the

processing speed is a major predictor in performance across cognitive tasks in older adults (Birren & Fisher, 1995; Eckert, Keren, Roberts, Calhoun & Harris, 2010; Salthouse, 1996; Salthouse, 2000). The speed of a response, however, is not a unitary phenomenon but tasks usually involve several cognitive processes, from simpler perceptual to more complex executive and motor functions which might decline differently during lifespan (Eckert, 2011).

Studies in visual modality use a wide scale of tasks measuring processing speed, for example pegboard, inspection time, symbol coding (Ebaid, Crewther, MacCalman, Brown & Crewther, 2017), trail making, letter connection (Eckert et al., 2010), etc. tasks (for a review and enumeration of tests, see Salthouse, 2000). The results suggest that although older adults are systematically slower when motor response is needed as predicted by the theory of general slowing (Ebaid et al., 2017; Eckert et al., 2010; Kerchner et al., 2012; Salthouse, 1996; Salthouse, 2000), no difference was found between groups in case when only inspection time (that is, the time needed to correctly identify an object as target) was compared between older and younger adults (Ebaid et al., 2017). More importantly, the pattern of decline in inspection time was correlated with age within older adults group, suggesting that it might be a more accurate predictor of cognitive aging than reaction times per se (Ebaid et al., 2017). Comparable results were demonstrated by Deary, Johnson and Starr (2010) who tested several cognitive abilities longitudinally at ages 11 and above 70. They found that the inspection time was the only measure with correlated more strongly with cognitive abilities in older age than in childhood, proposing that inspection time might be a useful biomarker of cognitive aging (Deary, Johnson and Starr, 2010; Ebaid et al., 2017).

In contrast with the manifold task categories in visual modality, auditory studies in the topic of processing speed were mostly limited to speech understanding or to gap detection tasks. For example, Wingfield, Poon, Lombardi and Lowe (1985) demonstrated that the increased presentation rates of speech led to a significantly steeper rate of decline in speech understanding in older adults compared to the younger ones. Moreover, when the rate of speech was increased by deleting its particular segments without affecting the critical features of the speech signal, older adults identified significantly less words correctly than younger adults, suggesting a slowing in their auditory sensory perception (Schneider, Daneman & Murphy, 2005). In paradigms testing speech perception in noise, participants typically identify words perfectly in the

absence of noise, but their performance decreases with the introduction of noise. At a certain signal-to-noise ratio, listening becomes effortful. Older adults typically enter this zone at lower higher signal-to-noise ratios as younger adults, that is, their performance starts to decline earlier (Pichora-Fuller, 2003a, 2003b). When following conversations either in silence or in background noise, adequate processing of fine temporal resolution of the auditory scene is essential and can be measured with gap detection tasks. While older and younger adults detected gaps with similarly high accuracy in sinusoid tones (Alain, McDonald, Ostroff & Schneider, 2004), processing of short gaps in noise was found to be slowed in older adults (Harris, Eckert, Ahlstrom & Dubno, 2010; Harris, Wilson, Eckert & Dubno, 2012) and they also missed more gaps compared to the younger adults (Harris, Wilson, Eckert & Dubno, 2012). Moreover, slower processing speed was correlated with higher gap detection thresholds when task difficulty increased (Harris, Eckert, Ahlstrom & Dubno, 2010).

2.1.2 Inhibitory deficit theory

While the idea of general slowing suggests that aging affects both perceptual and motor speed in a general way, the inhibitory deficit theory introduced by Lustig, Hasher and Zacks (2007) emphasizes more strongly the role of controlled top-down processes. According to their theory the cognitive capacity available for information processing is limited, and in order to achieve efficient cognitive functioning, the processing of task-irrelevant information need to be inhibited but this efficiency declines with aging. As the concept of inhibition is broad, Hasher, Lustig and Zacks (2007) proposed three functions of inhibition. The first function is to control access to the focus of attention, that is, one should prevent irrelevant information from catching attention. Second, once irrelevant information gets in the focus of attention, it needs to be deleted from there and should also be excluded from working memory. Third, suppression of strong, often automatic but incorrect responses is essential. All three functions may decline with aging. It has been suggested that older adults are susceptible to keep a larger amount of irrelevant information in their focus of attention and in their working memory compared to younger adults, even though the capacity of the two systems do not differ between the two age groups. Moreover, the time needed to select and suppress inappropriate prepotent responses was also assumed to be longer in older adults (Guerreiro, Murphy & Van Gerven, 2010; Lustig, Hasher & Zacks, 2007).

Although the theory provides an appealing framework, its weakness is that modality was not originally specified, suggesting implicitly that the inhibitory deficit in older adults is a global phenomenon, affecting several modalities similarly. However, in order to get a more detailed picture, it is important to disentangle different modalities from each other (Guerreiro, Murphy & Van Gerven, 2010; Van Gerven & Guerreiro, 2016). The vast majority of studies on inhibitory deficits in older age utilized visual tasks with mixed results as pointed out by Guerreiro and colleagues (2010) in their review of studies from the past 30 years. In visual modality, older adults' performance significantly decreased in the incongruent condition of the Stroop task in which color names are printed with different colors and participants need to respond to the color, suppressing the automatic response from word processing (e. g. Andrés, Guerrini, Phillips & Perfect 1998; Borella, Delaloye, Lecerf, Renaud & de Ribaupierre, 2009). Enhanced reaction times and error rates were also found in older adults in reading-with-distraction tasks in which participants need to read a text including distracting words, strengthen the results from Stroop task that aging is associated with decline in suppressing concurrent distracting semantic information (e. g. Duchek, Balota & Thessing, 1998; Kemper, McDowd, Metcalfe & Liu, 2008). Younger adults outperformed older adults in Simon task requiring response to a relevant dimension of a stimulus (for example color or direction of an arrow) with left and right buttons while ignoring its position (left or right) on the screen: the reaction time cost between compatible and incompatible response button and location was larger in older adults, suggesting that they were less able to suppress irrelevant spatial information (e. g. Germain & Colette, 2008; Van der Lubbe & Verleger, 2002). Tasks involving negative priming (selecting a target stimulus which was a distracter in the previous trial) or flankers (two-choice response to a target while ignoring flankers) did not show a consistent pattern, however.

The number of studies administering the auditory versions of the above-mentioned studies is much lower than those utilizing visual tasks. In auditory Stroop tasks participants need to identify a perceptual feature of spoken words (e. g. gender of the speaker) while ignoring the meaning. In the auditory Simon task, left or right buttons are coupled to high or low pitch tones presented in the left or right ear. Both tasks showed similar pattern to the visual versions, that is, older adults seemed to be able to suppress irrelevant location or semantic information to a lesser degree when

presented in the auditory modality (e.g. Pick & Proctor, 1999; Sommers & Danielson 1999; Wurm, Labouvie-Vief, Aycock, Rebucal & Koch, 2004). Older adults also tended to exhibit impaired performance on listening-in-noise-tasks, especially when they had to recall sentences later (Helfer & Freyman, 2008; Tun & Wingfield, 1999). Unfortunately, oddball paradigms which can reflect the impact of distracters more directly were mentioned only in the auditory-visual modality suggesting that older adults are more impacted by distracters when they are presented in the auditory modality (Guerreiro, Murphy & Van Gerven, 2010), therefore in the following I discuss results from studies investigating at which levels are older adults distracted by rare, task-irrelevant auditory stimuli.

2.2 Age-related changes reflected in oddball paradigm

The alterations in auditory and cognitive abilities described above result in a shift in the balance of attention and distraction with aging. Beside of the subjective reports, studies also characterize older adults as being more susceptible for distraction than younger adults. When comparing behavioral results between older and younger adults, despite the diverse pattern of results, one can suggest that older adults either perform tasks comparably to younger adults or they are slower or make more errors. Nevertheless, faster response times and higher accuracy are not typical. Similarly, the amount of distraction effect (performance difference between rare and frequent stimuli) is either larger in older adults or similar to the younger group.

In go-nogo tasks participants typically attend to streams of tones and rare stimuli (for example pitch deviants) serve as targets, that is, only one type of stimuli require response. In such target detection tasks (without preceding task-irrelevant distracting stimuli), older adults responded to targets with similar reaction times than younger adults (Amenedo & Díaz, 1998; Iragui, Kutas, Mitchiner & Hillyard, 1993) or slightly slower (Gaeta, Friedman, Ritter & Cheng, 1998). Accuracy was typically high and either did not differ between age groups (Amenedo & Díaz, 1998; Gaeta, Friedman, Ritter & Cheng, 1998) or older adults identified significantly less targets than younger adults (Iragui et al., 1993). In the study of Woods (1992), the identification of target tones (pitch deviants) was similarly fast and accurate in both groups in general, however distraction was larger in the older adults when target tones were preceded by salient novel stimuli. On the other hand, when the pitch belonged to the irrelevant dimension and short tones were targets and long tones were nontargets, rare pitch changes at the

tone onsets (deviants) impacted the reaction times and target detection accuracy of older and younger adults similarly (Horváth et al., 2009), that is, both groups were equally distracted.

In two-alternative-forced choice tasks (2-AFC) participants need to respond not only to one but two types of stimuli, for example by pressing one button to one type and another button for another type of target stimulus. In such a forced-choice discrimination task, older adults tended in general slower than younger adults (Falkenstein, Yordanova & Kolev, 2006; Salthouse, 2000) but otherwise the results are similarly diverse than in case of the go-nogo tasks as described above. When participants' task was to discriminate whether the presented digits are odd or even, the pitch-deviance in the preceding task-irrelevant tones led to similar amount of slowing both in the older and younger groups (Leiva, Parmentier & Andrés, 2015) but novel sounds distracted older adults at a larger extent (Andrés, Parmentier & Escera, 2006). Rare pitch deviants in duration discrimination tasks were accompanied by similar response slowing both in younger and the older groups in the studies of Getzman, Gajewski and Falkenstein (2013) and Mager and colleagues (2005); however, in the study of Mager and colleagues (2005) older adults were marginally less accurate. In contrast to these studies, Berti, Grunwald and Schröger (2013) demonstrated more pronounced distraction effect in the reaction times of older adults but not in case of accuracy. Woods (1992) found that distraction was larger in the older adults only when target tones were preceded by salient novel stimuli, otherwise their reaction times increased similarly to young adults.

The inconsistencies in the results mentioned above could be brought about by the small age difference between groups (see Berti, Grunwald & Schröger, 2013), the small number of participants and the low statistical power to detect potential effects, therefore Leiva, Andrés and Parmentier (2015) administered a tone duration discrimination paradigm with larger group sizes. Similarly to the majority of studies using this paradigm, no difference was present between younger and older adults, and more importantly, Bayes factor-based analysis also supported the null effect. According to authors, beside the low effect and group sizes, participants with undetected cognitive impairment or strategy for maximizing accuracy at the expense of response speed could lead to the group-difference in the study of Berti, Grunwald and Schröger (2013).

When interpreting the null effects, it is also important to note the possibility that compensational mechanisms in older adults also could enhance their performance and lead to the lack of age differences (Getzman, Gajewski & Falkenstein, 2013; Reuter-Lorenz & Cappell, 2008; Zanto & Gazzaley, 2014) or because the low cognitive demands of the tasks, strategical and motivational strategical differences between groups also could arise (Horváth et al., 2009; Iragui et al., 1993; Leiva, Andrés & Parmentier, 2015). First, because of age-related slowing or decreased inhibitory control, older adults might need invest attention in order to solve a task, that is, they compensate (Lustig, Hasher & Zacks, 2007; Zanto & Gazzaley, 2014) and this overall enhanced attention might make them more susceptible to be distracted by rare stimuli. A second factor might be present because they are more cautious in general. That is, as an additional factor to the general slowing, it is also possible that they press a button only when they are sure about the response even when they are instructed to favor speed against accuracy while younger adults might respond in a more impulsive manner (Forstmann et al., 2011). Third, motivation might be an essential difference between the two groups. While younger adults are often recruited for course credit or as a part-time student job, the motivation of older adults might originate from more incentive factors; besides, the perceived difficulty of the task can also modulate the motivation level (Horváth et al., 2009). In order to understand the effects of aging on cognitive processes and to interpret results from behavioral studies more accurately, it is essential to review what kind of changes happen to the brain in the older adults.

2.3 The aging brain

The behavioral results mentioned above are supported by data from brain imaging studies revealing structural and functional changes with age. Although the size of the brain shrinks in general at older age, specific areas are more affected than other, including anterior insula, inferior, medial and superior frontal areas and cerebellum (Eckert, 2011). Recent studies suggest the presence of at least two distinct networks responsible for processing speed at frontal (anterior cingulate cortex, dorsolateral prefrontal cortex) and at cerebellar areas which play an essential role in motor functions (Eckert et al., 2010; Eckert, 2011; Hogan, 2004). In these areas, both grey and white matter are affected by aging: frontal grey matter modulation was found to be dependent on the frontal white matter change (Eckert, 2011) and grey matter volume in cerebellum modulated processing speed (Hogan, 2004). While grey matter consists mainly of

neuronal cell bodies, white matter contains myelin-coated neural projections which enable efficient neural communication, deterioration will affect processing speed as well (Nilsson, Thomas, O'Brien & Gallagher, 2014). The loss of white matter integrity might be caused by ischemia, microvascular disease, myelin degradation, fiber loss or arteriosclerosis (for a review see Cabeza and Dennis, 2012) and it was demonstrated at frontal and parietal areas as a significant cause of decreased processing speed in otherwise cognitively healthy older adults (Kerchner et al., 2012). Moreover, fewer functional connections were found at frontal cortex compared to other brain areas in older than in younger adults due to de-afferentation (Eckert, 2011).

Frontal and prefrontal areas of the brain play an essential role in inhibitory functions as well, and form a common network including anterior cingulate cortex, dorsolateral prefrontal cortex, inferior frontal gyrus, posterior parietal cortex and anterior insula (Lustig, Hasher & Zacks; Wager et al., 2005) which show structural and functional changes during aging (Cabeza, 2002). The decreased grey matter volume in the prefrontal cortex also referred to as "the frontal lobe hypothesis" (Raz, 2004; West, 1996), emphasizing the role of top-down control functions which are declined with aging. It is important to highlight that the measures used to assess either inhibition deficit or processing speed share mutual variance both in processes contribute to the task performance (Albinet, Boucard, Bouquet & Audiffren, 2012) and also in their neural correlates.

Beside the structural changes demonstrated above that several brain areas are playing role both in the inhibitory and response speed processes, especially in the frontal and prefrontal locations, and the structural changes of these lead to decrease in cognitive performance. Apart from the structural differences, functional changes measured by blood flow or metabolic processes also show change with aging. Using functional imaging (PET, fMRI), numerous studies showed that older adults' brain often show overactivation at several areas which are not significantly active in younger adults. Overactivation occurs especially in the dorsolateral prefrontal cortex (Cabeza & Dennis, 2012; Reuter-Lorenz & Cappell, 2008) which is one of the most flexible brain structures (Park & Reuter-Lorenz, 2009) and a more distributed activation pattern also can be found at posterior regions (Lustig, Hasher & Zacks, 2007). In parallel with activation enhancement, underactivation might occur at other areas (Cabeza & Dennis, 2012; Reuter-Lorenz & Cappell, 2008). Underactivation usually characterizes brain

locations where declines are present, for example memory or sensory areas at occipital and temporal lobes. For the first sight it could seem controversial that this area exhibits the largest volume and connectivity decline but also the largest activation in the same time. This seemingly paradoxical pattern can be explained well by the compensation hypothesis, that is, older adults recruit extra neural support in order to shore up declining structures whose function become inefficient or noisy (Lustig, Hasher & Zacks, 2007; Park & Reuter-Lorenz, 2009) but only to a certain point at which age-related decline is not too progressed (Persson & Nyberg, 2006).

A major advantage of using functional brain imaging techniques is that they are highly informative when defining which brain structures are damaged or function less effectively than in the younger persons. Beside structural differences, these methods also shed some light on the rough time course of different cognitive processes. However, they can reflect the temporal proceeding in steps about 1 sec which is considerably too slow to capture distinct stages of cognitive processing. In contrast, the event-related potentials (ERPs) based on electro-encephalography (EEG), are a highly suitable tool to measure the timing of cognitive processes since its temporal resolution can be defined in milliseconds (Luck, 2005). For this reason, I also utilized this method across the studies in my thesis to characterize the different stages of processing between attention and distraction.

Chapter 3: Electrophysiological correlates of the attention and distraction

In Chapter 3, I describe the method of ERPs in detail, focusing on components reflecting sensory and attentional processes. After the introduction of the method in general, I enumerate ERP components indexing the various stages of distraction in the so-called "distraction potential" (Escera & Corral, 2003), such as the detection of irregularity (mismatch negativity – MMN), orienting of attention (P3a) reorienting it to the original task after distraction (reorienting negativity – RON). I mention the effects of attentional control on these components as well. In the second part of the chapter, I argue why the utilization of sensory potentials (N1, processing negativity – PN) and their attention-related modulation could be a highly effective alternative when following-up the time course of attention, especially in case when comparing different age groups.

3.1 The method of event-related potentials

Psychophysiology is a domain of psychology which is based on the presumption that physical (e. g. neural or hormonal) responses and events can be regarded as signals of human nature, such as perception, emotion, action or thought, analyzed on the transactions between the environment and the functional organism (Cacioppo, Tassinary & Berntson, 2000). Because the present thesis makes extensive use of the method of event-related potentials (ERPs) derived from electro-encephalogram (EEG) data, the following section introduces how this method and different ERP waveforms can be utilized to identify cognitive processes, with special focus on those related to the attention-distraction balance.

Although Hans Berger was the first to register human EEG in 1929 and the first sound-evoked sensory EEG change was reported 1939 by Pauline and Hallowell Davis (Davis, 1939), the modern era of ERP research began in the 1960s when Grey Walter (Walter, Cooper, Aldridge, McCallum & Winter, 1964) and his colleagues discovered the first cognitive component, named contingent negative variation (CNV) eliciting following warning signals and indicated the participants' preparation to the upcoming target (Luck, 2005). Since these discoveries, the method of ERPs became a favored and widely used technique in cognitive neuroscience (Woodman, 2010) reflecting

electrophysiological response to a certain sensory, motor or cognitive event (Luck, 2005).

In comparison to the brain imaging techniques mentioned in the previous section (fMRI, PET), EEG has several advantages: it can record signals which originate from the brain in a noninvasive way, the device is relatively inexpensive, and most importantly, it has a high temporal resolution. That is, we can investigate the unfolding of cognitive processes at millisecond resolution. Importantly, several aspects of perception and attention are characterized at such a time scale, ERPs provide essentially useful information when following-up the different stages of attention. ERPs can be quantitatively characterized by three main parameters: amplitude (indexing the extent of neural activity), latency (their temporal course) and scalp density maps (scalp areas where the component typically manifests). Although several components might arise in a certain time window overlapping each other, calculating difference waveforms between experimental conditions might be a promising way to isolate them (Luck, 2005).

3.2 Event-related potentials reflecting distraction

In the oddball paradigms, a widely used method to identify the effects of rare stimuli (e. g. 20%) is to calculate a difference wave between rare and frequent events (that is, subtracting frequent from rare). This subtraction method typically results in waveform consisting of three deflections: first a negative one between 100 and 250 ms (mismatch negativity – MMN; Alho, Paavilainen, Reinikainen, Sams & Näätänen, 1986; Näätänen, 1982), followed by a positivity around 250-400 ms (P3a; Polich, 2007) and a late negative deflection arises at about 400-600 ms (reorienting negativity – RON; Schröger & Wolff, 1998a). The complex of these three distinct waveforms was named “distraction potential” (Escera & Corral, 2003) and is thought to reflect distinct stages of cognitive processing, beginning with detection of change in regularity of stimulus sequence, followed by the orientation of attention triggered by the rare event or stimulus evaluation and finally, the re-orientation of attention to the original task. Figure 3.2.1 illustrates a schematic “distraction waveform” as a result of subtraction of frequent standards from rare deviants. Note that the negative voltages are plotted upwards which is a common method in the ERP research.

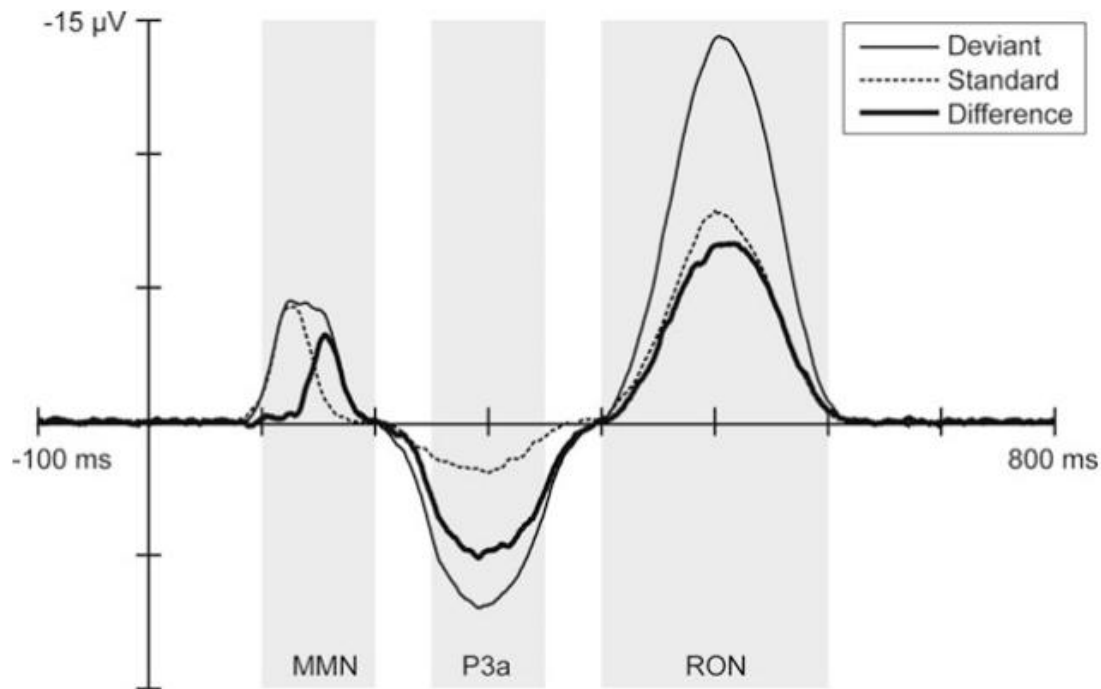


Fig. 3.2.1 Schematic illustration of the distraction potential in a passive oddball task in which tones are unattended. The dotted line corresponds to the frequent standard and the solid line corresponds the rare deviant tones. The bold line marks the deviant-minus-standard difference including MMN, P3a and RON (that is, the distraction potential) and their typical latency windows are highlighted with grey shading (Honig, Bouwer & Håden, 2014; Figure 2., pp. 312.).

3.2.1 MMN

The MMN is a negative-going waveform peaking between 100 and 250 ms around the fronto-central areas resulted from subtraction of frequent events from rare ones. It can be easily identified to frequency, duration, intensity (Giard et al., 1995), location deviants or to gaps inserted to the middle of tones (Garrido, Kilner, Klaas & Friston, 2009; Näätänen, Pakarinen, Rinne & Takegata, 2004), eliciting with an increased amplitude and decreased latency to larger differences between stimuli (Alho, 1992; Näätänen, 2008). The evolutionary significance of MMN is presumably to automatically switch one's attention to the auditory change as an attention-call process (Alho, 1992; Escera & Corral, 2007). MMN was originally thought to be elicited by sudden changes in the auditory environment based on automatic memory-based change-detection which is independent of attention (Alho, 1992; Näätänen, Kujala & Winkler, 2011). The automaticity of MMN and the sensitivity of auditory system to violations is

supported by its elicitation in coma patients (Morlet, Boucher & Fischer, 2000) or in sleeping newborns (Winkler et al., 2003) who cannot exhibit overt responses.

Regarding the origin and function of the MMN component, two main sets of theories are dominating the scientific literature which are based either on neural adaptation or on violation of expectations. The idea of MMN as a simple indicator of change or rarity detection might be underpinned well by the adaptation hypothesis stating that continuous or repetitive auditory stimulation leads to the decreased responsiveness of neurons in general in the auditory cortex to repeated standard auditory events. This decreased firing rate can be evolutionary adaptive in the protection against overstimulation which is one of the major functions of neural adaptation. This process is observable at several stages of auditory processing, from the auditory nerve to the cortex (Pérez-Gonzales & Malmierca, 2014). It was also suggested that neural adaptation processes play role in deviance detection, leading to MMN elicitation (Pérez-Gonzales & Malmierca, 2014). Besides, the repetition of tones might facilitate the processing of the same stimuli and allows information to flow more rapidly, leading to shorter latencies of neural responses (Grill-Spector, Henson & Martin, 2006) as depicted in Fig. 3.2.1 as well. Since both the decreased latencies of neural firings and the attenuated neural responsiveness in general might result in the same EEG amplitudes measured on the cortex, both processes can manifest in MMN when subtracting frequent standards from neural response to deviant or novel stimuli, for example based on frequency difference (Jääskeläinen et al, 2004).

MMN was found to be elicited not only to the simple feature deviance but also when stimulation with a more complex structure was applied. According to the present models of MMN including the framework of hierarchical predictive coding, a memory trace is built-up cumulatively during auditory stimulation (Cowan, Winkler, Teder & Näätänen, 1993) which is violated by infrequent irregularities (Näätänen, Kujala & Winkler, 2011). It was also proposed that MMN is sensitive to the abstract sequence rules (Näätänen, Kujala & Winkler, 2011), for example to language-related disruptions like pseudowords (Pulvermüller et al., 2001), syntactic or semantic violations (Hasting, Kotz & Friederici, 2007) or violations in music (Koelsch & Seibel, 2005). These results go far beyond the simple physical difference between subsequent stimuli and suggest a mismatch between the auditory input and the predictions formed based on rules in the recent auditory stimulation (Garrido et al, 2009; Winkler, 2007; Winkler & Schröger,

2015). The Auditory Event Representation System (AERS) model proposed by Winkler and Schröger (2015) attempts to explain how representations from such highly complex auditory scenes are processed. They suggest that the auditory system continuously updates its representations based on comparisons of the predictions originating from existing representations from previous experiences and the incoming sensory inputs. More importantly, several regularities can be maintained in parallel in AERS with different levels of activation, which makes easier to detect small violations even when the stimulation is complex (Winkler & Schröger, 2015).

A recent study by Symonds and colleagues (2017) aimed to distinguish MMN effects from the neural adaptation and predictive coding hypotheses. In the vast majority of the studies in the topic of deviance detection the deviant tones or patterns physically differed from standard ones. In contrast, Symonds and colleagues (2017) utilized sequences in which the pattern of deviant and standard sequences was physically the same and occurred in the same blocks. Participants listened to tone pips separated in 200 ms and every 4th tone was presented with a higher pitch (standards pattern). Two deviant patterns could occur infrequently: the higher pitch tone was presented either too early (following the first low tone) or too late (the lower tone was repeated 5 times instead of 3). In these terms, early deviant patterns both violated the expectations and involved physical change from the previous tone, while late deviants violated predictions only while no physical change was present. The results showed that the early deviants elicited a negativity with larger amplitude and shorter latency compared to the late ones, suggesting that the MMN traditionally measured in oddball tasks usually involves processes related both top-down predictions and physical change detection via neural adaptation and that MMN response can be elicited without physical change in the stimulation (Symonds et al., 2017). It is also important to highlight that adaptation is a broad concept which occurs at different levels of the auditory pathway, and it plays a crucial role in processing of more complex regularities from the environment and also contributes to higher order cognitive mechanisms like attentional control (Pérez-Gonzales & Malmierca, 2014). That is, although the framework of predictive coding can explain well how brain does extract regularities from the complex environment and build expectations whose violations are manifested in MMN, it is not enough per se to completely rule out the presence of neural adaptation processes

and of synaptic changes during the elicitation of MMN (Garrido et al., 2009; Symonds et al., 2017).

Several studies revealed that besides of passive and automatic change-detection, attentional factors, regularity of the presentation and sound context may play a significant role in the elicitation and modulation of MMN (Sussman, 2007). For example, although no difference was found in MMN when standards and deviants were presented in random versus regular order (every 5th tone was deviant, stimulus separation in 1.3 sec) in case of slow presentation (Scherg, Vajsar & Picton, 1989), faster presentation rate (stimulus onset interval = 0.1 sec) elicited MMN to rare sounds in case of random presentation only, suggesting that the unit of representation was not a single tone but the microsequence (Sussman, Ritter & Vaughan, 1998). MMN in regular tone sequences was also found when the dimension of deviance (for example pitch) was ignored (for review, see Sussman, 2007). When participants attended one ear and actively detected intensity deviants in low and high frequency tones, intensity deviants in the unattended ear elicited smaller amplitude MMN compared to the attended ear (Woldorff, Hackley & Hillyard, 1991). However, it is ambiguous whether attention directly influences deviance detection and leads to a pure MMN modulation because such effects are rather an overlap with other cognitive components and motor or premotor potentials (Alho, 1992; Sussman, 2007).

In the scalp distribution of MMN the fronto-central areas are dominating, besides, it gets contribution from the auditory cortex as well (Winkler, 2007) as evidenced by the polarity reverse at the mastoid electrodes (Alho et al., 1986). Moreover, studies using magneto-encephalography (MEG) provide more precise information about the generator structures of different components because magnetic signals are not distorted by the tissues of the brain. The role of primary auditory cortex in auditory change detection was demonstrated by Hari and colleagues (1984) and Sams and colleagues (1985) who found the magnetic counterpart of MMN (MMNm) in healthy adults to rare deviant auditory events in the supratemporal plane over Sylvian fissure. Besides, evidence from generators in the frontal lobe in humans were also found healthy adults (Giard et al., 1995) and in patients with unilateral frontal lesions (Alho, Woods, Algazi, Knight & Näätänen, 1994) which might be related to the triggering of involuntary attention switch. Animal models suggest comparable results (intracranial recording from cats: Csépe, Karmos & Molnár, 1986) and indicate contributing activity

from thalamic and hippocampal areas as well (reviewed by Alho, Huotilainen & Näätänen, 1995).

3.2.2 P3a

Once infrequent violations alerted the system as indicated by elicitation of MMN, attention shifts toward that event (Escera & Corral, 2007; Schröger & Wolff, 1998a, 1998b). This orienting response or displacement of attention is thought to be reflected by the P3a eliciting around 250-400 ms which is the second deflection of the distraction-potential and considered as a subcomponent of P3 waveform (Polich, 2007; Soltani & Knight, 2000). The P3 (or P300) component was reported first by Sutton, Braren, Zubin and John in 1965, who manipulated the uncertainty of the presented stimuli and found that the amplitude of the late positive component was larger for uncertain auditory (clicking tone) and visual (light flash) stimuli (Sutton et al., 1965).

Subsequent studies utilized oddball tasks to investigate this late positive waveform and its relationship to uncertainty, and they suggested that it might play role in task-relevance and probability representations, irrespectively of modality (Courchesne, Hillyard & Galambos, 1975; Squires, Squires & Hillyard, 1975). It is important to note, however, that P300 waveform consists of two, partly independent subcomponents which must be interpreted separately (Spencer, Dien & Donchin, 1999): the earlier P3a and the later P3b (Squires, Squires & Hillyard, 1975). P3b is a slower waveform typically elicited by rare target stimuli – or by events requiring decision – at posterior parietal areas (Friedman, Cycowitz & Gaeta, 2001). Since the “distraction potential” involves P3a which is more relevant regarding the present paper, in the following section I describe it in detail.

Although the P3a usually evokes to infrequent stimuli – therefore often called as “novelty-P3” (Polich, 2007; Soltani & Knight, 2000) – there is no agreement regarding its functional significance. A highly prevalent explanation suggests that it reflects *involuntary* attention shift (Escera & Corral, 2003; Polich, 2007; Soltani & Knight, 2000) and the amount of its amplitude change is in line with the salience of distracters which prepares the organism to deal with the novel stimulus (Friedman, Cycowitz & Gaeta, 2001). For example, rare sounds with larger frequency separation from frequent ones lead to larger P3a amplitudes (Berti, Roeber & Schröger, 2004; Wetzell, Widmann, Berti & Schröger, 2006; Yago, Corral & Escera, 2001). Similar amplitude enhancement

was found in case of novel stimuli both in auditory (sinusoid vs environmental tones, for example drill, telephone ring etc.; Escera, Alho, Winkler & Näätänen, 1998; Escera, Yago & Alho, 2001; Spencer, Dien & Donchin, 1999) and in visual modality (simple geometric shapes vs complex colorful figures: Courchesne, Hillyard & Galambos, 1975).

Beside the stimulus salience, several other factors modulate the amplitude of P3a, leading to diverging explanations of its role in information processing. For example, when comparing novel stimuli during the time course of the task, gradually decreased P3a amplitudes were found toward the end of the task, suggesting that the novelty value decreases after a few repetitions (Friedman & Simpson, 1994). The amplitude decrease was more pronounced when sounds were presented in the background, that is, they were unattended, compared to the condition when participants had to perform a decision task about the tones (Friedman, Kazmersky & Cycowitz, 1998). Enhanced P3a amplitudes were demonstrated in difficult discrimination tasks as well with a more frontal distribution (Katayama & Polich, 1998; Muller-Gass & Schröger, 2007) but P3a decreased when cues preceding distracters indicating whether it will be a deviant or standard helped participants to prepare for them (Horváth & Bendixen, 2012; Sussman, Winkler & Schröger, 2003; Wetzel & Schröger, 2007; a tendency: Wetzel, Schröger & Widmann, 2013). More importantly, the P3a decrease was accompanied by decreased behavioral distraction effects as well (see Chapter 1.2.1), suggesting the role of attention and context in P3a generation and arguing against the complete involuntariness of attention switch.

An other set of studies proposes that the cognitive system needs to constantly monitor the environment in order to manage goal-directed behavior efficiently and P3a amplitude might reflect such update processes to decide whether an actual stimulus is relevant regarding our further actions. Based on the continuously incoming stimuli, the current mental representations of the environment (Dien, Spencer & Donchin, 2004; Donchin & Coles, 1988) and the allocation of the attentional resources must be revised and updated (Polich, 2007). Barceló, Escera, Corral and Periañez (2006) utilized Wisconsin Card Sorting Task in which participants had to select the matching card based either on shape, color or number. An acoustic cue induced before each trial whether participant needed to respond to the same feature than at previous trial or to a different one; that is, whether any task-set change needed. Such task-switch cues

elicited identical P3a responses to the novel tones, which might reflect the activation of a neural network associated with updating task-set information in order to select goal-directed action depending on context (Barceló et al., 2006). Similarly, when deviant tones required evaluation in an otherwise irrelevant dimension (e. g. pitch), more pronounced P3a was found compared when no overt response was needed, suggesting that the attention switched completely only when distracters were task-relevant and triggered task-switch as well (Berti, 2008; Hölig & Berti, 2010). Horváth, Winkler and Bendixen (2008) also proposed that instead of attention switch per se, P3a reflects the detection of events for further processing because these provide new information or are significant regarding the organization of further behavior.

Not only the exact functional role of P3a is ambiguous but its generator processes as well (Luck, 2005; Polich, 2007). Patients with unilateral dorsolateral prefrontal cortex exhibited reduced frontal P3a amplitudes while P3b remained intact (Knight, 1984). Besides, temporo-parietal junction (including superior temporal plane and inferior parietal cortex) (Knight, Scabini, Woods & Clayworth, 1989) and posterior hippocampal (Knight, 1996) injury impaired P3a elicitation as well while parietal lesions had no effect on it (Knight, 1984; Knight et al., 1989). Frontal lobe was also found to contribute to detection to rare or alerting events in fMRI studies (McCarthy, Luby, Gore & Goldman-Rakic, 1997), suggesting the elicitation of P3a when such stimuli are processed, or sufficient attentional focus is engaged (Polich, 2007). Beside the frontal cortex, studies using MEG identified the magnetic counterpart of P3a in the auditory cortex during auditory stimulation (Alho et al., 1998; Kropotov et al., 1995). Results about the role of frontal areas and temporo-parietal junction in the generation of P3a potential are similar to the neural network responsible for the orienting to novel events (Posner, 2016) and orienting of attention in general (Mesulam, 1990), strengthening the ERP results described above and highlighting the role of attention to the potentially significance of distracters.

3.2.3 RON

According to the theory of distracting potential, attention should be oriented back to the primary task following momentary distraction as indexed by the so-called reorienting negativity (RON) (Escera & Corral, 2003, 2007; Schröger & Wolff, 1998a). Reflecting its name, RON is a negative displacement between 400 and 600 ms with a typically frontal/prefrontal scalp distribution (Schröger, Giard & Wolff, 2000). RON

was recorded first by Schröger and Wolff in 1998, following P3a only when participants actively attended to the auditory stimulations and rare deviant stimuli acted as behavioral distractors (Schröger & Wolff, 1998a) and was registered later in visual modality as well (Berti & Schröger, 2001). Although for the first sight its role in cognition seems well-defined, its functional characterization is still debated (Berti, 2008; Escera, Yago & Alho, 2001).

In auditory-visual oddball paradigms in which task-irrelevant tones preceded visual targets, it was also observed that RON consisted of two subcomponents, an early and a late RON. They showed different scalp distributions and the late one was associated more with the processing of the task-relevant stimulus (Escera, Yago & Alho, 2001). On the other hand, the early part of the component elicited when working memory was included into the task (classification task of odd/even numbers and colors), but when participants discriminated physical features, only the late subcomponent was present (Munka & Berti, 2006). Besides, RON was elicited to trials which triggered object switch in the working memory (that is, operating with a previously processed or with a new stimulus) (Berti, 2008). However, when the task was presented in the auditory modality only, response withhold (which is also a component of working memory) attenuated RON amplitude (Berti & Schröger, 2003) while working memory load enhanced its amplitude in a visual-auditory task (SanMiguel, Corral & Escera, 2008).

Similarly to P3a, cues presented before deviant tones lead to reduced or abolished RON amplitudes (Horváth & Bendixen, 2012; Horváth, Sussman, Winkler & Schröger, 2011; Horváth, Winkler & Bendixen, 2008; Sussman, Winkler & Schröger, 2003; Wetzell, Widmann & Schröger, 2009), proposing that since predictability theoretically reduces distraction, re-orientation should be required to a lesser degree than in case when deviants are completely unexpected. Besides, RON might also involve processes which integrate information both from alerting cues and target stimuli (Horváth & Bendixen, 2012) suggesting that even it reflects processes related re-orientation of attention, it is not a "pure" indicator of that, but other higher order cognitive processes might be incorporated as well (Horváth, Winkler & Bendixen, 2008).

The cortical generator mechanisms of RON are not well mapped yet. According to some suggestions that multiple cortical generators might play role in the elicitation process of RON located mainly in the frontal areas (Schröger, Giard & Wolff, 2000) as well as in the superior temporal cortex, ventral and dorsal mid-cingulates and in the anterior cingulate (Rissling, Miyakoshi, Sugar, Braff, Makeig & Light, 2004). Besides, RON can get contributions from the primary motor areas which are related to the selection of action (Horváth, Maess, Berti & Schröger, 2008).

3.2.4 The independence of MMN, P3a and RON

Although the three-phasic distraction potential seems to be a unitary chain response of the brain to the attention capture by unexpectedly occurring distracter and then to the release from that, MMN, P3a and RON are at least partly independent from each other. In most studies examining top-down processes such as prediction or working memory, MMN remains the same between conditions (e. g. Berti & Schröger, 2003; Horváth et al., 2011; Sussman, Winkler & Schröger, 2003) suggesting the automaticity of deviance detection. The later components were, however, more sensitive to top-down manipulations and either changed systematically (e. g. Berti & Schröger, 2003; Sussman, Winkler & Schröger, 2003) or independently from each other (e. g. Berti, Roeber & Schröger, 2004; Munka & Berti, 2006), hinting that probably they do not follow each other in an obligatory way. To investigate this systematically in an auditory oddball paradigm, Horváth, Winkler and Bendixen (2008) utilized a duration discrimination task (200 vs 400 ms) and compared micro-sequences differing in the number of repetition trials (2, 3, 4 or 5 standards) before a change trial (deviant). The change (deviant) minus repetition (standard) waveform exhibited MMN, P3a and RON deflections. However, P3a to the low amount of stimulus repetition (1 or 2) changed differently not only from RON but from MMN as well strengthening results from further studies suggesting the dissociation of MMN and P3a (Rinne, Särkkä, Degerman, Schröger & Alho, 2006; Winkler, Tervaniemi, Schröger, Wolff & Näätänen, 1998) and of P3a and RON (Bendixen, Roeber & Schröger, 2007).

When using difference waveforms to get information about cognitive processes, it is important to keep in mind that subtraction might smear overlapping components. For example, in the time window of RON, ERP components regarding target detection (P3b; Horváth et al., 2011) or remaining from processing of preceding distracters might be present (Escera, Yago & Alho, 2001). Because of the possible shifts in temporal

characteristics of these components with aging or within clinical groups, difference waveforms should be explained and interpreted especially carefully. Moreover, studies using duration discrimination tasks often average short and long trials together which might be problematic in the 200-400 ms interval since tone offsets also elicit sensory ERP responses (Hillyard & Picton, 1978), leading to misinterpretation of P3a or RON effects (Horváth, 2014a). In the next session I introduce how sensory ERPs might be used for investigating distraction with the avoidance of overlapping effects.

3.3 The role of sensory ERPs in the time-course of attention

3.3.1 N1

Once a selective attention set is established, the possibility to process task-relevant auditory events across different stages of auditory processing is provided as suggested by Broadbent (1970; see Knight & Parkinson, 1975). When an auditory event occurs, its onset elicits a markable negative deflection around 50-150 ms named N1 which – similarly to MMN – reflects sensory change detection, however, they are two separate components (Näätänen, 1982; Näätänen & Picton, 1987; Näätänen et al., 2011) corresponding to two different steps in the auditory processing (Näätänen et al., 2011). Their cortical generators might overlap in the supratemporal areas (see the more detailed description below) but the temporal source of MMN is more anterior than of N1 (Garrido et al., 2009; Näätänen, Paavilainen, Rinne & Alho, 2007) and probably involves different neural processes as well. Besides, generation and amplitude modulation of N1 is more likely to be related neural adaptation and refractory processes than of MMN (Näätänen et al., 2011). The auditory N1 was originally thought to be the part of the so-called vertex potential (coupled with a positive deflection around 200 ms named P2) representing a nonspecific sensory change and notifying the brain that something happened (Näätänen & Picton, 1987) and serving as an attention-call signal (Lange, 2013).

The auditory N1 wave was found to get contribution from several distinct brain areas. Intracranial animal and human recordings revealed superior temporal, frontal, midbrain reticular formation and thalamic activation when N1 was measured at scalp, suggesting that not only a specific area leads to N1 elicitation (summarized by Näätänen & Picton, 1987). According to Näätänen (1982), the “true” N1 wave consists of three components originating from different regions. Two of these subcomponents are related

to the auditory areas: the frontally distributed negative deflection coupled with positivity at mastoid sites under the Sylvian-fissure originates from the supratemporal cortex at primary auditory areas when measured with nose reference (Näätänen & Picton, 1987; Vaughan & Ritter, 1970). Magnetic recordings also support the presence of this generator (Hari, Aittoniemi, Järvinen, Katila & Varpula, 1980; Pantev et al., 1995). The supratemporal N1 is organized tonotopically, which means that the location of the generator depends on the frequency of the pure tone; besides, the pure tone amplitudes also affect the generator locations (Winkler, Denham & Escera, 2015). Second, the idea of multiple generators was stated first by Wolpaw and Penry (1975) who discovered the T-complex which is a positive-negative going waveform between 50 and 170 ms measured at temporal cortical areas originating from the superior and lateral temporal gyrus, corresponding to the secondary or supplementary auditory areas. T-complex consists of further subcomponents (Ta, Tb, Tc) overlapping the N1-P2, and subsequent studies confirmed its independent origin from N1 measured at vertex (e. g. Pantev et al., 1995; Ponton, Eggermont, Khosla, Kwong & Don, 2002; Scherg & Von Cramon, 1986). Besides, Näätänen and Picton (1987) suggested the presence of a third, non-specific generator which elicits a negative deflection at vertex around 100 ms. Its exact origin is unspecified, but the authors propose that it might be generated in frontal motor and premotor cortices influenced by thalamic areas.

As one the main functional role of N1 is to “alert” the organism that something happened in the environment (Lange, 2013), it was found to be sensitive to transient acoustic events or to sounds presented with longer temporal separation (Berti, Vossel & Gamer, 2017; Teder, Alho, Reinikainen & Näätänen, 1993; Näätänen & Picton, 1987). Rare acoustic events (deviants or novels) also lead to amplitude enhancement (Näätänen & Picton, 1987; Winkler, 2007) and N1 amplitude was found to be sensitive to processes linked to feature extraction and sensory memory (for example to loudness: Lu, Williamson & Kaufman, 1992). Besides, auditory stream segregation and sound organization (Szalárdy, Böhm, Bendixen & Winkler, 2013) as well as general arousal changes also affected N1 amplitudes (Näätänen & Picton, 1987).

3.3.2 Attention effects on the N1 waveform

Although the N1 ERP basically reflects sensory processes as introduced above, several studies suggest that it is sensitive to top-down cognitive processes as well and significantly affected by selective attention. In their classic study, Hillyard, Hink,

Schwent and Picton (1973) presented short tone pips concurrently to the two ears with short temporal separation (100-800 ms) and participants' task was to count randomly occurring frequency deviants delivered to one designated ear while ignoring the other one. They found significantly larger N1 amplitudes to tones in the attended ear compared to the unattended one. The authors interpreted the results as the N1 enhancement reflects the stimulus-set mode of attention as suggested by Broadbent (Knight & Parkinson, 1975), that is, providing a selection criterion to participants before the presentation of the stimulus will lead to more efficient processing. In this case, a stimulus set admits all sensory inputs to an attended channel while blocking or attenuating inputs from other task-irrelevant channels, already at the early stage of processing (Hillyard et al., 1973).

However, later studies argued against the interpretation that amplitude enhancement was due to a pure N1 modulation, but an overlapping negative shift emerged which was especially pronounced when the inter-stimulus-interval was longer and constant (800 ms). This negative displacement started slightly later than N1 and was observable both at vertex and at auditory areas at temporal cortex (Näätänen, Gaillard & Mäntysalo, 1978). The authors named this deflection "processing negativity", reflecting its endogenous, attention-related nature (Näätänen, 1982) generated by a matching process between the sensory input and the attentional trace (Alho, 1992; Alho, Töttölä, Reinikainen, Sams & Näätänen, 1987). Processing negativity (PN) was found to be generated at independent sources from the N1 and consists of two subcomponents, and early and a late PN. The early PN begins around 50-100 ms and lasts until the end of the processing of the auditory stimulus and originates from the auditory sensory and associational areas on the supratemporal plane and on the lateral temporal areas (Näätänen & Picton, 1987). The function of early PN is thought to select stimuli for further processing (Alho, 1992). In contrast, late PN acts as an attentional supervisor which feeds back to the auditory sensory areas and is probably generated in the anterior frontal cortex (Näätänen & Picton, 1987). The lack of polarity reversal at mastoid electrodes when recorded with nose reference also strengthens the independence from pure N1 (Alho et al, 1986).

During selective listening an attentional trace is actively formed and each incoming stimulus is compared with the trace. As attended relevant stimuli elicit enhanced PN compared to the irrelevant unattended ones, their difference is also

informative regarding the amount of time the attentional trace needs to reject the stimulus (Alho, 1992). Hansen and Hillyard (1980) named this fronto-centrally distributed difference waveform “negative difference”, reflecting selective attentional processes eliciting with larger amplitudes and shorter latencies when acoustic channels were easy to discriminate.

Irrespective of contribution of PN, the enhanced N1 amplitudes tend to suggest that a specific acoustic event is in the focus of attention, therefore the modulation of this component might be a plausible tool to follow-up the balance between attention. The first study suggesting this was produced by Schröger (1996). In his study, participants listened to pairs of discrete tones separated by 200 or in 560 ms and they had to ignore the first tone of each pair (Stimulus 1 – S1) and make decision about the second one (Stimulus 2 – S2). In most cases, the S1 was presented with the same pitch than the task-relevant S2 but occasionally it was a pitch deviant differing from standard slightly or largely. He found that irrelevant deviant tones led to reduced accuracy and slowing in case of 200 ms separation in parallel with a significant decrease in N1 amplitude to S2 stimulus. These effects, however, abolished in case of 560 ms separation interval in which preceding deviants did not decrease either behavioral performance or N1 amplitudes. Deviant S1 tones also elicited a positive deflection, probably a P3a which overlapping with S2-related N1 could cause its attenuation.

Later studies using continuous stimulation paradigm attempted to measure more systematically the effect found by Schröger (1996). The continuous stimulation paradigm introduced by Horváth and Winkler (2010) mirrors the classical duration-discrimination go/nogo (participants have to respond to short tones) oddball task in terms of its temporal parameters but instead of discrete tones, auditory stimulation consists of long, continuous tones. Tones alternate between two frequencies by occasional, quick glissandos (glides), corresponding to deviants and contain short gaps which serve as target events. Because glides serve as deviant events, they occur with the same temporal probability as discrete deviant tones in oddball tasks. Variations in the temporal separation between distracter glides and target gaps, the modulation of gap-related N1 amplitudes provides information of the focus of attention and about the time when attention set is restored after distraction. In the study of Horváth and Winkler (2010), 50% of glides was followed by gaps either in 150 ms (50% of gaps) or were presented without any preceding glide (“gap only” trials; 50%). In this way, successive

glide-gap pairs reflect short deviant tones while gaps without any preceding glides correspond to standard tones. Glides presented without any succeeding gaps mirror long deviant tones (nontargets). They found that when participants maintained the go/nogo task, they responded significantly slower and less accurately to gaps preceded by glides in 150 ms compared to gaps without any preceding glides. Importantly, N1 amplitudes to these gaps were also significantly reduced compared to “gap only” trials. On the other hand, when participants’ attention was directed to a silent movie and auditory stimulation was presented in the background (passive condition), the N1 modulation showed an opposite pattern: 150 ms glide-gap separations lead to enhanced gap-related N1 amplitudes.

Utilizing the same active continuous stimulation paradigm, Horváth (2014a) compared the effect of rarely or frequently occurring glides to gaps presented in 150 ms or in 650 ms. He replicated the effect of attenuated gap-related N1 and lower behavioral performance following rare glides in 150 ms and also showed that these occasionally presented distracters had a much smaller impact to gaps separated from glides in 650 ms. These results suggest that in the active conditions, infrequent, task-irrelevant distracter glides disrupted the attention set which restrained the overall processing of briefly succeeding gaps (in 150 ms). On the other hand, in case of “gap only” trials and in case of 650 ms glide-gap separations, the attention set could be restored. The lack of polarity inversion to gaps preceded by glides in 650 ms also suggests the presence of enhanced attention to these events as well (Horváth, 2014a). These results are also in line with those related to attentional blink. Attentional blink paradigms typically use rapid presentation of tones and participants have to respond to two targets separated by nontargets in various time intervals (Shen & Mondor, 2006; Tremblay, Vachon & Jones, 2005). When the two targets are separated briefly (270 ms or less), the processing of second target is impaired, that is, participants detect it less accurately (Horváth & Burgyán, 2011; Shen & Alain, 2010)

In contrast, when participants watched a movie or read a book and tones were presented in the background, the N1 enhancement to gaps closely following glides probably indexed an attention switch to the auditory modality, bringing the tones into the focus of attention which lead to the enhanced processing of the gaps closely following distracters (Horváth, 2014a; Horváth & Winkler, 2010). This result is in line with former studies in which identical tones presented separated by short intervals (<400 ms)

while participants' attention was directed to somewhere else. For example, in the study of Loveless, Hari, Hämäläinen and Tiihonen (1989) found the largest N1 amplitudes to the second tones when tones followed each other in 150 ms. Similarly, when tones followed each other in trains, the largest N1s were measured to the second tones in trains when separated in 400 ms or shorter intervals (Budd & Michie, 1994; McEvoy, Levänen & Loveless, 1997; Sable, Low, Maclin, Fabiani & Gratton, 2004; Wang, Moraux, Liang & Iannetti, 2008).

Beside of the attention switch, N1 enhancement in passive paradigms can be explained in the context of the latent inhibition model as well: according to this theory, a general facilitation occurs in the auditory cortex following tone onsets which lasts until about 400 ms. After that, inhibitory processes start to dominate (Budd & Michie, 1994; McEvoy, Levänen & Loveless, 1997; Sable et al., 2004). That is, it is also possible that in absence of attention, automatic excitatory neural processes modulate N1 amplitudes, resulting in enhancement when tones are separated shortly, irrespectively of attentional orienting.

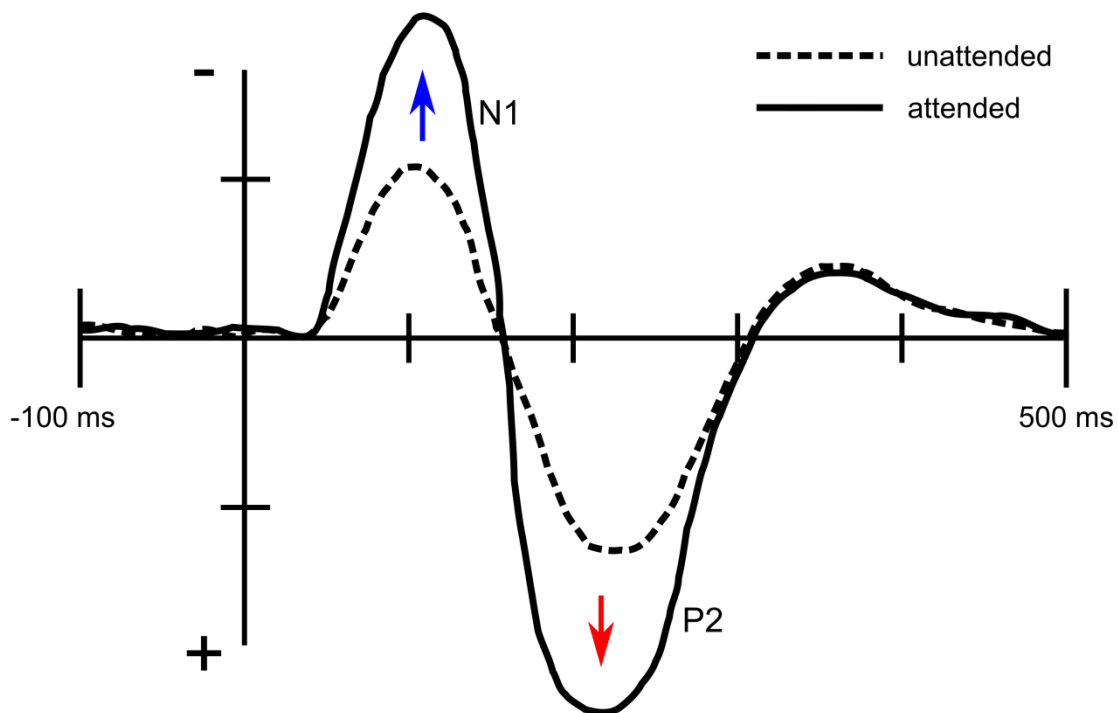


Fig. 3.2.2 Schematic illustration of the attention-related modulation of the N1 and P2 amplitudes. Sensory events in the focus of attention elicit enhanced amplitudes.

In summary, irrespectively of the exact nature of neural processes leading to N1 amplitude modulation, the above-mentioned results unambiguously suggest that N1 amplitude is enhanced when the auditory events are in the focus of attention, whereas attentional disruptions lead to the decrease of N1. The time course of this process is also clearly followable when varying the temporal separation between distracter and target (or probe) auditory events. Therefore, patterns of the N1 component might allow more exact and direct interpretations than components in the “distraction potential” such as P3a or RON.

3.3.3 Age-related changes in distraction-related event-related potentials

Therefore, characterizing different (age) groups with the attentional modulation of N1 and the neighboring negativities may be more readily interpretable than approaches based on the “distraction potential”. Regarding the “distraction potential”, results with older adults are diverse in oddball paradigm: amplitudes tend to be similar or smaller (sometimes larger) compared to younger adults; and latencies either delay or do not differ from the younger adults’. Amplitude-results show a high variability both for MMN (no age difference: Amenedo & Díaz, 1998; Berti, Grunwald & Schröger, 2013; Gaeta et al., 1998; Mager et al., 2005; attenuation with aging: Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009) and P3a (no age difference: Berti, Grunwald & Schröger, 2013; Getzman, Gajewski & Falkenstein, 2013; Mager et al., 2005; attenuation with aging: Gaeta et al., 1998; Iragui et al., 1993), which may reflect differences between the utilized tasks but also between individuals. Whereas the interpretation of amplitude differences may not be unequivocal, differences in latency may directly reflect between-group processing speed differences. While MMN latency basically remained unchanged with aging (Amenedo & Díaz, 1998; Gaeta et al., 1998; Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009; Mager et al., 2005), P3a was elicited systematically later in the older adults (Gaeta et al., 1998; Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009; Mager et al., 2005). As an exception, Berti, Grunwald and Schröger (2013) found delayed MMN in the older group and no group-differences in P3a; note that in their case, behavioral results were also incongruent with the rest of the studies assessing oddball tasks (Leiva, Andrés & Parmentier, 2015).

In case of N1 elicited by tone onsets, older adults usually exhibited larger (Amenedo & Díaz, 1998; Anderer, Semlitsch & Saletu, 1996; Chao & Knight, 1997) or

similar (Berti, Vossel & Gamer, 2017; Getzman et al., 2013; Horváth et al., 2009; Mager et al., 2005; Tomé, Barbosa, Nowak & Marques-Teixeira, 2014; Woods, 1992; but see Berti, Grunwald & Schröger, 2013) amplitudes than younger adults, suggesting that transient detection – irrespectively of the direction of attention – is probably intact in healthy aging (Berti, Vossel & Gamer, 2017). However, gaps inserted to tones resulted in lower N1s in older compared to younger adults which could be linked to the less efficient processing of temporal resolution (Alain, McDonald, Ostroff & Schneider, 2004; Harris et al., 2011). Although inconsistencies regarding N1 are also present between age groups, these results are less ambiguous compared to the MMN-P3a-RON measured on deviant-minus-standard difference waveforms. This also suggests that N1 amplitude modulation pattern might be superior to “distraction potential” in characterizing the temporal structure of attention-distraction balance between age groups.

Chapter 4: Research questions

This dissertation includes four ERP studies investigating the balance between attention and distraction and the changes of its dynamics with aging. The focus of the first two studies was directed to the role of predictability in prevention of distraction and in cue utilization reflected by the distraction potential and behavioral indices. While the first study applied an auditory distraction paradigm with discrete tones, the remaining three studies utilized continuous stimulation (Horváth & Winkler, 2010). In the first two studies younger adults participated only.

Study III and Study IV compared older and younger adults in terms of the duration of the distracted state by manipulating the temporal separation between distracter and target events during continuous stimulation. While Study III investigated event-related processing in the context of a gap detection task, Study IV explored the ERP reflections of cognitive processes in a passive arrangement. All data were analyzed in R (see the different versions in the corresponding studies); for variance analyses, we utilized the ezANOVA function from package ez (Lawrence, 2016).

The main research questions and hypotheses were the following:

Study I: Numerous studies found that predictability enabled by cues presented before distracting events leads to decreased distraction effects both behaviorally and in the ERPs (Horváth & Bendixen, 2012; Horváth, Sussman, Winkler & Schröger, 2011; Sussman, Winkler & Schröger, 2003; Wetzel, Widmann & Schröger, 2007). However, it is debated whether the reduced ERP amplitudes result from preparation or they are rather a byproduct of the processing of the previously presented cues. The aim of Study I (Volosin & Horváth, 2014 – Chapter 5) was to investigate whether knowledge of the sequence structure leads to decreased distraction effects similarly to the presentation of cues.

Hypothesis: Behavioral distraction effect will be reduced, and the amplitude of the P3a and RON will diminish when participants can predict the occurrence of deviant event compared with the condition when no such predictions are available to be formed.

Study II. The main question of Study II (Volosin, Grimm & Horváth, 2016 – Chapter 6) was whether task-irrelevant distracter events can be utilized as cues to prepare for the

presentation of the forthcoming task-relevant event. In one condition, task-irrelevant events preceded task-relevant ones with a fixed 400 ms time interval (informative condition) while in the other (uninformative) condition, no such temporal relationship was present. In order to manipulate the distractive value of task-irrelevant events, they could be presented either rarely or frequently.

Hypothesis: In the informative condition the task-irrelevant distracters will elicit larger N1/PN and P3a ERPs, reflecting enhanced attention to these events.

Study III: Study III (Volosin, Gaál & Horváth, 2017a – Chapter 7) compared the duration of distracted state between younger and older adults in an active gap-detection task as reflected in N1 amplitudes. We manipulated systematically the temporal separation between distracter and target (gap) events (150, 250, 650 ms or longer).

Hypothesis: The distracted state manifested in reduced N1 amplitudes will take longer in the older compared to younger adults.

Study IV: Study IV (Volosin, Gaál & Horváth, 2017b – Chapter 8) utilized the same paradigm than Study III (distracter-probe event separation in 150, 250, 650 ms or longer) but instead of a gap detection task, participants watched a self-selected silent movie with subtitles. Because in the active task, the utilization of compensatory mechanisms might be assumed, the passive arrangement provides essential information on the changes in the sensory processing and the enhanced sensitivity of acoustic system following rare changes in the background.

Hypothesis: As in Study III, sudden changes in the background acoustic stimulation will affect the sensory processing in the older adults longer than in younger adults.

Chapter 5: Knowledge of sequence structure prevents auditory distraction⁷

5.1 Introduction

Many tasks in our everyday life require the filtering of task-relevant and task irrelevant sensory events: Task-relevant events have to be processed as fast as possible, while task-irrelevant events should not consume processing resources at all. Such a “perfect” selective attention set, however, cannot be established: Unpredictable, rare stimuli easily capture our attention and disrupt the ongoing task-related behavior, that is, we get *distracted*. A number of studies show that the sensory system automatically responds to unpredictable, rare stimulus events (for a summary, see Escera et al., 2000), which may lead to involuntary allocation of attention to such events (Schröger, 1997). Recent studies show that when forthcoming, potentially distracting events are preceded by informative cues, the effects of distraction are reduced or eliminated (Sussman et al., 2003; Horváth et al., 2011; Horváth and Bendixen, 2012; Wetzel and Schröger, 2007; Wetzel et al., 2009, 2012). The goal of the present study was to investigate whether the prevention of distraction was also possible by providing information on forthcoming distracters without relying on explicit cues.

Cognitive processing related to distraction is usually investigated in oddball-paradigms, in which the presentation of frequent *standard* stimuli is interrupted by infrequent *deviants*. A variant of the oddball paradigm developed by Schröger and Wolff (1998b) allows unique insights into distraction-related processing. In this paradigm, long and short tones are presented equiprobably, and participants perform a duration discrimination task. Occasionally, randomly, the task-irrelevant tone pitch is changed (in about 10% of the trials). For such deviants, prolonged response times, reduced hit rates and more false alarms were found than for standards. Distraction effects can be found at the electrophysiological level as well: After deviance onset, a characteristic waveform can be observed in the deviant-minus-standard event-related potential (ERP) difference, starting with an enhanced N1 and mismatch negativity

⁷ Volosin, M., & Horváth, J. (2014). Knowledge of sequence structure prevents auditory distraction: An ERP study. *International Journal of Psychophysiology*, 92, 93-98. <http://dx.doi.org/10.1016/j.ijpsycho.2014.03.003>

(MMN) at 100-250 ms, followed by a positivity at around 300 ms (P3a), and finally a negative deflection occurs peaking around 500 ms (reorienting negativity – RON). The N1-effect and MMN reflect the activity of sensory change detection processes (Näätänen, 1982). P3a is generally assumed to reflect involuntary attention switching (Friedman et al., 2001; Polich, 2007), while RON is theorised to reflect the reorientation of attention to the original task (Schröger and Wolff, 1998a; Sussman et al., 2003). Similar results were found in auditory-visual paradigms in which targets were visual stimuli (e. g. odd or even numbers) and the distractors were sounds (Escera et al., 1998, 2000, 2001). Although the early studies using either auditory (Berti and Schröger, 2003; Schröger and Wolff, 1998a; Schröger and Wolff, 1998b) or auditory-visual (Escera et al., 1998, 2000, 2001) paradigms consistently found prolonged response times (RTs) and decreased accuracy, recent studies found abolished or even reversed behavioral effects (Li et al., 2013; Parmentier et al., 2010; SanMiguel, et al., 2010a; 2010b; Wetzels et al., 2012). These studies suggest that alerting and fore-period effects differ between standards and deviants, and these differences influence the behavioral results.

Interestingly, the paradigm can be also utilized to assess whether distraction can be prevented or reduced. Sussman et al. (2003) utilized the paradigm developed by Schröger and Wolff (1998b) but they presented visual cues before each tone. In the predictable condition, cues indicated whether the forthcoming tone was a standard or a pitch-deviant. In the unpredictable condition, the cues did not allow predicting whether the forthcoming tone was a standard or a deviant. In the unpredictable condition, the expected distraction effects were found: (delayed RTs to deviants in comparison to standards, and the elicitation of N1/MMN, P3a, and RON). In the predictable condition, however, the RT-delay, P3a and RON were abolished (predictability had no effect on the N1/MMN). These results were replicated in several studies using different experimental designs and manipulations of presentation (Horváth et al., 2011; Horváth and Bendixen, 2012; Wetzels and Schröger, 2007; Wetzels et al., 2009).

These studies showed that cues providing different degrees of predictability allow the reduction of distraction, but the mechanism behind the cuing effect is not fully understood yet. Although the prevalent interpretation of the cuing effect is that cues allow one to prepare for, and prevent distraction caused by deviants (“preparation”-hypothesis), other interpretations are also possible. The main alternative interpretation is that distraction-prevention is a “byproduct” of cue-processing: Because cues deliver

information commensurate to that of the forthcoming deviant (i.e. their presentation frequencies are necessary the same, therefore deviant cues are deviants themselves within the cue sequence), processing this sudden “burst” of information may temporarily deplete processing resources, which in turn, may lead to reduced distraction effects. Direct evidence against the “byproduct”-hypothesis is scarce. There is only one study, conducted by Parmentier and Hebrero (2013), which showed that cues allowing the prediction of forthcoming deviants reduced distraction-related response-time delays even if the cues preceded the deviants by as much as 2250 ms (i.e. the reduction of RT-delay did not differ from that at 250 ms cue-tone separation). Because it seems unlikely that cue-related processing would block further processing for such a long time, this result supports the “preparation” account of the cuing effect.

The goal of the present study was to investigate distraction-prevention using the method of ERPs in a setting in which information on forthcoming distracters was not delivered in “bursts”, but was available continuously. Investigating whether distraction can be reduced in this setting is important, because such an arrangement would allow the comparison of distraction-prevention ability between groups potentially differing in their ability to process and utilize “bursts” of information. That is, the continuous availability of cue-information would eliminate confounds due to potential between-group cue-processing abilities. For example, if processing “burst”-like cues required 300 ms on average in one group, but required 500 ms in another, then cues appearing 400 ms before distracters would allow one group to fully prepare for the forthcoming distracters, while leaving the other group prone to their distracting effects. In this example, one would measure between-group differences in the efficiency in distraction-prevention, but these differences would not reflect the ability to prevent distraction, rather, they would reflect a difference in cue information processing speed. Furthermore, even if the cue-distracter separation allowed both groups to process cue information in time, the utilization of this information depends on the willingness of participants to do so. The amount of effort needed to process cue information in the short time available may reduce the participants’ motivation to utilize cue information at all (Horváth, 2013).

We administered an auditory distraction paradigm in which the presentation order of tones was either predictable (every 7th tone was pitch-deviant) or random (with 1:6 deviant:standard ratio). The tones virtually moved either to the left or to the right

and participants responded to the direction of the movement, ignoring sound frequency. As in previous studies, deviants in the predictable condition should be less distracting than those in the random condition because of the availability of information on forthcoming deviants. This arrangement, however, still provides a challenge: participants have to keep the current position within the sequence in mind to be able to prepare for forthcoming deviants. In order to minimize the effort needed, a visual counter showing the sequence position was presented as a constant reminder, which made information on forthcoming tones continuously available throughout the experimental blocks of the predictable condition. We hypothesized that knowledge about the stimulus sequence would reduce or abolish behavioral and ERP effects of distraction.

5.2 Material and methods

5.2.1. Participants

14 healthy young volunteers participated in the experiment (9 women, aged: 19-26 years, mean age: 22 years). All participants reported normal hearing and normal or corrected-to-normal vision. They received either modest financial compensation or course credit for participation, and gave written informed consent before the experiment, after the experimental procedures were explained to them.

5.2.2. Materials and procedure

Participants were sitting in a comfortable chair in a sound-attenuated room during the experiment. Each experimental block consisted of either random or predictable sequences of complex spatial sounds with 1300 ms SOA, through a Sennheiser (HD-600, Sennheiser, Wedemark, Germany) headphone. The intensity of sounds was individually calibrated to 50 dB sensation level above the hearing threshold, determined by the method of limits.

Tones were generated with Csound version 5.7.11, using the head related transfer function tool “hrtfmove2” to simulate virtual movement. Due to a programming error, tones were generated with 44.1 kHz sampling frequency, but replayed with 48.0 kHz, which did not substantially alter the perceived virtual movement. The frequency and velocity data values reported below correspond to what participants actually heard.

The duration of each tone was 643 ms, with 9 ms rise and fall times. Each tone started on the virtual midline (they could be heard in both ears equally), then after 184 ms they moved 20° toward the left or right (50-50% probability) with constant angular velocity in 459 ms, i.e. angular velocity was 43.54°/sec. The tones were complex tones with six harmonics. The fundamental frequency of the tones was either 254 Hz (high) or 202 Hz (low). The amplitudes of the five harmonic overtones were 80%, 40%, 50%, 30% and 90% of the amplitude of the fundamental. Both frequencies could function as deviant (14.28%) or standard (85.71%). The role of frequencies (standard or deviant) was counterbalanced between participants: For seven participants, standards were high, for the other seven standards were low.

The participants' task was to indicate whether the tone moved to the left or to the right (regardless of its frequency), by pressing the key held in their corresponding hand. The instruction was to respond as fast and accurately as possible, immediately when the direction of the virtual movement could be assessed (without waiting for the sound-offset). Participants were informed before each block whether the presentation of the block was predictable or random. Each block consisted of frequent standard and rare deviant stimuli, presented with a 6:1 ratio. Thus, 154 tones were presented in each block (132 standards and 22 deviants). In predictable blocks every 7th tone was deviant, in random blocks the tone order was randomized while keeping the 6:1 standard:deviant ratio.

To support keeping the current sequence position (and the forthcoming deviant tone) in mind, a visual counter was presented on a screen. Black digits from 1 to 7 were presented continuously in linear order in the middle of the gray screen, under a viewing angle of about 7°. The transition between digits occurred 44 ms before each tone. In the random condition where the order of the standards and deviants was completely unpredictable, the digits and their transition gave information only about the onset of the forthcoming tone (i. e., that it will be presented in 44 ms) but not about its pitch (deviant or standard). In contrast, in the predictable condition, one of the transitions indicated that the next will be a deviant. The transition that was followed by the deviant was varied randomly between the participants (e.g., for some participants, the 1-to-2 transition was followed by a deviant, for others it was the 4-to-5, etc). Participants were explicitly told which transition was followed by the deviant. Each block started with a so-called "reminder" sequence, that is, the first four tones were presented in alternating

order to the left and right directions, in order to make the direction discrimination easier. These four tones were not included in the analyses.

Estimating the effect of predictability is not trivial. Because in the predictable condition every 7th stimulus was a deviant, one could select micro-sequences ending with a deviant and preceded by exactly six standards (but not seven, that is, the micro-sequence should end but also start with a deviant) from the random condition as a comparison. However, the proportion of such sequences is quite small. Therefore, we included deviants preceded exactly by 4, 5, 7 or 8 standards as well. It is well-known that deviance-related processing activity is stronger when the deviant follows a longer regular stimulus sequence (Bendixen et al., 2007; Horváth et al., 2008; Sams et al., 1983; Winkler et al., 1996). Furthermore, it is plausible that the activity-increase in deviance-related processing brought about by adding further stimuli to the preceding regular sequence decreases with each addition: For example, the activity increase when a deviant is preceded by 5 instead 4 standards is larger, or at least not smaller, in comparison to when it is preceded by 6 instead of 5. Because of this, adding the deviants preceded by 4-, 5-, 7- and 8-standard micro-sequences results in less (or at least equal) deviance-related activity on average than for the deviants preceded by a 6-standard micro-sequence. That is, this selection of deviants results in an *underestimation* of the distraction-effects. Furthermore, in a random sequence, the frequency of micro-sequences with deviants preceded by a given number of standards decreases as the function of the number of preceding standards (e.g. there are less deviants preceded by exactly 5 standards than that preceded exactly by 4), which results in an even more conservative estimate (because more deviants with shorter preceding standard-micro-sequences are included in the average). Because we only included deviants preceded by 4-5-6-7-8 standards in the random condition, in order to achieve a similar number of trials as in the in predictable condition, about 2.5 times more random blocks were needed. Therefore, the experiment consisted of 5 predictable and 13 random blocks. The order of blocks was randomized with the constraint that predictable blocks could never immediately follow each other. The approximately 3.5 minutes-long blocks were separated by 1-2 minute long breaks, depending on the participant's preferences, with a longer, 10-15 minute break after 9 blocks. After each block, feedback on behavioral performance was given, which consisted of correct response

rates, average response time and a distribution plot of correct response times within the block.

Before administering the experiment, the participants were familiarized with the task: Two practice blocks were presented, one before mounting the electrodes and one when the electrodes were already mounted. The practice blocks were about 3.5 minutes long and consisted of either only low or only high tones.

5.2.3. EEG recording

The EEG was recorded with a sampling rate of 500 Hz with a Neuroscan Synamp 2 (Compumedics Inc., Victoria, Australia) amplifier, from 63 Ag/AgCl electrodes mounted on an EasyCap (EASYCAP GmbH, Herrsching, Germany) arranged according to the 10% system (Nuwer et al., 1998), and filtered online with a 100 Hz lowpass filter. The reference electrode was placed on the tip of the nose, the ground electrode on the forehead. Horizontal electro-oculogram was measured from two electrodes placed at the outer canthi of the eyes. Vertical electro-oculogram was calculated off-line as the difference between the signals of the Fp2 and an electrode under the right eye.

The EEG data were filtered offline, using a 20 Hz lowpass filter (Kaiser-windowed sinc finite impulse response filter, beta of 10.06, 1603 coefficients; 2 Hz transition bandwidth, and stopband attenuation at least 100 dB). 1344 ms long epochs were extracted from each trial, including a 144 ms pre-tone interval. Amplitude calculations were referred to the first 100 ms of the epochs (i.e. the interval before the visual stimulus transition). Epochs with a signal range exceeding 150 μ V on any channel, as well as the first four epochs of each experimental block (“reminder sequence”) were discarded from the analyses. The epochs selected according to the preceding micro-sequences as described above were averaged separately by condition (predictable or random) and stimulus type (deviant or preceding standard), so predictable standard, predictable deviant, random standard and random deviant tones were included in the analyses.

5.2.4. Statistical analysis

For each participant medians of the response times were calculated, which gives more accurate results than means because of the skewed distribution of response times. Only correct responses between 300 and 1200 ms (following tone onset, i.e. between

100 and 1000 ms after the onset of virtual movement) were included in the response time analysis. d' sensitivity scores were calculated according to the signal detection theory (MacMillan and Creelman, 1991). Response times and d' were analyzed in repeated measures Condition \times Stimulus analyses of variance (ANOVAs).

Distraction-related ERPs (N1/MMN and P3a) were identified in the group average deviant-minus-standard waveforms of the random condition. Individual ERP amplitudes were calculated in both conditions as the average signals in 40 ms long windows centered at peak latencies at the FCz electrode (where these ERPs typically peak in similar experiments, see e.g. Horváth et al., 2011; Horváth and Bendixen, 2012; Jankowiak and Berti, 2007). Additionally, and unexpectedly, two slow ERP waveforms were also observed, which were analyzed in 200 ms long windows. The amplitudes were submitted to Condition (random vs. predictable) \times Stimulus (deviant vs. standard) repeated measures ANOVAs. Mean square error (MSE) and generalized effect sizes (η^2_G) are reported (Bakeman, 2005; Olejnik and Algina, 2003).

5.3 Results

5.3.1. Behavioral performance

Neither the analyses of d' nor that of response times showed significant effects. The group-mean response time in the predictable condition was 576 ms in standard (standard deviation, $SD=50$ ms) and 579 ms in deviant trials ($SD=55$ ms), while in the random condition 577 ms was the average speed on standards ($SD=49$ ms) and 578 ms on deviants ($SD=59$ ms). These response times are referred to the onset of the tones (and not the time point the virtual movement started). Neither the main effect of Condition ($F[1,13]<.001, p=.99, MSE<.001, \eta^2_G<.001$), nor the main effect of Stimulus: standard or deviant ($F[1,13]=.015, p=0.7, MSE<.001, \eta^2_G<.0001$) was significant; and the Condition \times Stimulus interaction did not show any significant effect either: ($F[1,13]=.133, p=.133, MSE<.001, \eta^2_G<.001$). Regarding sensitivity, the mean of d' -s in the predictable condition was 2.91 for standards ($SD=0.65$) and 2.8 for deviants ($SD=0.58$). In the random condition, the mean of d' -s was 2.98 for standards ($SD=0.79$) and 2.85 for deviants ($SD=0.73$). No significant effects were found (Condition main effect: $F[1,13]=.22, p=.65, MSE=.183, \eta^2_G=.002$, Stimulus main effect: $F[1,13]=.72, p=.408, MSE=.287, \eta^2_G=.008$, Condition \times Stimulus interaction: $F[1,13]=.011, p=.916, MSE=.034, \eta^2_G<.001$).

5.3.2. ERPs

After excluding artifact-contaminated epochs, individual ERPs were averaged for 88 deviants in the predictable condition (SD: 13.6); for 65 deviants in the random condition (SD: 13.44); 81.5 standards in the predictable condition (SD: 12.19) and 64.6 standards in the random condition (SD: 14.36). The group-average ERPs elicited at midline electrodes in the two types of trials and conditions, and corresponding deviant-minus-standard waveforms are presented in Fig. 5.1.

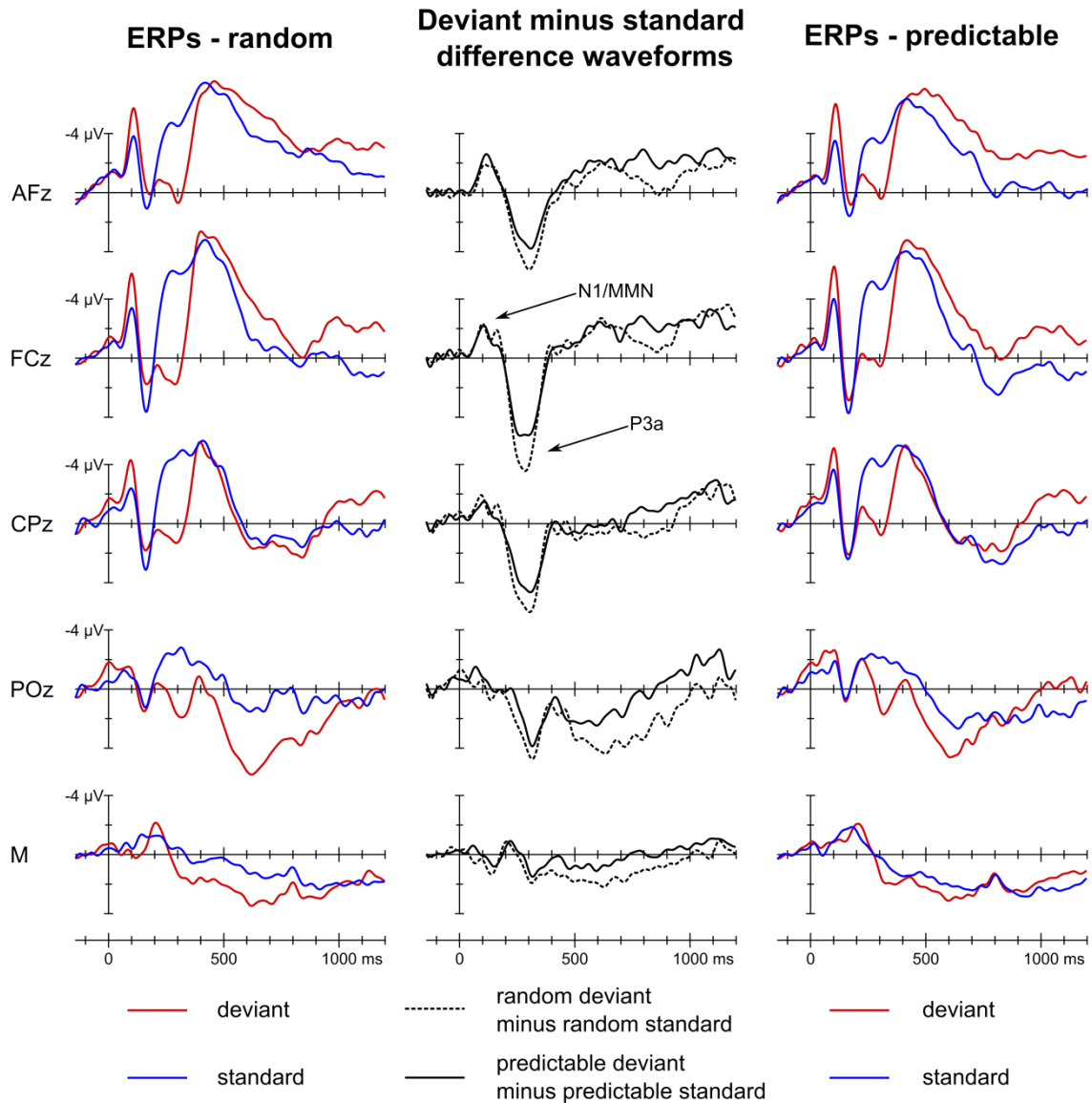


Fig. 5.1 Group-average ($N = 14$) ERPs to deviants, and standards preceding them in the random (left) and the predictable (right) conditions, and the corresponding deviant-minus-standard difference waveforms (middle column) at selected midline and averaged mastoid leads.

The ERP waveforms at FCz showed a negative-going trend before tone onset suggesting preparatory activity for the forthcoming tone. Tones elicited an N1 and a P2, which was followed by a negativity between 200 and 300 ms and a negative sustained activity of duration comparable to that of the tone. For deviants, the second negativity was overlapped by a positive waveform, and the sustained negativity persisted longer than for standards. This suggests that participants probably kept their attention slightly longer on deviants than on standards. The deviant-minus-standard difference waveform in the random condition showed an early negative difference (N1-effect/MMN/N2b) with two negative peaks at 100 ms and 162 ms, and a fronto-central P3a peaking at 286 ms. In parallel with the differential fronto-central negativity resulting from the persistence of the sustained negativity for deviants, the difference waveform also showed a slow positive activity after 500 ms, peaking at 634 ms on the POz lead in the random condition (identifiable as a P3b).

The ANOVA of the amplitudes at the first peak of the early negativity showed a significant Stimulus main effect: $F(1,13)=39.766$, $p<.001$, $MSE=1.667$, $\eta^2_G=.102$, indicating larger (more negative) N1 (and possibly MMN) amplitudes. Neither the Condition main effect ($F[1,13] = 2.14, p = .16$, $MSE=1.69$, $\eta^2_G=.006$) nor the Stimulus \times Condition interaction ($F[1,13] = .019, p = .89$, $MSE= 2.629$, $\eta^2_G < .001$) was significant. For the second peak only a marginal Stimulus main effect was found: $F(1,13)=3.75, p=.075$, $MSE=6.53$, $\eta^2_G=.034$. Neither the main effect of Condition: ($F[1,13]=.75, p=.4$, $MSE=5.53$, $\eta^2_G=.006$), nor the interaction of Stimulus \times Condition ($F[1,13]=1.02, p=.32$, $MSE= 3.048$, $\eta^2_G=.004$) reached statistical significance. The ANOVA of the amplitudes in the P3a latency-range showed a significant Stimulus main effect: $F(1,13)=25.05, p<.001$, $MSE= 22.15$, $\eta^2_G=.35$ and a Condition \times Stimulus interaction: $F(1,13)=8.20, p=.013$, $MSE=2.04$, $\eta^2_G=.016$, showing that P3a amplitude was smaller in the predictable than in the random condition. A significant Condition main effect was not found: $F(1,13)=.095, p=.76$, $MSE=4.52$, $\eta^2_G<.001$. The topography of the P3a in the two conditions, and the modulatory P3a-effect (the difference of the deviant-minus-standard differences) are presented in Fig. 5.2. The ANOVA of the P3b activity on POz lead showed significant stimulus effect: $F(1,13)=30.366, p<.001$, $MSE=3.837$, $\eta^2_G=.053$, indicating that deviants evoked larger positive responses than standards. Neither the main effect of Condition ($F[1,13]=.008, p=.92$, $MSE=8.813$, $\eta^2_G<.001$) nor the Stimulus \times Condition interaction was significant ($F[1,13]=1.64, p=.22$,

MSE=8.033, $\eta^2_G=.014$). The ANOVA of the negative difference on AFz electrode showed a stimulus main effect: $F(1,13)=4.80, p=.047$, MSE=8.495, $\eta^2_G=.028$, indicating that amplitudes for deviant tones were more negative than for standards. No significance was present regarding the Condition main effect ($F[1,13]=.69, p=.42$, MSE=8.654, $\eta^2_G=.028$) and the Stimulus \times Condition interaction ($F[1,13]=.92, p=.76$, MSE=6.37, $\eta^2_G<.001$).

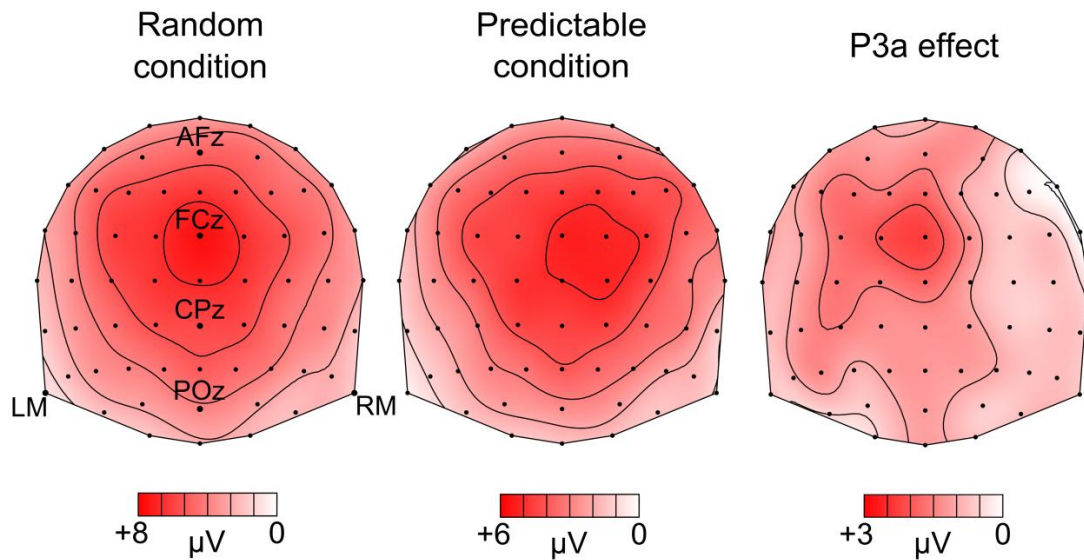


Fig. 5.2. Group-average ($N = 14$) topographical distribution of the P3a in the random (left panel) and in the predictable condition (middle panel). The P3a-effect (right panel) is calculated as the between-condition difference of the deviant-minus-standard ERP difference.

5.4 Discussion

The present study introduced an oddball paradigm in which the prevention of distraction was supported by the constant availability of information on the temporal structure of the stimulus sequence instead of supplying information on forthcoming distracters “in bursts” shortly before the distracter was presented. The results generally fit current views on distraction-related processing. Deviants elicited an N1-effect/MMN, P3a, a longer sustained frontal negativity, and a parietal P3b in comparison to standards preceding them. Importantly, P3a amplitude was significantly reduced in the predictable condition, despite using a conservative estimate of this effect. This supports the “preparation”-hypothesis, that is, this suggests that information on forthcoming deviants allowed participants to reduce the effects of distraction. The results also show that the present stimulation arrangement, which was designed to allow the elimination of

confounds stemming from (between-group) differences in cue-processing abilities, is a viable alternative to the typically used cueing arrangements.

Although at first sight, the absence of distraction-related behavioral effects may seem to contradict the assumption that distraction had happened, it has to be kept in mind that behavioral responses in such paradigms are influenced by a number of factors (for example, differences in stimulus-triggered arousal level changes), which, in sum, may lead to reduced, but also to enhanced performance in a given paradigm (Li et al., 2013; Parmentier et al., 2010; SanMiguel et al., 2010a, 2010b; Wetzels et al., 2012). It is also possible that the lack of a significant behavioral distraction-effect is partially due to the “natural” stimulus-response mapping (congruent stimulus- and response side), which may allow for a faster response, and less interference than in studies with arbitrary mappings (e.g. duration discrimination). Note that although behavioral distraction effects have been observed in previous studies using a laterality-based discrimination task (Wetzels et al., 2009), in these studies distracters were unique, spectrally rich, novel sounds (i.e. highly deviant sounds, differing in a number of features from standards), while in the present study deviants differed only in their pitch from standards.

Although P3a was significantly reduced in the predictable condition, the N1-effect/MMN was not similarly modulated by predictability. This is in consonance with previous studies, in which cue-information on forthcoming distracters did not affect the N1-effect/MMN (Horváth et al., 2011; Horváth and Bendixen, 2012; Wetzels and Schröger, 2007; Wetzels et al., 2009). In contrast with these studies, however, in the present study there was a definite theoretical possibility that knowledge of the sequence structure could lead to MMN reduction. It has been demonstrated that that under the right circumstances the deviant-detection system underlying MMN elicitation can represent regularities similar to that in the present study, and therefore, it may not respond to predictable deviants: Sussman et al. (1998) showed that in a passive arrangement (i.e. participants were reading during tone presentation), in a tone sequence in which every fifth tone was a deviant, deviants did not elicit an MMN, presumably, because the unit of representation was not the single tone, but the five-tone micro-sequence. The lack of MMN elicitation depended, however, on the rate of presentation: MMN was not present when the onset-to-onset interval (stimulus onset asynchrony – SOA) was 100 ms, but a clear MMN was elicited when it was 1300 ms (see also Scherg

et al., 1989). In a further study (Sussman et al., 2002), in which tones were presented with an SOA of 1000 ms, and participants *actively monitored* whether the repeating five-tone-pattern was violated, no significant MMN was observed. Importantly, a significant MMN was, however, present in a condition in which participants actively monitored the sequence, but were *unaware* of the five-tone repeating structure. Similarly, significant MMNs were found in the study by Jankowiak and Berti (2007), in which deviants were presented at regular sequence positions (SOA of 2500 ms) and participants were unaware of the regularity. This set of results suggests that *top-down processes* may influence the regularity representation underlying MMN elicitation even at a 1/s presentation rate, but the presence of the regularity *in itself* is insufficient to influence the MMN-mechanism. Based on these findings, one might expect that MMN would be reduced in the predictable condition of the present study, however, no such effect was found. The lack of modulation may be due to a number of differences between the paradigms: First, we used a relatively long SOA (1.3s vs. 1.0s) and micro-sequence length (every 7th was a deviant vs. every 5th was a deviant). Second, also, in contrast with Sussman et al.'s (2002) study, in which the feature defining the micro-sequence pattern and the task-relevant feature was the same (pitch), in our study the two features were different (pitch and lateral movement). Third, in Sussman et al.'s (2002) study the task was to detect a highly infrequent (2%) pitch variant (which required a response only rarely), whereas in the present study the task was a 50-50% discrimination (which required a response on each trial).

The reduction of P3a in the predictable condition indicates that knowledge about the stimulus sequence allowed the reduction of distraction. This result fits previous studies which used cues preceding deviants to prevent distraction (Horváth et al., 2011; Horváth and Bendixen, 2012; Sussman et al., 2003; Wetzel and Schröger, 2007; Wetzel et al., 2009). Because information on the tone sequence and forthcoming deviants was constantly available during stimulation, a “burst”-like cue processing was not required. This supports the notion that distraction is actively prevented by the use of predictive information, and the prevention is not (solely) a by-product of cue processing. In summary, the present study showed that knowledge of the stimulus sequence allowed one to prevent distraction as reflected by the P3a. This result is compatible with the notion that distraction can be prevented when information is available on forthcoming distracters. Moreover, the constant availability of information on forthcoming

distracters eliminates potential processing bottlenecks inherent in other cue presentation based procedures. Therefore, the present stimulation arrangement may be more suitable to assess between-group differences in the ability to prevent distraction.

5.5 Acknowledgements

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Chapter 6: Exploiting temporal predictability: Event-related potential correlates of task-supportive temporal cue processing in auditory distraction⁸

6.1 Introduction

When performing tasks requiring overt or covert reactions to stimulation events, the predictability of the stimulation can often be exploited to streamline processing. If we know what types of stimulus events may occur, we can establish *selective attention sets*, which makes it possible to prepare for task-relevant sensory events while ignoring task-irrelevant ones (e. g. Parmentier, 2014). We can also make use of cues that predict *when* task-relevant events can occur, and prepare for their processing at a given moment in time (Holender and Bertelson, 1965). Numerous studies have shown that selective attention sets can be disrupted by rare, unpredictably occurring, or conspicuous stimulus events (distracters). In the present study, using the method of event-related potentials (ERPs), we investigated whether such distracters can nonetheless be utilized as temporal cues to support task-related processing in a continuous auditory stimulation paradigm.

Variants of the oddball paradigm especially suitable for investigating distraction-related processing have been introduced by Schröger and Wolff (1998b) and Escera, Alho, Winkler and Näätänen (1998). In these *distraction paradigms*, a discrete stimulus sequence is presented, and participants perform a discrimination task related to one aspect of the stimulation. Distraction is induced by infrequently, unpredictably changing a task-irrelevant aspect of the stimulation. In the paradigm introduced by Schröger and Wolff (1998b), participants perform a duration discrimination task in a sequence of short and long tones, in which (the task-irrelevant) tone pitch is occasionally changed (distracter trials). In the paradigm introduced by Escera et al. (1998), participants perform odd/even discrimination for visually presented numbers. Each number is preceded by a task-irrelevant sound, and distraction is induced by

⁸ Volosin, M., Grimm, S., & Horváth, J. (2016). Exploiting temporal predictability: event-related potential correlates of task-supportive temporal cue processing in auditory distraction. *Brain Research*, 1639, 120-131. <http://dx.doi.org/10.1016/j.brainres.2016.02.044>

occasionally replacing the (task-irrelevant) sound with a different sound. The rationale of these arrangements is that behavioral and ERP response-differences between distracter and non-distracter trials reflect processes related solely to distraction because participants perform the same task on both types of trials.

Variations of these initial paradigms (see e.g.; Berti and Schröger, 2003; Escera et al., 1998; Escera et al., 2000; Escera, Yago and Alho, 2001; Polo et al., 2003; Roeber, Berti and Schröger, 2003; Roeber, Widmann and Schröger, 2003; Schröger and Wolff, 1998a, 1998b) showed a consistent pattern of results. Response times in distracter trials were longer than in non-distracter trials, and more mistakes were made. In the ERPs (Escera et al., 2000; Escera and Corral, 2007) the distracter-minus-non-distracter difference waveforms showed an enhanced N1 and mismatch negativity (MMN) between 100-250 ms following the onset of the distracting stimulus event, followed by a P3a in the 250-400 ms interval; and finally a negative waveform termed reorienting negativity (RON) could be observed between 400 and 600 ms. These ERPs are usually described in a three-stage model of distraction. The deviant-related N1 enhancement and MMN are generally thought to reflect processes related to auditory change detection (e.g. Näätänen, 1982; Näätänen et al., 2007). P3a is thought to reflect an involuntary selective attention set change, that is, distraction (Friedman, Cycowicz and Gaeta, 2001; Polich, 2007). Finally, RON may reflect processes involved in the restoration of the task-optimal attention set after the distracting event (Berti, 2008; Schröger and Wolff, 1998a; Sussman, Winkler and Schröger, 2003).

To better understand information processing in these paradigms, it is useful to point out that all of these paradigms feature two types of *stimulation events* which differ in terms of their task-relevancy: 1) One type of event is task-relevant in the sense that the occurrence of the event provides the information necessary to select the correct response. For example, in the paradigm introduced by Escera et al. (1998), the onset of the number is the task-relevant event. In the paradigm introduced by Schröger and Wolff (1998b), the task-relevant event occurs at the time point of the short tone offset, at which the tone either stops or continues. 2) The second type of event is task-irrelevant in the sense that it does not convey information regarding the response to be given, but nonetheless, it is a well-detectable transient change in the stimulation which allows the temporal structuring of the stimulation. In the Schröger and Wolff (1998b)

paradigm, this event is the tone onset, whereas in the paradigm introduced by Escera et al. (1998) such events are the tone-onsets and -offsets.

These task-irrelevant events may play an important role in distraction paradigms, because these events can be used as *temporal cues* to predict the onset of the task-relevant events, especially if they precede the task-irrelevant events by a constant interval (foreperiod effect, see e. g. Capizzi, Correa and Sanabria, 2013; Holender and Bertelson, 1975; Leynes, Allen and Marsh, 1998). Indeed, this is the case for all the studies referred to above: in these studies, irrelevant and relevant events were presented with constant temporal separation, typically in the range of 100-200 ms (e.g. Wetzel, Widmann and Schröger, 2012; Berti and Schröger, 2001; Schröger and Wolff, 1998a, 1998b), but even as high as 600 ms in some experiments (Ruhnau et al., 2010). Because of this, it seems reasonable to assume that task-irrelevant events play a “supportive” role in performing the task by allowing temporal preparation for the forthcoming task-relevant event.

There is substantial evidence for the supportive, temporal cueing function of the irrelevant events in these paradigms. In some arrangements, task-irrelevant events cannot be disregarded at all: in a duration discrimination task (Schröger and Wolff, 1998b) the stimulus onset is a crucial reference point, and therefore even small deviations – for example, otherwise hardly noticeable (1%) pitch changes – occurring at the onset result in robust distraction effects (Berti, Roeber and Schröger, 2004). Recent behavioral studies, in which the separation of task-relevant and –irrelevant events was manipulated, as well as whether the irrelevant event was followed by a relevant one on each trial, showed that the distraction-related response time delay was reduced when the foreperiod was not constant and the irrelevant event was unreliable (50% or less) in signaling the forthcoming task-relevant event (Berti, 2013; Jankowiak and Berti, 2007; Li, Parmentier and Zhang, 2013; Parmentier, 2014; Parmentier, Elsley and Ljungberg, 2010; Wetzel, Widmann and Schröger, 2012). These results suggest that in distraction paradigms, participants actually use the “task-irrelevant” events as temporal cues to enhance their task performance, that is, these events are not disregarded at all, but are incorporated in the task-behavior of the participants.

One may even argue that “distraction”-effects observed in these paradigms actually reflect the disruption of the regular task-behavior: That is, despite having the

same between-event relationship as for the standard stimulation, distracters may not enable the same preparatory activity for the task-relevant event. The goal of the present study was to investigate whether it was at all possible to exploit a regular temporal relationship between a task-irrelevant *distracter* and a task-relevant event, that is, whether distracting events could be utilized as temporal cues to support task performance.

In contrast with previous studies, in which the discrete, trial-based stimulation protocol established a standard between-event relationship and occasionally changed the identity of the cue event on a low proportion of trials, we used a continuous stimulation protocol in which the identity of the cue events was not varied at all, and distraction was induced by manipulating the presentation frequency (the probability of presenting an event within a given time interval). We administered a continuous stimulation paradigm (Horváth and Winkler, 2010), in which 4-5 minutes long, continuous tones are presented, which feature occasional gaps and frequency glides (rapid – 10 ms long – transitions from one pitch to another). In the present study, the task-relevant events were the gaps: participants performed a gap discrimination task: they indicated by key presses whether a long (100 ms) or short (10 ms) gap was presented (note that due to the short gap duration, the gap onset is too close to the task-relevant moment to be useful in any preparation). The glides were task-irrelevant.

Similarly to discrete paradigms, in which distraction is induced by introducing rare task-irrelevant stimulus variations, in the present study, the probability of the glides was manipulated to induce distraction: glides occurred frequently or rarely in separate conditions, and based on previous studies (Horváth and Winkler, 2010; Horváth, 2014b) it was assumed that rare glides lead to distraction. Note that although numerous studies compare responses elicited by rare and frequent stimuli presented within the same condition to assess the effects of distraction, these effects (as detailed above) are mainly brought about by the difference in presentation frequency, and not by the difference in tone identity (see e.g. Horváth, Winkler and Bendixen, 2008; but see also Horváth, 2014b, and Horváth, in press).

The temporal cue function of the glides was manipulated by randomly inserting glides and gaps independently in one condition, while creating an 80% reliable, predictive temporal glide-gap arrangement in another (glides preceded gaps by 400 ms,

see Fig 6.1). 80% predictability was chosen because this level of reliability seems to be sufficient to compel participants to exploit cues (Posner et al., 1980; in the context of the distraction paradigm: Horváth and Bendixen, 2012). 400 ms separation was chosen, because this would allow efficient preparation (Holender and Bertelson, 1965), while allowing the observation of the relevant ERPs (see below). The orthogonal combination of the two manipulations resulted in four conditions: an informative frequent glide, an informative rare glide, an uninformative frequent glide, and an uninformative rare glide condition. In this design, ERPs related solely to distraction would be observable in the uninformative rare-minus-frequent waveforms as described above, whereas solely cue utilization-related ERP effects would be observable in the frequent informative-minus-uninformative difference waveforms, and the main question of interest is whether interactions between these “pure” effects would occur in the informative rare glide condition.

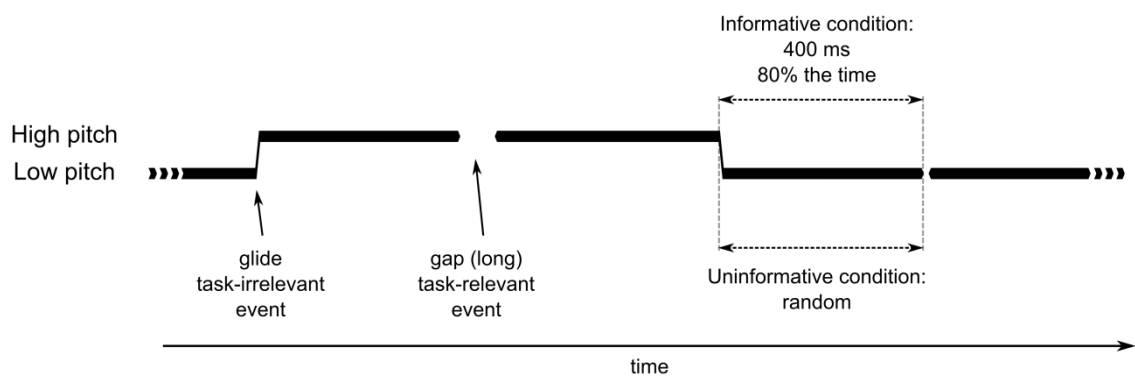


Fig. 6.1 The schematic design of the experimental paradigm, including glides, short gaps and long gaps. The thick black line represents the continuous tone alternating between two pitches (non-target glides) and the short breaks mark the gaps (short and long targets). The difference between glide – gap time intervals and the predictive values in the informative and uninformative conditions are marked with dashed lines.

In this paradigm, the utilization of temporal cues may be manifested in the ERPs in various ways: First, participants may form a selective attention set allowing the enhanced detection of the cue, which may be manifested as the enhancement of the N1 waveform (e.g. Hillyard et al., 1973; Kauramäki, Jääskeläinen & Sams, 2007; Lange, 2013), which may include contributions from the processing negativity (PN) or negative difference (Nd; Alho et al., 1986; Alho, 1992; Mueller et al., 2008) signaling that an attentional trace for the cue was established (Näätänen, 1982). Second, rare temporal cue events may also elicit an N2b (Alho et al., 1986; Folstein and Van Petten, 2008;

Näätänen and Gaillard, 1983; Näätänen et al., 2007; Ritter, 1979, 1982, 1992), signaling that the event was registered as being task-relevant. Third, preparatory activity for the task-relevant event is likely to be manifested in a contingent negative variation following the cue (CNV; Dien et al., 2004; Donchin et al.1975; Leynes, Allen and Marsh, 1998; Liu et al., 2013; McCallum, 1988; Mento, 2013; Smith, Barry and Steiner, 2013; Tecce, 1972; van Rijn et al., 2011; Verleger et al., 2012; Walter et al., 1964), even if the following, target event is omitted in 15-25% of the cases (Bauer, 1993; Walter et al., 1964).

Interestingly, some studies also hint at the possibility that the P3a, which is generally regarded as a reflection of distraction, may be sensitive to cue predictability and cue utilization. Wetzel, Schröger and Widmann (2013) compared a condition with a constant (100 ms) foreperiod between task-irrelevant and -relevant events, and a condition in which the foreperiod varied between 0, 50, 100, 150 and 200 ms. Although individual P3a assessments did not show a between-condition amplitude difference, the group average ERP waveforms seem to show a P3a amplitude increase for constant foreperiods (Wetzel et al., 2013, p. 926, Fig.3; and also a negative shift, potentially a CNV). A further hint for the potential effect of predictability on the P3a amplitude comes from the continuous stimulation distraction paradigm (Horváth and Winkler, 2010). In the study by Horváth and Winkler (2010) although glides occurred unpredictably, the glide-gap separation was 150 ms for 50% of the glides, therefore, participants may have used the glides as a temporal cue for the forthcoming, task-relevant gap. In this arrangement glides elicited a P3a. When glides and gaps were interspersed independently, and therefore the glides could not be used as cues, the glides did not elicit a P3a (Horváth, 2014a). Although fully independent and coupled glide-gap presentation protocols were not compared directly, these results also hint at the possibility that P3a may be enhanced by the temporal predictive value of the distracter with respect to the task-relevant stimulus event. In a variant of the paradigm introduced by Schröger and Wolff (1998b), Hölig and Berti (2010) made the distracting events explicitly task-relevant: for the distracters participants had to discriminate the distracter pitch (high or low), instead of its duration. Such distracters elicited an N2b and an enhanced P3a in comparison to the condition when distracter events did not require such a task-change, which may indicate that P3a, at least in part, is involved in task-switching or task-set activation (Berti, 2008; Hölig and Berti, 2010, for similar

suggestions see Dien, Spencer and Donchin, 2004; Barcelo et al, 2006; Horváth, Winkler and Bendixen, 2008).

In the present study, we hypothesized that in the informative conditions glide-related ERPs will feature an enhanced N1 (possibly involving PN or Nd) due to the establishment of a selective attention set for the glide, and that the glide will be followed by a CNV reflecting preparation for the forthcoming gap. It was further hypothesized that the rare-minus-frequent glide difference waveforms would show the characteristic distraction waveform: an enhanced N1, as well as MMN and P3a. Importantly, we hypothesized that the cue value of the glides would modulate the rare-minus-frequent glide difference waveforms: informative glides would lead to the emergence of an N2b, and the enhancement of the P3a in the difference waveform. Conversely, if cue utilization would be interrupted by distraction, the CNV would be elicited with lower amplitude in the informative rare glides condition than in the informative frequent glide condition.

6.2 Methods

6.2.1 Participants

16 paid volunteers took part in the experiment but data of 2 participants were excluded from further analyses (one performed the task at chance level, i.e. accuracy between 46% and 58%; d' -s between -.2 and .4; and one had a high number of movement artifacts resulting in the rejection of about 85% of all epochs). The remaining 14 participants (mean age: 23, from 19 to 31 years, all right-handed, 12 women) reported normal hearing and normal or corrected-to normal vision. They received either modest financial compensation or course credit for participation. All participants gave written informed consent after the experimental procedures were explained to them.

6.2.2 Stimuli and procedure

During the experiment, participants listened to continuous tones (through headphones, Sennheiser HD 25-1, Wedemark, Germany) generated off-line with Csound 5.16 (www.csounds.com), with a sampling rate of 44.1 kHz. The tones consisted of three harmonics with equal amplitude: the fundamental, the second and third harmonics (the first harmonic was missing). The fundamental frequency was either 220 Hz (low) or 277 Hz (high). Tone intensity was 68 dB SPL (measured with an artificial head, HMS III.0, Head Acoustics, Germany). The tone featured two types of

events: pitch changes with an exponential transition over a duration of 10 ms from low to high or back (*glides*), and short silent periods (*gaps*) breaking the continuous tone for 10 or 100 ms (with additional 10 ms linear fall and 10 ms linear rise times). Participants performed a gap discrimination task: they indicated by keypresses whether a long or short gap was presented, while ignoring frequency glides. The assignment of left and right keys to short and long gap durations was counterbalanced between participants. Participants were familiarized with the gap duration discrimination task in two 4-minute-long training blocks at the beginning of the experiment. These blocks did not feature any frequency glides in order to demonstrate the difference between long and short gaps (i.e. the pitch was constant in these blocks - in one it was high, in the other it was low). The probability of the two gap durations was 50 per cent each and they followed each other in random order. The between-gap intervals (measured between the onsets of the amplitude decreases) was random: it contained a fixed, 1.3 s period and an additional time period randomly drawn from an exponential distribution characterized by a mean of 1.5 s. Glides were presented either frequently or rarely in different conditions. The glide-to-glide interval was chosen randomly from a uniform distribution of intervals between 4.0 and 16.0 s in rare glide blocks, and between 1.0 and 4.5 s in frequent glide blocks. (On average, frequent glide blocks featured 87 glides and 85 gaps, whereas rare glide blocks featured 23 glides and 85 gaps). Because glide and gap presentation times were independently generated, glides and gaps could occur temporally close to each other. To avoid glide-gap overlaps, for gap and glide events scheduled to occur within 150 ms, the starting point of a long gap was re-scheduled to a time point 150 ms earlier, whereas short gaps were re-scheduled to be presented 80 ms earlier. If the gap was scheduled to be preceded shortly by a glide, the gap was re-scheduled to be presented 80 ms later, irrespectively of its duration. In the uninformative conditions, no further manipulations were administered. In the informative condition, however, gaps immediately following glides were re-scheduled to exactly 400 ms following glide onset in 80% of the cases (randomly chosen), thereby creating an event sequence in which 80% of the glides were followed by a gap exactly by 400 ms. To be able to collect a similar number of ERP epochs in each condition, and for each glide presentation frequency (with timing parameters described below) without overlaps from other events, a simulation of the scheduling was run. Based on the results of this simulation, the informative glide condition was administered in 5 rare and 2

frequent glide blocks, the uninformative glide condition in 6 rare and 2 frequent glide blocks.

The experiment was conducted at the University of Leipzig. Participants were sitting in a comfortable chair in a sound-attenuated chamber. The experiment was run in two parts. The first part featured the informative condition blocks for seven participants, while seven others started with the uninformative condition blocks. The duration of an experimental block was approximately 4 minutes. Before each condition, a short (2 minutes long) practice block reflecting the structure of forthcoming experimental blocks was presented.

During each block a black fixation cross was presented on grey background on a screen in front of the participants. At the beginning of each block, the task instruction was displayed on the screen, and stimulation started when participants pressed a key. Data from the practice blocks were not analyzed. Between the blocks short (1-2 min) pauses were available, and at about the half of the experiment, participants had the opportunity for a longer (5-15 min) break. At the end of each block, feedback about the accuracy was displayed on the screen.

6.2.3 EEG recording

The EEG was recorded with 512 Hz sampling rate with an Active Two (BioSemi B. V., Amsterdam, Netherlands) amplifier, from 64+2 active electrodes mounted on a headcap according to the 10% system (Nuwer et al., 1998). A further electrode was placed on the tip of the nose for off-line re-referencing. Horizontal electro-oculogram was measured by two electrodes placed to the outer canthi of the eyes, and vertical electro-oculogram was measured from electrodes attached above and below the left eye. Because of the malfunction of the electrode at Fp1 position this channel was discarded from the analyses.

The continuous EEG was referenced to the nose and was filtered offline, using a 30 Hz lowpass filter (Kaiser-windowed sinc finite impulse response filter, beta of 5.65, 929 coefficients; 2 Hz transition band width, stop-band attenuation at least 60 dB). 500 ms long glide-related epochs were extracted, including a 100 ms pre-glide interval. Only epochs corresponding to glides not preceded by any event in 600 ms and not followed by any event in 390 ms were retained for analysis. Epochs with a signal range exceeding 100 μ V on any channel were also discarded from the analyses. The

remaining epochs categorized according to Cue Function (informative / uninformative) and Glide Frequency (frequent / rare) were averaged separately, that is, rare informative, frequent informative, rare uninformative and frequent uninformative glides were included in the analyses.

6.3 Statistical analyses

Only correct responses occurring within 120 to 1000 ms after the beginning of a gap were included in the reaction time analysis. Individuals were characterized by the median reaction time, because it better represents the typical response time than the mean due to the skewed individual reaction time distribution. d' sensitivity scores for gap discrimination were calculated according to the Signal Detection Theory (MacMillan and Creelman, 1991). Reaction times and d' -s were analyzed in repeated measures ANOVAs including the factors Cue function (informative / uninformative) and Glide Frequency (rare / frequent).

The glide-related N1 latency and maximum was measured in the group-average uninformative frequent glide condition: it reached its maximum (negative) peak at Fz, at 107 ms. The N1/MMN deflection was identified in the rare-minus-frequent difference waveform of the uninformative condition: it peaked at 129 ms at FCz. For identifying informativeness-related negative ERP waveforms, and the P3a, however, the informative condition was chosen since these components should be elicited with maximal amplitudes in this condition. The negative peak overlapping the N1/MMN peaked at 158 ms at FCz in the informative rare-minus-frequent difference waveform; the P3 peaked at 346 ms at Pz. Finally, as an exploratory step, we calculated the difference of the frequent-minus-rare difference waves, to better characterize this negative difference. For all analyses individuals were characterized by the average amplitude measured in 20-ms windows centered on these peak latencies, at the electrodes, and the data were submitted to Cue Function \times Glide Frequency ANOVAs. To assess whether amplitude differences were caused by topographical differences between ERP waveforms or difference waveforms (and not by genuine amplitude modulations), the effects were compared in ERP \times Electrode (for N1/MMN and N2b: AFz, FCz, CPz, POz; for P3: Fz, Cz, Pz, Oz, respectively) ANOVAs, in which the amplitudes were vector-normalized as described by McCarthy and Wood (1985). In such analyses a significant interaction would mean that the shapes of the two ERP topographies differ, that is, that the manipulations result in the activation of different

ERP generators as well. Statistical analysis was conducted in R (version 3.1.0, R Core Team, 2014). Generalized eta squared (η^2_G) effect sizes are also reported (Olejnik and Algina, 2003; Bakeman, 2005).

6.4 Results

6.4.1 Behavioral results

Although the present study was not designed for the investigation of the gap-related behavioral and electrophysiological responses, a liberal trial-selection procedure still made it possible to assess distraction- and cue function-related effects manifested in the accuracy and reaction time data. To make meaningful and unbiased between-condition comparisons, we selected glide-gap pairs with a similar temporal structure: we selected gaps which were preceded by a glide in 300-500 ms and were not followed by any glides in 1 s. The 300-500 ms interval was used for the following reason: In the informative conditions, 80% of the glides were followed by a gap in 400 ms. In the uninformative conditions, however, this 400 ms glide-gap separation is extremely rare because of the independent presentation of glides and gaps. To include a reasonable number of trials with close to 400 ms separations, gaps with 300-500 ms glide-gap intervals were selected. The 1 s glide-free interval following the gap was chosen to make sure that no interference from glides presented during the response interval contaminated the data. Even with the liberal trial selection, two participants did not have trials with responses, that is, they failed to respond to gaps in the selected trials in the rare uninformative condition. For this reason they were not included in the following accuracy and reaction time analyses.

To assess gap-related accuracy, correct response rates were calculated. The 2×2 ANOVA of the correct response rates showed no significant main effect of Glide Frequency ($F(1, 11) = .38, p = .55, \eta^2_G = .002$) or Cue Function ($F(1, 11) = .04, p = .848, \eta^2_G < .001$). The Glide Frequency \times Cue Function interaction was not significant ($F(1, 11) = 3.74, p = .08, \eta^2_G = .004$) either. Participants performed the task in average with 88.9% (SD = 9.4) correct response rate.

Gap discrimination performance was assessed in a 2×2 ANOVA of the d' -s. Although a tendency of Glide Frequency \times Cue Function interaction effect ($F(1, 11) = 4.14, p = .067; \eta^2_G = .023$) was found, the main effect of Glide Frequency ($F(1, 11) = .029, p = .86, \eta^2_G < .001$) and Cue Function ($F(1, 11) = .164, p = .69, \eta^2_G = .004$) were

not significant. The mean gap duration discrimination sensitivity was 2.62 (SD = .88) in the sample.

For the reaction times, a significant Cue Function main effect was found ($F(1, 11) = 9.19, p = .011, \eta^2_G = .125$), showing that informative foreperiods allowed faster responses than uninformative ones. The average response time was 526.76 ms (SD = 70.92) in the informative and 591.02 ms (SD = 99.98) in the uninformative conditions. Neither Glide Frequency main effect ($F(1, 11) = .11, p = .75, \eta^2_G < .001$), nor the Glide Frequency \times Cue Function interaction ($F(1, 11) = .12, p = .735, \eta^2_G < .001$) was significant.

Due to the nature of the task, participants may also inadvertently respond to glides and not only to gaps. The tendency to respond to task-irrelevant glides was assessed by selecting sequences where a response to a gap was preceding a glide at least in 100 ms, and where these glides were not followed by any other event (glide or gap) in 1 s. Then, the ratio of keypresses to such glides in 1 s was calculated. Using this method, we ensured that the keypress is actually a response to the glide and not a late reaction to a previously presented gap. The number of keypresses to such glides was rare (in average between 0% and 18%), suggesting that participants did understand the task properly, and followed the instructions.

6.4.2 ERPs

Individual ERPs were on average calculated from 109 epochs (range: 79 to 130; SD = 14.4) from the frequent informative condition, 64 (range: 50 to 83; SD = 9.33) from frequent uninformative condition, 54 (range: 30 to 73; SD = 11.47) for the rare informative condition, and 56 (range: 38 to 77; SD = 11.02) for the rare uninformative condition.

The group-average ERPs and the corresponding difference waveforms are presented in Fig. 6.2. Glides elicited a clear N1, which was peaking at 107 ms in the frequent uninformative condition at Fz. The rare-minus-frequent glide difference waveform in the uninformative condition showed a fronto-centrally negative deflection (labeled as N1/MMN, because this may include both change-detection-related waveforms), peaking at FCz at 129 ms, with its polarity inverted on the mastoids. In the

informative condition, an additional negativity following the N1/MMN was observable peaking slightly later (158 ms) at FCz. This peak showed no polarity-inversion at the mastoids. These negative deflections were followed by a centro-parietally distributed positive waveform peaking at 346 ms at the Pz electrode, which was present in the uninformative condition as well. Due to its parietal distribution, we labeled this waveform P3 instead of P3a (which usually exhibits a fronto-central maximum).

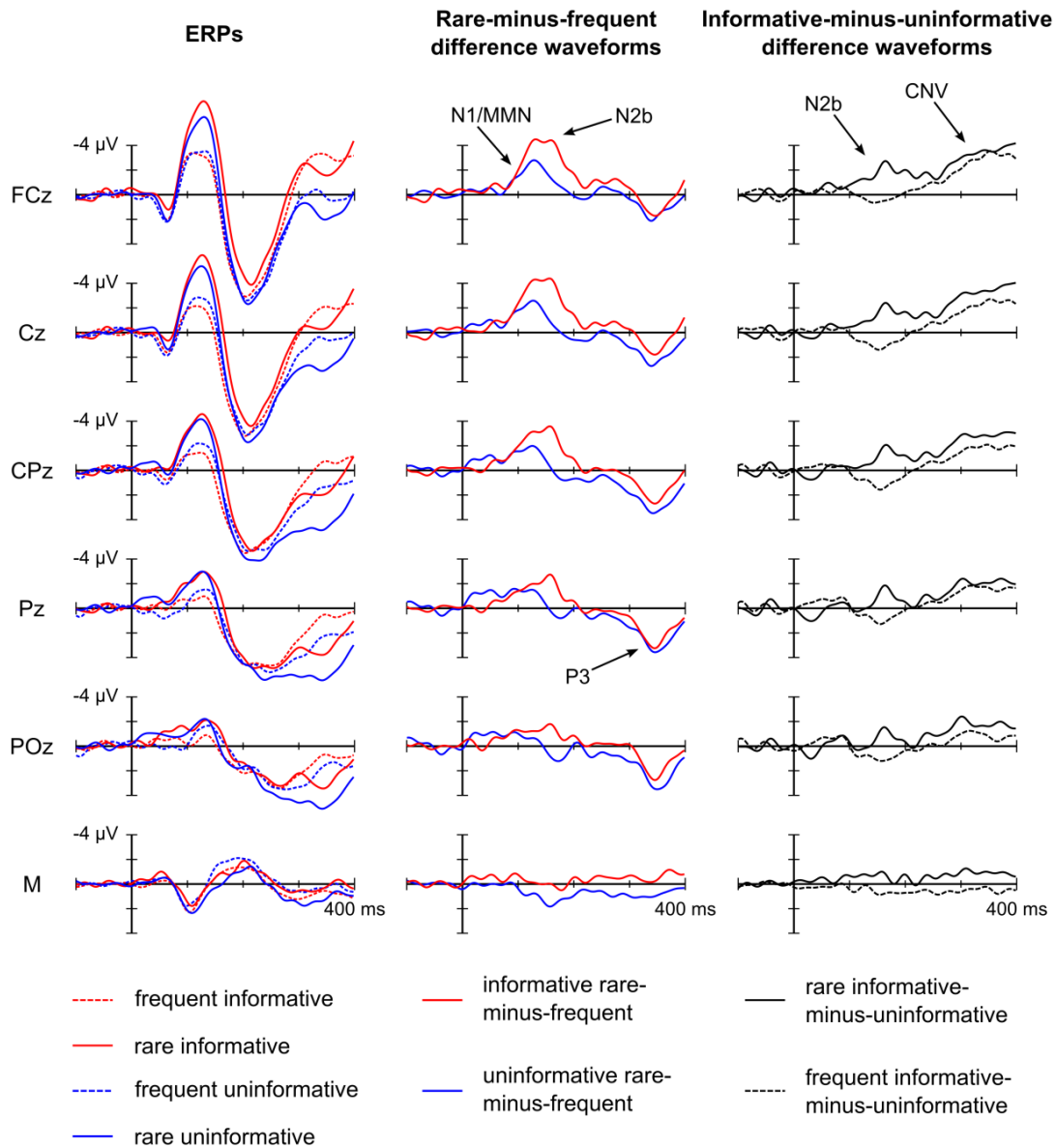


Fig. 6.2 Group-average ($N=14$) glide-related ERPs in the frequent informative, rare informative, frequent uninformative and rare uninformative conditions (left column) and the rare-minus-frequent difference waves measured at midline electrodes (FCz, Cz, CPz, Pz, POz) and at the averaged mastoids (M) in the informative and uninformative condition (middle column). The

informative-minus-uninformative difference waveforms showing the effect of informative foreperiod are presented in the right column.

The Glide Frequency \times Cue Function ANOVA of the amplitudes measured the N1 time range (97-117 ms), at Fz showed only a Frequency main effect: $F(1, 13) = 16.788$, $p = .001$, $\eta^2_G = .123$, indicating that rare glides elicited higher N1 amplitudes than frequent ones. Neither the Cue Function main effect ($F(1, 13) = .466$, $p = .507$, $\eta^2_G = .005$), nor the Glide Frequency \times Cue Function interaction ($F(1, 13) = 1.061$, $p = .321$, $\eta^2_G = .007$) was significant.

The Glide Frequency \times Cue Function ANOVA of the N1/MMN amplitudes (measured in the 119-139 ms interval at FCz) showed only a significant Glide Frequency main effect: $F(1, 13) = 41.009$, $p < .001$, $\eta^2_G = .27$, showing that rare glides elicited higher (more negative) N1/MMN amplitudes than frequent ones. Neither the main effect of Cue Function ($F(1, 13) = .457$, $p = .52$, $\eta^2_G = .006$) nor the Glide Frequency \times Cue Function interaction were significant ($F(1, 13) = 2.9$, $p = .11$, $\eta^2_G = .02$). The comparison of the N1/MMN topographies showed no Cue Function \times Electrode interaction ($F(3, 39) = .338$, $p = .80$, $\eta^2_G = .003$), that is, N1/MMN topographies were not significantly different in the informative and uninformative conditions.

The Glide Frequency \times Cue Function ANOVA of the amplitudes of the early negative waveform overlapping the MMN (measured at FCz in the 148-168 ms interval) showed a significant Glide Frequency main effect ($F(1, 13) = 24.08$, $p < .001$, $\eta^2_G = .075$), but the main effect of Cue Function failed to reach statistical significance ($F(1, 13) = 1.19$, $p = .296$, $\eta^2_G = .008$). In addition, a significant Glide Frequency \times Cue Function interaction was present ($F(1, 13) = 23.01$, $p < .001$, $\eta^2_G = .02$) indicating that the ERP was larger (more negative) in the informative than in the uninformative condition. The topographical comparison of the rare-minus-frequent glide difference waveforms showed a significant Cue Function \times Electrode interaction ($F(3, 39) = 9.2$, $p < .001$, $\eta^2_G = .077$), suggesting that the topographical distributions differed between the informative and uninformative conditions across electrodes, that is, this effect was not a modulation of the N1/MMN. Additionally, the difference of the two difference waveforms (i.e. the Glide Frequency \times Cue Function interaction effect) was explored in

a 150-ms long window (from 90 to 240 ms), to determine the latency of its (negative) maximum. The negativity peaked at Cz, at 162 ms (see topography in Fig 6.3).

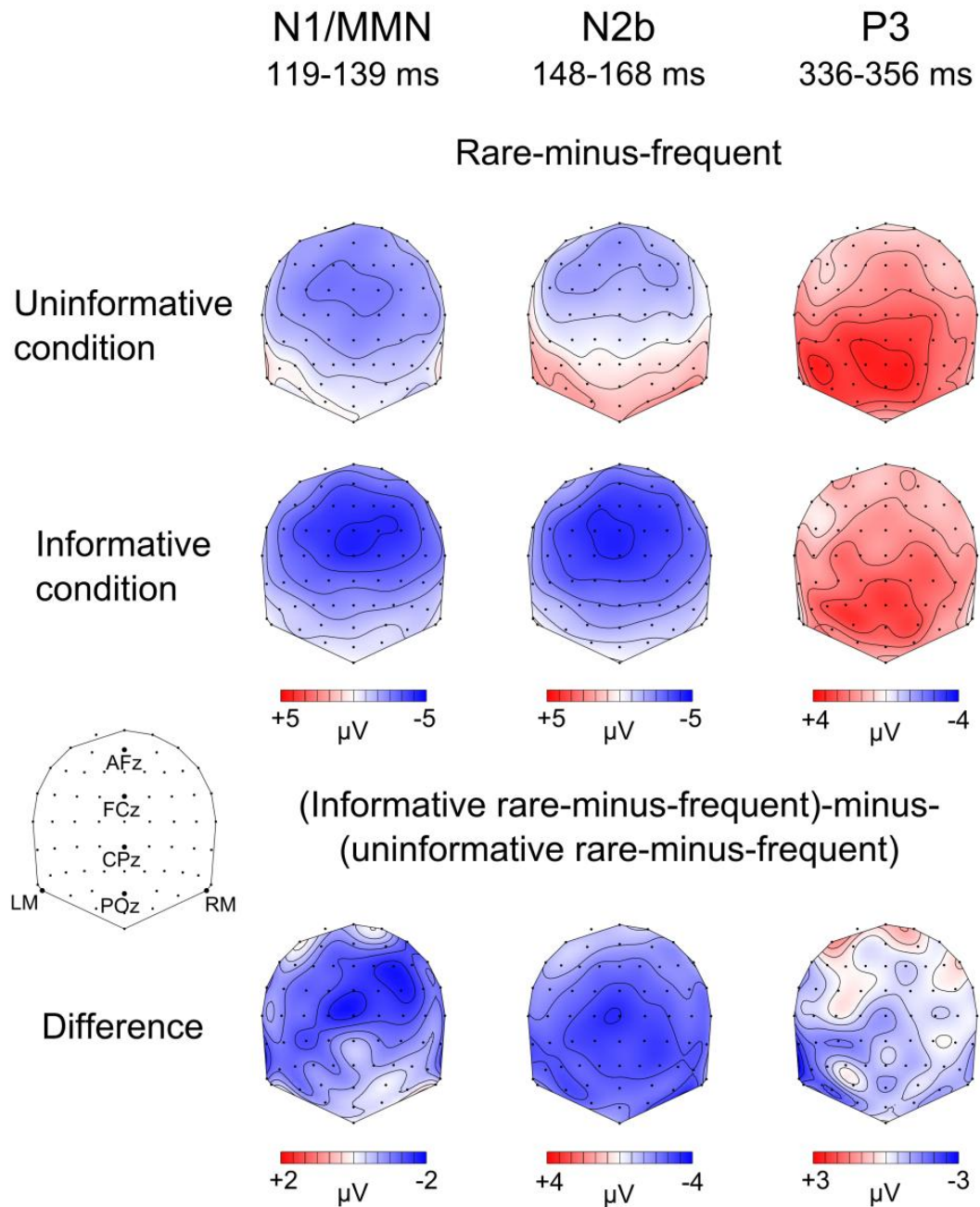


Fig. 6.3 Group-average ($N=14$) topographical distribution of the MMN, N2b and P3 waveforms in the uninformative (first row) and in the informative condition (second row). The MMN, N2b and P3 are based on rare-minus-frequent difference waveforms and the between-condition difference is plotted in the third row. Note that the scales differ in order to highlight differences and similarities in the shape of the distributions.

Based on its topographical and latency characteristics, this cue function-related negativity might be labeled both as N2b and PN/Nd. Both waveforms are typically elicited by active attention (Alho et al., 1986; Alho, 1992; Mueller et al., 2008) to register task-relevant events (Ritter, 1992) and reflecting template matching processes (Alho, 1992; Näätänen, 1982; Näätänen et al., 2007; Ritter et al., 1992). However, since N2b is related more strongly to attended rare deviations (Patel and Azzam, 2005; Ritter et al., 1992) than PN/Nd, it is more likely that the overlapping negativity is an N2b effect to the attended task-irrelevant events, as it can be seen in the right panel of Fig. 6.2, elicited by rare informative glides.

The Glide Frequency \times Cue Function ANOVA of the P3 peak showed a significant Glide Frequency main effect: ($F(1, 13) = 27.783, p < .001, \eta^2_G = .148$). The main effect of Cue Function ($F(1, 13) = 2.96, p = .11, \eta^2_G = .05$) and the interaction were not significant ($F(1, 13) = .08, p = .783, \eta^2_G = .001$). The topographical comparison of the rare-minus-frequent glide difference amplitudes showed no Cue Function \times Electrode interaction at Fz, Cz, Pz, and Oz electrodes (after scaling: $F(3, 39) = .018, p = .908, \eta^2_G = .001$), that is, the P3 topographies were not significantly different in the two conditions. The informative-minus-uninformative difference waveforms are also presented in Fig 6.2, in the right panel. These difference waveforms show that the lack of the hypothesized P3 difference might be due to the overlap of CNV in the time window of P3, and Fig. 6.4 represents its topographical distribution.

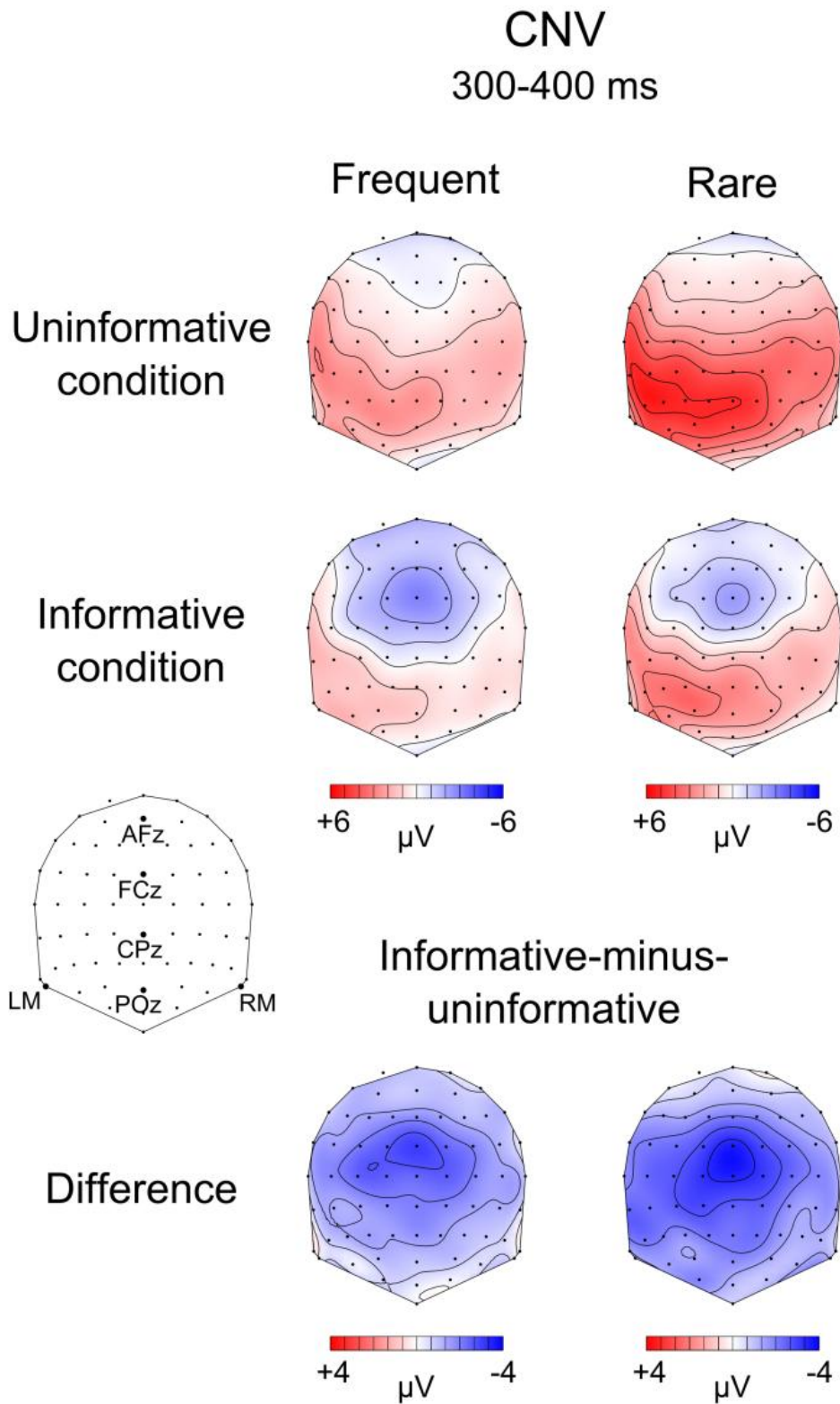


Fig. 6.4 Group-average ($N=14$) topographical distribution of CNV in the uninformative (first row) and in the informative condition (second row). Since CNV is basically elicited under informative foreperiod, the informative-minus-uninformative differences are relevant in this case.

6.5 Discussion

The goal of the present study was to investigate whether it was possible to exploit a regular temporal relationship between a task-irrelevant *distracter* event (a glide) and a task-relevant event (a gap) to prepare for the moment the task-relevant event (gap) was likely to occur. Distraction was induced by the manipulation of glide presentation frequency (rare vs. frequent), which resulted in a characteristic distraction ERP waveform: Rare glides elicited an early negative deflection (probably composed of an enhanced N1 and MMN) in comparison to frequent glides, indicating that rare glides triggered automatic auditory change detection mechanisms. The N1/MMN was followed by a similar P3 in both informative and uninformative conditions. The manipulation of cue function (i. e. whether the glide allowed the prediction of the task-relevant moment) was also successful, as evidenced by the N2b elicited by the rare informative glides, and CNV elicited in both informative glide conditions. An N1 difference between informative and uninformative conditions, which would reflect the establishment of a selective attention set for the informative, but not for the uninformative glides, was, however, not observable.

The rareness-related early negativity (presumably the mixture of an enhanced N1 and MMN) reflects auditory change detection, potentially leading to the orientation of attention to the eliciting event (Näätänen, 1982; Näätänen et al., 2007). Importantly, this negative waveform was further modulated by the cue function of the glides: somewhat later, an N2b was observable in the informative rare-minus-frequent glide waveform but not in the uninformative one. This finding is in line with previous findings, which showed that N2b is elicited only by sounds which are rare in the terms of a sound-related task (Sams, Alho and Näätänen, 1983; Ritter et al., 1992). In the present context the presence of the N2b indicates that participants included the informative glides into their task-behavior, that is, they utilized the distracter glides as temporal cues. It is important to note, however, that we found no evidence that participants formed an attention set tuned for glides in the informative glide conditions, as no N1-enhancement was observed in the informative-uninformative glide contrast. That is, the inclusion of the glides into the task-behavior seems to be limited to a post-perceptual level: whereas the N1 reflecting the auditory processing of the glides was unaffected, the task-relevance was nonetheless reflected by the elicitation of the N2b, and the following CNV.

The hypothesized P3a enhancement in the informative condition was not observable and the measured waveform also showed a parietal distribution, therefore we labeled it more generally as P3. Beyond the trivial explanation (i.e. the predictability of the task-relevant moment has no effect on the P3), the lack of the expected effect has at least two further explanations. First, it is possible that the rare informative glides may have elicited ERPs which overlapped, and presumably cancelled the P3a-effect. Beside the N2b, the CNV observed in the informative conditions may have contributed to such an overlap. Since the CNV is a long lasting negative deflection, it might affect the later components in the time window of the foreperiod, including the P3a related to the first event (Dien, Spencer and Donchin, 2004; Verleger et al., 2012; Wetzel, Schröger and Widmann, 2013). In the study of Wetzel, Schröger and Widmann (2013) P3a and CNV waveforms were also observable when the distracter was informative regarding the presentation probability and occurrence time of the target (300 ms following distracter, that is 300 ms foreperiod). In their study, similarly to our results, P3a amplitude did not differ significantly between informative and uninformative conditions either, although for informative distracters a P3a latency shortening was present and informative distracters elicited a late negative shift interpreted as CNV, but it did not overlap P3a. The lack of overlap of these two waveforms could be explained by the relatively early occurrence of P3a (between 220 and 300 ms) compared to CNV (between 330-400 ms) and the utilization of cross-modal stimulation (auditory distracters and visual targets). In the present study, however, CNV started around 300 ms, which coincided with the P3 time-range. There is also evidence that rare cue events are followed by enhanced CNVs in comparison to frequent cues (Bauer et al., 1992), suggesting that an enhanced CNV to rare informative glides could cancel a potentially significant P3a-increase which might explain both the null-effect and the parietal distribution of the component in the present study.

Second, one might also argue that participants were not motivated enough to rely on glides as cues and to extract the temporal information they provided because this would essentially transform the single-task into a – more difficult – dual-task situation (detect the glides as well as discriminate the gaps). Because cue utilization is voluntary, and cue utilization behavior was not measured on-line, participants could “opt-out” from using the cues without notice (as demonstrated by Horváth, 2013). However, this explanation is not convincing, because of the presence of the attention- and preparation-

related negativities to rare informative glides (N2b, CNV), indicating that participants evaluated these as task-relevant events.

In line with the ERP data, the behavioral results also suggest that informative glides were utilized as cues allowing task-related preparation: although correct response rate and gap duration discrimination scores were not affected, participants responded significantly faster when an informative foreperiod was provided. It is important to note that data from two participants were excluded from the reaction time- and accuracy analysis, because they did not respond in the selected trials in the uninformative rare glide condition. Such response omission to task-relevant stimuli following a distracting event has also been reported by Pacheco-Unguetti, Gelabert & Parmentier (2016), who interpreted it as a temporary suspension of cognitive activity after distraction.

The behavioral results basically fit into the literature using either discrete (e. g. Li, Parmentier and Zhang, 2013; Parmentier, 2014; Parmentier, Elsley and Ljungberg, 2010; Wetzel, Widmann and Schröger, 2012) or continuous (Horváth, 2014a; Horváth and Winkler, 2010) stimulation. In studies where temporal intervals between task-irrelevant and task-relevant events (in audio-visual paradigms: distracter tone onset and offset and the onset of visual target stimuli) were manipulated, the fixed foreperiod between rare distracters and targets had the potential to enhance behavioral performance (e. g. reduced reaction times or at least reduced distraction effect) on a second, task-relevant event in a 2-choice task, even though the task-irrelevant first event did not provide any specific information on the type of the succeeding second one (Holender and Bertelson, 1975; Parmentier, Elsley and Ljungberg, 2010; Wetzel, Widmann and Schröger, 2012, but see Li, Parmentier and Zhang, 2013), and implicit timing expectations improved reaction times and accuracy as well (Rimmele, Jolsvai and Sussmann, 2011). In the present study, participants also responded faster when the task-relevant event was preceded by an informative foreperiod, which is in correspondence with the studies cited above, suggesting that they exploited the temporal cue value of the glides.

Most of the studies cited above did not find any change in hit rates when a temporally informative foreperiod was present in discrete stimulation protocols (Li, Parmentier and Zhang, 2013; Wetzel, Schröger and Widmann, 2013; Wetzel, Widmann and Schröger, 2012, but see Parmentier, Elsley and Ljungberg, 2010), which is in line

with the present findings. Using continuous stimulation, in Horváth and Winkler's (2010) study, gap detection rate was significantly reduced and participants got slower as well when only 50% of the glides were followed by a gap. However, when glides and gaps were presented in a fully independent manner, reaction times were not impacted (Horváth, 2014a), which suggests that randomly presented glides did not enhance readiness for response, while in case of 50% gap probability, participants might have treated task-irrelevant glides and succeeding gaps as a common unit and glides as potential cues. In the present study, the 80% gap presentation chance after glides in the informative condition let participants to form stronger associations between the two types of stimuli and to mark glides as task-relevant events exploiting their cue value as reflected in ERPs (enhanced N2b, CNV) and in decreased reaction times to gaps. Correct response rates and d' -s were, however, not significantly impacted by glide presentation frequency. This difference to Horváth's (2014a) study might be explained by the task-difference between the two studies: while in Horváth's (2014a) experiment, the task was gap detection, which required fast simple responses, the present study, however, featured a discrimination task, in which the frequently presented glides without any information regarding the correct answer (i. e. the duration of the target) might have interfered with the discrimination process.

In summary, the present study showed that the constant foreperiod between task-irrelevant distracter and task-relevant target events allowed participants to exploit the temporal cue value of rare distracters and to support the temporal preparation for the task-relevant second event. This supportive effect was not manifested in an enhanced perceptual processing of the informative glides (as no cue function-related N1 differences were found), but it was manifested in ERPs reflecting post-perceptual processing: the characteristic rare-minus-frequent difference waveform featured an N2b in the informative condition, and informative glides were also followed by a CNV, suggesting preparational effects. The task-supporting effect was present behaviorally as well: the presence of informative glides enhanced participants' response-behavior to the gaps reflected by decreased reaction times, even though it did not increase accuracy. Our results basically fit the results of studies varying the temporal cue value of the distracter events not only in discrete (Hölig and Berti, 2010; Parmentier, Elsley and Ljungberg, 2010; Wetzels, Schröger and Widmann, 2013; Wetzels, Widmann and Schröger, 2012) but in continuous stimulation paradigms (Horváth, 2014a; Horváth and

Winkler, 2010) as well. Finally, and most importantly, the present study supports the idea that both prediction- and distraction-based information processing are manifested in various distraction paradigms.

6.6 Acknowledgments

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Chapter 7: Task-optimal auditory attention set restored as fast in older as in younger adults after distraction⁹

7.1 Introduction

Aging is associated with deteriorated frontal lobe functions which result in a decreased ability to inhibit the processing of irrelevant information (Guerreiro, Murphy & Van Gerven, 2010; Hasher, Lustig & Zacks, 2007; Zanto & Gazzaley, 2014). This leads to greater susceptibility to distraction, that is, an inability to filter out task-irrelevant aspects of stimulation (Chao & Knight, 1997; Lustig, Hasher & Zacks, 2007; Mager et al., 2005). Numerous studies demonstrated that the impact of distracters on task-performance was stronger in older than in younger adults (e.g. Berti, Grunwald & Schröger, 2013; Carlson, Hasher, Connelly & Zacks, 1995; Woods, 1992). Distraction, however, is not a unitary phenomenon, and ageing may affect some distraction-related processes while sparing others, which might be reliably delineated by method of event-related potentials (ERPs). Differences in distraction-related processes can be reflected by amplitude- or latency-differences in specific ERP components (Escera & Corral, 2003; Horváth, Winkler & Bendixen, 2008). For example, Chao and Knight (1997) suggested that the age-related enhancement of the Pa mid-latency auditory ERP reflected decreased inhibition of incoming stimulation. Moreover, based on P3a latency differences, Horváth, Czigler, Birkás, Winkler and Gervai (2009) suggested that involuntary attention switching took longer in older than in the younger adults. The goal of the present study was to investigate how fast younger and older adults could restore the task-optimal attention set after distraction occurred. We utilized a recently developed, continuous stimulation distraction paradigm (Horváth & Winkler, 2010; Horváth, 2014a), which relies on the attentional modulation of the auditory N1 ERP.

In most studies investigating the effect of aging on distraction and its electrophysiological correlates, involuntary attention switching was induced by rare (oddball) stimuli which broke the regularity of a sequence comprising frequent stimuli.

⁹ Volosin, M., Gaál Zs. A., & Horváth, J. (2017a). Task-optimal auditory attention set restored as fast in older as in younger adults after distraction. *Biological Psychology*, 126, 71-81. <http://doi.org/10.1016/j.biopsycho.2017.04.007>

Distraction was characterized by rare-minus-frequent (behavioral or ERP) response differences. Studies comparing distraction effects between younger and older adults showed either no significant differences or differences with the same sign. Specifically, behavioral distraction effects (e.g. rare-minus-frequent reaction time differences) were mostly comparable between younger and older adults (Amenedo & Diaz, 1998; Gaeta, Friedman, Ritter & Cheng, 1998; Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009; Iragui, Kutas, Mitchiner & Hillyard, 1993; Leiva, Parmentier & Andrés, 2014; Mager et al., 2005), or, in some cases, older adults were more impacted by distracters (i. e. larger reaction time increase to rare stimuli, see Berti, Grunwald and Schröger, 2013; Woods, 1992).

The ERPs observable in the rare-minus-frequent difference waveform are generally interpreted as reflections of distraction-related processes: Sensory change- and deviance detection is thought to be reflected by the mismatch negativity (MMN, Näätänen, 1982), and the enhancement of the N1; the involuntary change in attentional orientation (distraction) is reflected by the P3a (Friedman, Cycowicz & Gaeta, 2001; Polich, 2007). Most studies found that in older adults the ERP amplitudes were smaller (MMN: Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009; P3a: Gaeta et al., 1998; Iragui et al., 1993), or similar to those recorded in younger adults (MMN: Amenedo & Diaz, 1998; Berti, Grunwald & Schröger, 2013; Gaeta et al., 1998; Mager et al., 2005; P3a: Berti, Grunwald & Schröger, 2013; Getzman, Gajewski & Falkenstein, 2013; Mager et al., 2005). Similarly, the distraction-related ERPs were delayed (P3a: Gaeta et al., 1998; Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009; Mager et al., 2005) or were elicited with similar latency as in younger adults (MMN: Amenedo & Diaz, 1998; Gaeta et al., 1998; Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009; Mager et al., 2005).

In the present study, we utilized a different approach to measure the effects of distraction (Horváth & Winkler, 2010). Instead of interpreting the ERPs observable in the rare-minus-frequent difference waveforms, the present study exploited the well-known attentional modulation of the auditory N1 waveform to measure the time of recovery from distraction. In the following, we first briefly summarize the literature on the effects of attention on the N1. Then an overview of the studies suggesting that N1 might be a suitable tool to measure the recovery time from a distracted state is presented. Finally, we discuss these phenomena in the context of aging.

N1 is associated with the detection of change in auditory stimulation (Näätänen & Picton, 1987). Numerous studies found that N1 was enhanced when the eliciting auditory event was in the focus of attention or the attention set was optimal to perform the task (Hansen & Hillyard, 1980; Hillyard, Hink, Schwent & Picton, 1973; Lange, 2013; Okamoto, Stracke, Wolters, Schmael & Pantev, 2007). In contrast, attentional disruptions led to reduced N1 amplitudes (Horváth & Winkler, 2010; Horváth, 2014a, 2014b). The attentional enhancements might not only reflect a genuine N1 modulation, but also the emergence of other ERP components (Woods & Clayworth, 1987), like the negative difference (Nd: Hansen & Hillyard, 1980) or processing negativity (PN: Alho, Paavilainen, Reinikainen, Sams & Näätänen, 1986; Alho, 1992; Näätänen, 1982), which may overlap with the N1 (Näätänen, 1982; Woods & Clayworth, 1987). However, Nd and PN can be separated from the N1, because in contrast to the N1, they do not show a polarity inversion at the mastoids when the EEG is recorded with a nose reference (Alho et al., 1986). While the enhancement of N1 is considered to reflect enhanced auditory event and feature detection (Näätänen & Winkler, 1999), Nd and PN are regarded as correlates of voluntary, task-relevant processes, possibly indicating template-matching to the attentional trace (Alho, 1992; Näätänen, 1982), and related to sustained attention (Jemel, Oades, Oknina, Achenbach & Röpcke, 2003).

That the modulation of the N1 amplitude could be used to measure the recovery time from a distracted state is supported by several studies. First, Schröger (1996) found that when tone pairs were presented to participants, response accuracy to the second tone was reduced when it was preceded by a distracter in 200 ms (in comparison to those preceded by a distracter in 560 ms). The performance decrease was accompanied by a positive shift in the ERP at around 100 ms following the tone onset. Because the positive shift also followed the distracter by about 300 ms, it could not be, however, decided whether it reflected an attenuation of the target-related N1, or the distracter-related P3a. Studies using the continuous stimulation paradigm introduced by Horváth and Winkler (2010) showed that task-relevant auditory events indeed elicited lower amplitude N1s when shortly preceded by distracter events. In this paradigm, continuous tones are presented, which alternate between two pitches by rare, short glissandos (glides). The participants' task is to detect and respond to frequently occurring short silent periods (gaps) while ignoring the glides. It was found that a 150 ms glide-gap separation resulted in reduced gap-related N1s and lower gap detection rates in

comparison to gaps not preceded by other events in at least 1300 ms. In a later study using the continuous stimulation paradigm Horváth (2014a) found that the distraction effects (N1 amplitude and detection rate reductions) did not last longer than 650 ms. These results fit well into the literature of the auditory attentional blink (see for example, Shen & Mondor, 2006; Tremblay, Vachon & Jones, 2005). In most attentional blink paradigms, two target stimuli are embedded in a rapid tone-sequence, and detection of the second target is impacted when the separation of the targets is short (e.g. shorter than 270 ms: Horváth & Burgyán, 2011; 90-150 ms: Shen & Alain, 2010). Furthermore, Shen and Alain (2010) found that the second target elicited lower-amplitude N1 when it was immediately preceded by the first target, in comparison to the case when the targets were separated by six intervening tones.

N1 elicitation also differs between age groups. For N1s elicited by tone onsets, N1 amplitude was mostly found to be higher in older adults (Anderer, Semlitsch & Saletu, 1996; Amenedo & Diaz, 1998; Chao & Knight, 1997), or no age-related differences were observed (Getzman, Gajewski & Falkenstein, 2013; Horváth et al., 2009; Mager et al., 2005; Pfefferbaum, Ford, Roth & Koppel, 1980; Woods, 1992; but see also Berti, Grunwald & Schröger, 2013). In contrast, gaps in continuous tones seem to elicit lower amplitude N1s in older than in younger adults (Alain, McDonald, Ostroff & Schneider, 2004; Harris, Wilson, Eckert & Dubno, 2012).

Experimental data on the duration of the distracted state induced by rare auditory events, and its dependence on age is scarce. Slawinski and Goddard (2001) presented short sinusoidal tones in a rapid auditory stream, and participants had to identify the pitch (low, medium, high) of the tone with higher sound pressure than the others. When only the probe stimulus was presented with higher sound pressure, both groups completed the task adequately, although the younger adult group slightly outperformed older adults. When both probe and targets were salient, the performance of older adults was significantly reduced compared to the younger adult group in general, and older adults showed an impaired performance in time intervals from 90 to 450 ms. Both groups detected probes poorly from 90 to 360 ms, suggesting that recovery from distraction – reflected by behavioral indices – happens by about 360 ms in younger adults and slightly later in the older adults.

Based on the studies summarized above, the aim of the present study was to compare the duration of the distracted sensory state induced by task-irrelevant, rare stimuli between older and younger adults, as reflected by the modulation of the N1 ERP. We administered the continuous stimulation paradigm introduced by Horváth and Winkler (2010) with minor modifications. The participants' task was to listen to the continuous tone and press a button when a gap occurred, while ignoring glides. The presentation frequency of the glides (serving as task-irrelevant distracter events) was identical to the one used in the study by Horváth and Winkler (2010), that is, they could occur with 1/7 probability at every 1300 ms. Glides preceded potential gap-positions by 150, 250 or 650 ms. Gaps were presented with 50% probability every 1300 ms at one of these time-points. Gaps not preceded by any glides in at least 1450 ms (gap only trials) allowed the measurement of the maximal gap-related N1 amplitude. We hypothesized that shorter glide-gap separations would lead to stronger N1 amplitude reductions because the optimal attention set for detecting a gap could not be fully restored after distraction occurred. We also hypothesized that in older adults, the effects of distraction – manifested in lower N1 amplitudes – would persist longer.

7.2 Methods

7.2.1 Participants

52 healthy adult women participated in the experiment: 25 younger (age: from 19 to 26; mean: 22.2 years) and 27 older (age: from 62 to 75; mean: 67.5 years) adults. Because of excessive amount of eye movement artifacts (3 younger adults) or poor task performance (false alarm rates above 40% - further 1 younger, and 9 older adults, or detection rates for 150 and 250 ms gaps below 66% - resulting in low epoch numbers – another 5 younger and 2 older adults), only 32 participants remained in the final analyses. That is, our results are based on the behavioral and ERP data of 16 younger (age: from 19 to 26; mean: 22.6 years) and 16 older (age: from 62 to 74 years, mean: 67.3 years) persons. Participants were free of any neurological or psychiatric disease by their own admission. They were compensated by modest amounts of money for taking part in the experiment. The study was approved by the United Ethical Review Committee for Research in Psychology (Hungary), and all participants gave written informed consent.

All participants reported correct or corrected-to-normal vision. Only persons with hearing threshold differences not more than 20 dB between the two ears in the 250 - 2000 Hz range (as measured by a SA-6 audiometer, MEDIROLL, Debrecen, Hungary) participated in the experiment. Older adults had higher thresholds than younger adults at all frequencies (see Table 1). To compensate for threshold differences, the amplitude of the experimental sounds was individually adjusted to 50 dB above the 75% hearing threshold for the continuous tone used in the experiment (as described below), using the single interval adjustment matrix (SIAM) method (Kaernbach, 1990; Shepherd, Hautus, Stocks & Quek, 2011). The older adult group was characterized with significantly higher IQ score than the younger adult group (Welch's unequal variances t-test: $t[29.521] = 4.963$, $p < .001$) as assessed by the Hungarian version of the Wechsler Intelligence Scale (WAIS-IV; Wechsler, 2008) administered in a separate session. The total mean score was 130.8 (SD = 14.18) in the older adults and 107.3 (SD = 12.4) in the younger adults group, suggesting that both groups were characterized with intelligence higher than the average as shown by one-sample Student's t-tests (older adults: $t[15] = 8.673$, $p < .01$; younger adults: $t[15] = 2.344$, $p = .03$).

| Group | 250 Hz | 500 Hz | 1000 Hz | 2000 Hz |
|---------|--------------------------|--------------------------|--------------------------|--------------------------|
| Younger | 14.38 (± 4.16) | 8.91 (± 5.34) | 2.81 (± 4.91) | 3.59 (± 4.62) |
| Older | 25.78 (± 7.94) | 23.125 (± 10.75) | 14.69 (± 10.54) | 23.125 (± 12.94) |
| | $t = 7.195$, $p < .001$ | $t = 6.695$, $p < .001$ | $t = 5.776$, $p < .001$ | $t = 8.043$, $p < .001$ |

Table 7.1. Group-mean hearing thresholds (dB) and standard deviations in the younger and older adults groups.

7.2.2 Stimuli and procedure

Participants were sitting in a comfortable chair in a dimly lit, sound-attenuated room and listened to 4-minutes-long continuous tones through Sennheiser (HD-600, Sennheiser, Wedemark, Germany) headphones. The tones were generated with Csound version 5.17.11 (www.csounds.com), with a sampling rate of 44.1 kHz. The tones consisted of three harmonics: the fundamental and the second and third harmonics (the first harmonic was missing), with equal amplitude. The base frequency was either 220 Hz (low) or 277 Hz (high), and the pitch of the tone changed occasionally from high to low, or low to high with a 10 ms transition time (glide). Glides could occur in the 4

minutes-long continuous tone at discrete time points separated by 1300 ms steps, and they occurred randomly with 14.28% probability at each time point, with the constraint that successive glides were separated by at least 3900 ms. That is, in average, 27 glides were presented in a block. Beside glides, short gaps (10 ms long silent periods preceded by a 10 ms linear fall and followed by a 10 ms linear rise) were also inserted in the tone. Gaps could occur at time points following the potential glide-time points within 650 ms with 50% probability. 35.7% of such gaps followed the potential glide time point by 150 ms, 28.6% by 250 ms, and 35.7% by 650 ms. Gaps following actual glides within 650 ms, are referred to as *150 ms*, *250 ms* and *650 ms gaps* in the following. The rest of the gaps (i.e. those which were not preceded by a glide within 1450 ms) are termed “*gap only*” trials. The schematic illustration of the tones including glides and gaps is presented in Fig. 7.1.

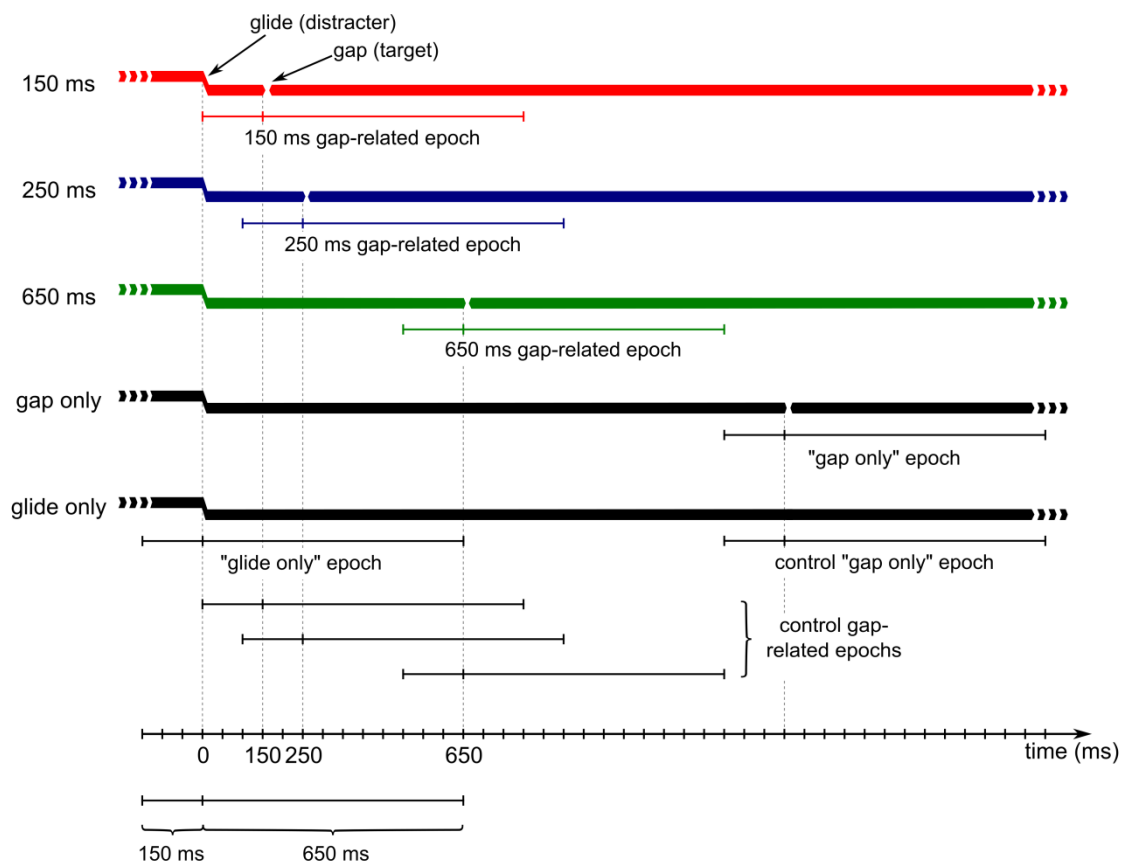


Fig. 7.1. The schematic design of the experimental tones reflecting glide-gap separation intervals and epoch types. The different colors represent the different glide-gap separations in the continuous tone.

Participants performed a gap detection task: they were instructed to press a button held in their dominant hand when they detected a gap, while ignoring the glides. The first block was a training block which allowed participants to get familiar with the task. After the training block, 15 experimental blocks were presented. Each block started with a black “START” text displayed on grey background. After 10 s, the “START” text changed to a black fixation cross and the tones started to play. At the end of each block, feedback about the gap detection rate (the ratio of correctly detected gaps to all presented gaps) and the mean reaction time was displayed on the screen. Between the blocks, short (1-2 min) pauses were available as needed, with a longer (5-10 min) break after the 7th experimental block.

7.2.3 EEG recording

The continuous EEG was recorded with a sampling rate of 500 Hz (with 100 Hz online lowpass filtering) with a Neuroscan Synamp 2 (Compumedics Inc., Victoria, Australia) amplifier with 61 Ag/AgCl electrodes mounted on an elastic cap (EASYCAP GmbH, Herrsching, Germany) arranged according to the 10% system (Nuwer, 1998). Two additional electrodes were placed at the mastoids. The reference electrode was placed on the tip of the nose and the ground electrode was attached on the forehead. Horizontal electro-oculogram was measured by electrodes attached near the outer canthi of the left and the right eye, and the vertical electro-oculogram was calculated offline as the difference of the signal between the Fp1 electrode and an additional electrode placed under the left eye. The continuous EEG data was filtered offline using a 30 Hz lowpass filter (Kaiser-windowed sinc finite impulse response filter, beta of 5.65, 907 coefficients; 2 Hz transition bandwidth, stopband attenuation at least 60 dB).

For an overview of the ERP epochs selected for the analyses, see Figure 7.2. For all the ERP analyses, glides and gaps with no keypresses in the preceding 300 ms were selected, as well as gaps following such glides in 150 ms, 250 ms or 650 ms. “*Gap only*” trials were also selected: these gaps were not preceded by a glide in at least 1450 ms or by another gap in at least 3400 ms, that is, no distracting events were present before them. To estimate the gap-related ERP activity without potentially overlapping glide-related ERP waveforms, timepoints were selected in which gaps could but did not occur (i. e. 150 ms, 250 ms and 650 ms after potential glide timepoints and after the

onset of glides which were not followed by any events in 650 ms), labeled as *control gaps*. 800 ms long epochs were extracted for each of these time-points including a 150 ms pre-timepoint baseline. Epochs with a signal range exceeding 150 μ V on any channel were discarded from further processing. Average ERPs calculated from the control epochs were subtracted from the corresponding gap-related (150 ms, 250 ms, 650 ms and gap only) average ERPs. The resulting waveforms are referred to as *corrected* waveforms in the following. The averaged ERPs, control gaps and the corrected waveforms are presented in Fig 7.2.

Glide-gap separation

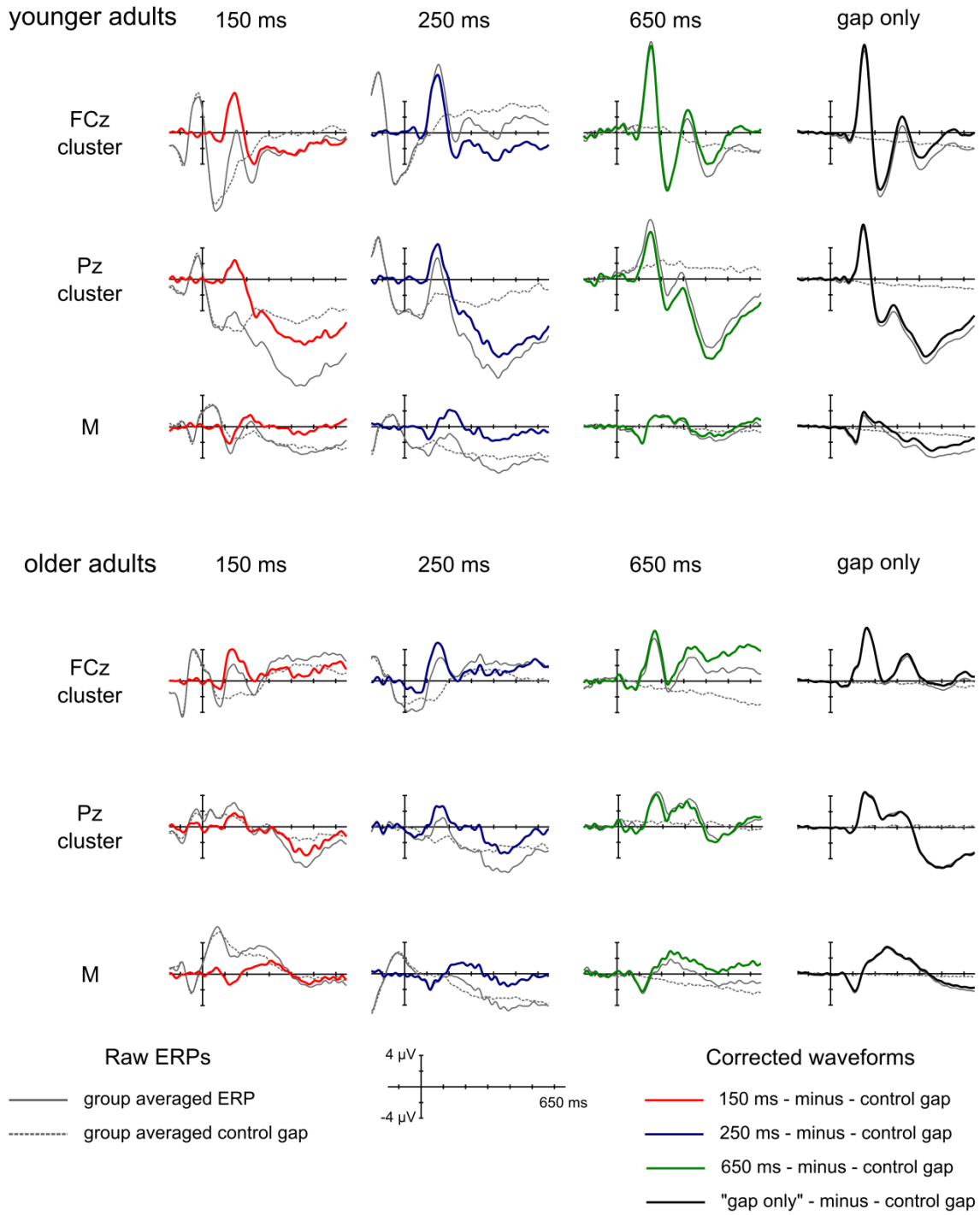


Fig. 7.2. The gap-related raw ERPs, the corresponding control ERPs and their difference (corrected waveforms) for each glide-gap separations.

7.2.4 Statistical analyses

Reaction times were analyzed only for detected gaps which were not preceded by any keypress in 300 ms, separately for each glide-gap separation (150 ms, 250 ms and 650 ms and gap only). Only responses which occurred between 120 ms and 1000 ms after the gap onset were included into analysis. Median reaction times were calculated for every participant, which were submitted to Group (younger adults / older adults) \times Gap Type (150 ms / 250 ms / 650 ms / gap only) ANOVA. Detection rates were submitted to an ANOVA of the same structure. The number of false alarms was also calculated by selecting glides with no preceding events in 300 ms which were followed by a keypress in 120 to 1000 ms. The ratio of these responses to all presented glides defined the false alarm rate which was compared between groups by Welch's t-tests.

Although our primary hypotheses were related to the modulation of N1 component, later waveforms (P2, N2, P3b) were elicited and modulated as well, therefore we included them into the analysis. Gap-related ERPs (N1, P2, N2, P3b) were identified in the group-average corrected waveforms for detected "gap only" trials. Individual N1, P2 and N2 amplitudes were measured as the average signal in a 20 ms long windows centered at the "gap only" peak latency in a fronto-central (FCz, Cz, Fz, FC1 and FC2) electrode cluster; P3b amplitudes were measured as the average signal in 100 ms long window centered at the "gap only" peak latency at a parietal cluster (Pz, POz, CPz, P1, P2) of electrodes to enhance signal-to-noise ratio. The "gap only" amplitudes were compared by Welch's t-tests between groups, then one-way ANOVAs were used to assess for different Gap Types (150 ms / 250 ms / 650 ms / gap only) separately for the two groups. Significant Gap Type effects were followed up by pairwise t-tests. To compare the glide-gap separation related modulation of the N1 amplitude between groups, the amplitudes were normalized by the gap-related N1 amplitudes measured in the corrected gap only waveforms for each group. These normalized amplitudes were submitted to Group (younger adults / older adults) \times Gap Type (150 ms / 250 ms / 650 ms) ANOVAs. Glide-related N1 and P2 amplitudes measured at the fronto-central cluster for glides which were not followed by any gaps in 650 ms (*glide only*) were compared between younger and older adults groups using Welch's t-test. All statistical tests were conducted by using R (version 3.1.0, R Core

Team, 2014). Generalized eta squared (η^2_G) effect sizes are also reported (Olejnik & Algina, 2003; Bakeman, 2005).

7.3 Results

7.3.1 Behavioral performance

Reaction times and gap detection rates are presented in Fig. 7.3. The Group \times Gap Type ANOVA of the reaction times showed a significant Gap Type main effect ($F[3, 90] = 16.45, p < .001, \eta^2_G = .07$), and a significant Group \times Gap Type interaction ($F[3, 90] = 4.83, p = .004, \eta^2_G = .022$). The Group main effect was not significant ($F[1, 30] = .002, p = .961, \eta^2_G < .001$). Analyzing the two groups separately, in older adults a Gap Type main effect was found: $F(3, 45) = 20.07, p < .001; \eta^2_G = .11$, which was followed up by pairwise t-tests. Responses were significantly slower with decreasing glide-gap separations (i.e. all but the 650 ms vs. gap only comparison showed significant differences: t-scores $> 3.238, p$ -values $< .01$). In contrast, no significant Gap Type effect was found in the younger adults group: $F(3, 45) = 2.67, p = .06, \eta^2_G = .04$.

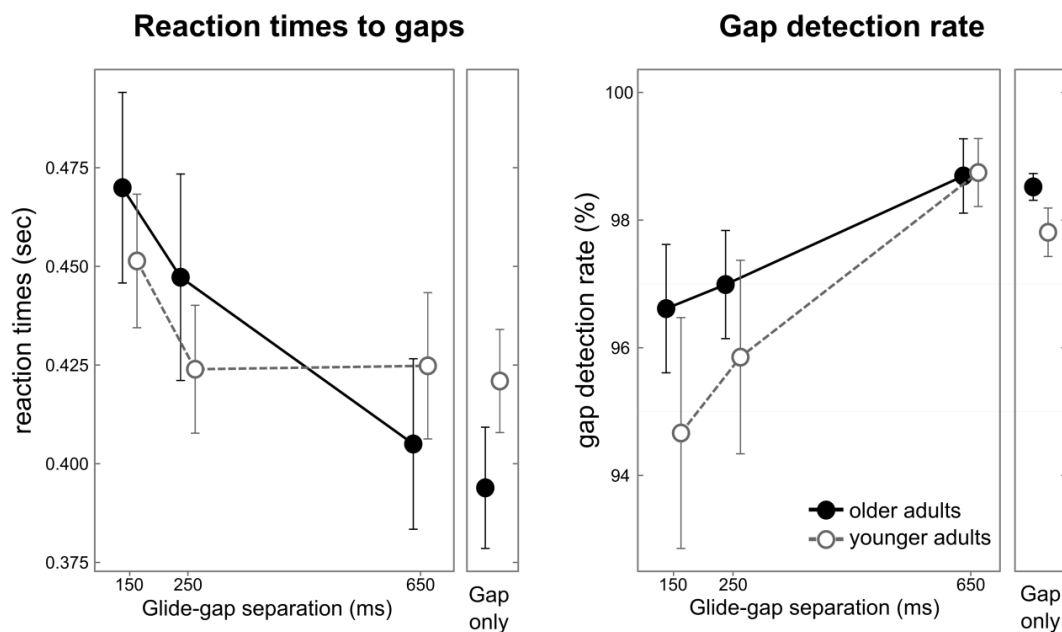


Fig. 7.3. Group mean reaction times (left) and gap-detection rates (right; both with standard errors of the means indicated by whiskers) in the younger and older adult group for the four types of gaps (150, 250, 650 ms glide-gap separation, and gap only trials).

The ANOVA of the gap detection rates (Fig. 7.3., right) showed a significant Gap Type main effect only: $F(3, 90) = 6.946, p < .001, \eta^2_G = .093$, indicating that participants in both age groups detected more gaps with increasing glide-gap separation. Neither the Group main effect ($F[1, 30] = .778, p = .385, \eta^2_G = .014$), nor the Group \times Gap Type interaction effects were significant ($F[3, 90] = .58, p = .63, \eta^2_G = .001$).

Participants could also inadvertently respond to glides as well, not only to gaps. To assess this, we selected glide only trials (no following gaps in 650 ms) and the ratio of keypresses to them in 120 to 1000 ms interval was calculated. The occurrence rate of such false alarms did not differ between the older and younger adults ($t[21.542] = .385, p = .703$): older adults responded in average to 11.72% of glides and younger adults in 12.74% (note that participants with higher than 40% false alarm rate were omitted from the original sample).

7.3.2 Event-related potentials

Individual ERPs were averaged separately for the two age groups and for the four gap types (gap only, 150 ms, 250 ms, 650 ms) on the corrected waveforms, as well as for glide only trials. The average number of epochs in the younger adults group was 50 (± 12) for 150 ms gaps, 41 (± 9) for 250 ms gaps, 51 (± 11) for 650 ms gaps, 604 (± 95) for gap only trials and 138 (± 20) for glide only trials. In the older adults group, the number of epochs was 58 (± 12) for 150 ms gaps, 44 (± 9) for 250 ms gaps, 55 (± 8) for 650 ms gaps, 666 (± 96) for gap only trials and 150 (± 20) for glide only trials.

On the corrected gap only waveforms, a negativity (N1) was peaking at 152 ms at FCz in the younger and at 160 ms at Cz electrode in the older adult group. However, the mastoid polarity inversion peaked earlier in both groups (114 ms in the younger and 110 ms in the older adults), suggesting that the fronto-central waveform included multiple components: a supra-temporal N1 and a PN (or Nd; Alho, 1986). Indeed, in the older adult group, two slightly overlapping peaks were elicited for short glide-gap separations. In the younger adults, these components might have completely overlapped, resulting in only a single observable peak. To investigate whether the supra-temporal N1 component was affected, an additional analysis was conducted in the time window of the earlier (mastoid) peak both at the fronto-central cluster and at the averaged mastoids. In the younger adults group, N1/PN was followed by a positivity

(P2) peaking at 218 ms at Cz lead but this component was absent in the older adults. Although a well identifiable P2 was not present in the older adult group, a positive peak was nonetheless observable at 230 ms at AF8 electrode in the group-average corrected gap only ERP, therefore, in the older adult group the P2 amplitude was characterized as the average signal in the 220-240 ms interval. P2 was followed by a negativity (N2), peaking for gap only trials at 326 ms at Fz in the younger adults and at 328 ms at C1 in the old adult group. The P3b waveform for gap only trials reached its maximum amplitude at Pz in both groups, with 428 ms latency in the younger adult group, and at 504 ms in the older adult group.

Glide only trials elicited a clear N1 in both groups, peaking at 130 ms at FCz in the younger, and at 106 ms at Fz in the older adults. The ERP amplitudes were compared between the two groups using Welch's t-test. In the younger adult group, N1 was followed by a P2 peaking at 206 ms at Cz. This component was less obvious in the older adult group (the maximum amplitude peak was at AF8 at 216 ms). The ERP results are plotted in Fig. 7.4 and the corresponding scalp topographies of the analyzed components are presented in Fig. 7.6 and Fig. 7.7.

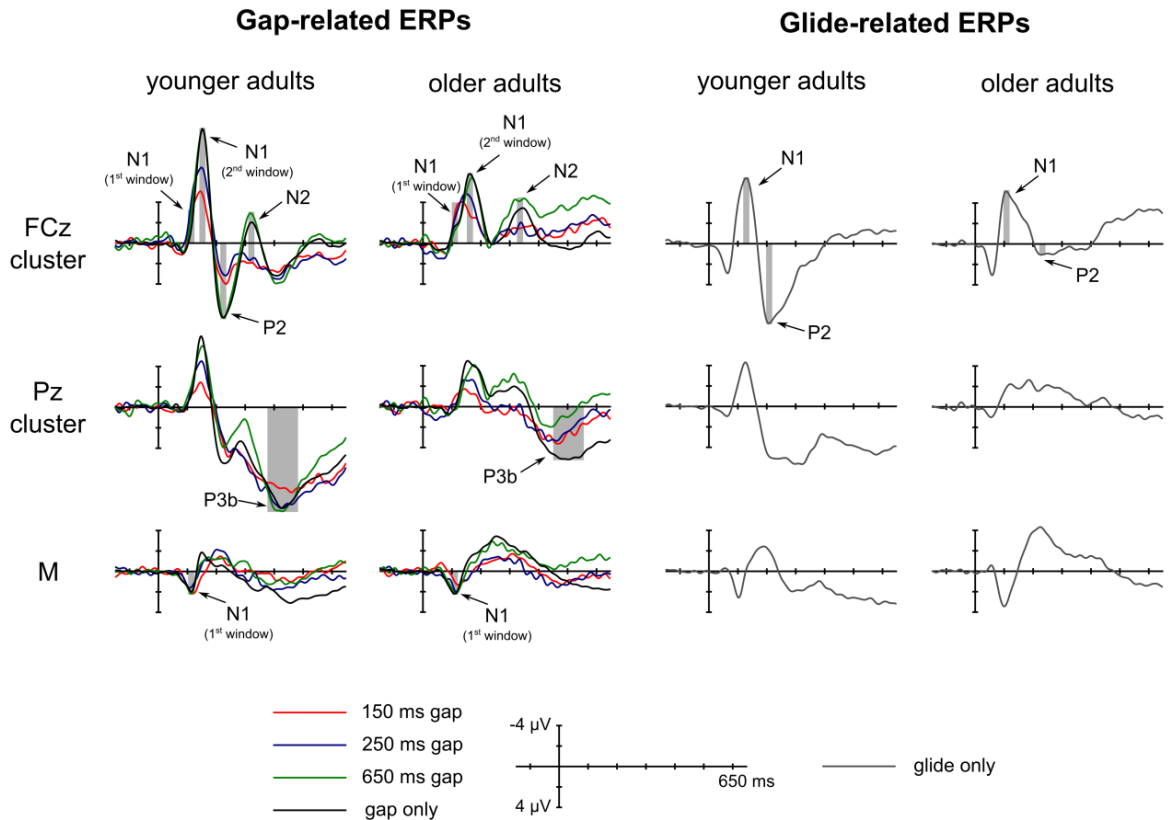


Fig. 7.4. The ERP results of the study. In the left side of the figure gap-related ERPs are presented plotted at the investigated clusters for younger and older adults separately. In the right side the control glide-related ERPs are shown. The grey bands index the time windows (20 ms for N1, P2 and N2 and 100 ms for P3b) where statistical analyses were assessed.

In the later N1 time window, younger adults exhibited significantly higher (more negative) amplitudes in the corrected gap only waveforms than older adults ($t[29.382] = -3.14, p = .004$). Therefore, we compared the amplitudes elicited by the four Gap Types, separately for the two age groups. Significant Gap Type main effects were present both in the younger ($F[3, 45] = 23.133, p < .001, \eta^2_G = .28$) and the older adult group ($F[3, 45] = 6.462, p < .001, \eta^2_G = .138$). The follow-up paired t-tests revealed that in the younger adults all four amplitudes differed from each other (all t values > 3.218 ; all p values $< .006$), except for the 650 ms gaps and gap only trials which were similar ($t[15] = .068, p = .947$). In the older adults, the 150 ms gaps amplitudes differed only from 650 ms ($t[15] = 2.739, p = .015$) and from gap only trials ($t[15] = 3.999, p = .001$); and the 250 ms gap amplitudes were also lower than amplitudes elicited by gap only trials ($t[15] = 2.459, p = .027$). For the normalized amplitudes, the Group \times Gap Type ANOVA showed only a significant Gap Type main effect ($F[2, 60] = 16.661, p < .001$,

$\eta^2_G = .163$), indicating that N1 amplitudes increased with increasing glide-gap separation (Fig. 7.5, left). Neither the main effect of Group ($F[1, 30] = .012$, $p = .914$, $\eta^2_G < .001$), nor the Group \times Gap Type interaction ($F[2, 60] = .335$, $p = .717$, $\eta^2_G = .004$) were significant, however. For normalized amplitudes, see Fig.7.3.

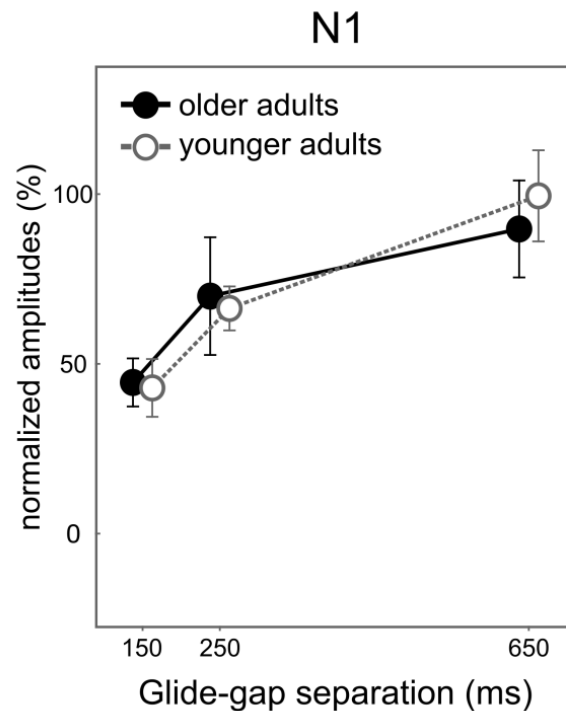


Fig. 7.5 ERP Group-mean normalized gap-related N1 amplitudes (with standard errors of the means indicated by whiskers) for of 150, 250 and 650 ms glide-gap separations measured at a fronto-central cluster (FCz, FC1, FC2, Fz, and Cz). The amplitudes were normalized by the corresponding group-mean ERP amplitudes for the corrected gap only trials.

In the earlier N1 time window (i.e. at the latency of the mastoid polarity inversion), amplitudes in the corrected gap only waveforms did not differ in the two groups at the fronto-central electrodes ($t[29.376] = .267$, $p = .792$). The Group \times Gap Type ANOVA for normalized amplitudes showed no significant effects (Group main effect: $F[1, 30] = 1.392$, $p = .247$, $\eta^2_G = .03$; Gap Type main effect: $F[2, 60] = 3.131$, $p = .051$, $\eta^2_G = .034$; Group \times Gap Type interaction: $F[2, 60] = 1.83$, $p = .169$, $\eta^2_G = .02$). No significant amplitude differences were found at the mastoids either (between-group amplitude differences in the corrected gap only waveforms: $t[29.976] = .748$, $p = .46$; for the Group \times Gap Type ANOVA for normalized amplitudes: Group main effect: $F[1, 30] = 1.863$, $p = .182$, $\eta^2_G = .026$; Gap Type main effect: $F[2, 60] = 1.136$, $p = .328$, $\eta^2_G = .021$; Group \times Gap Type interaction: $F[2, 60] = 1.806$, $p = .173$, $\eta^2_G = .033$).

Topographical distributions of gap- and glide-related N1 and P2

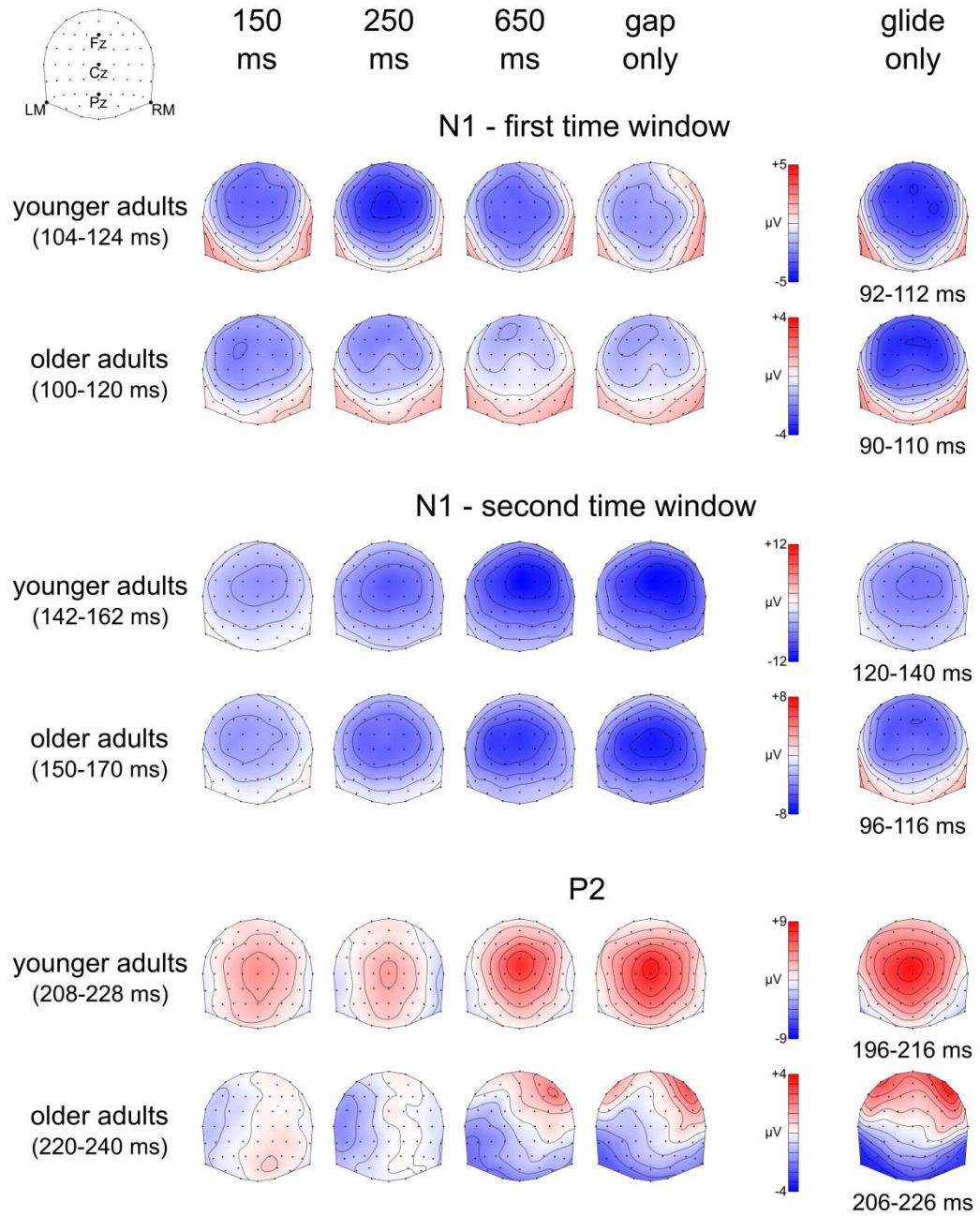


Fig. 7.6. Topographies of the group-mean gap- and the glide-related ERPs in the N1 (top and middle rows, measured at mastoid and at fronto-central peaks) and P2 (bottom) intervals in the younger and older adult groups. The amplitude scales differ between groups in order to adequately represent the shapes of topographies while showing the amplitude differences for each gap type within each group.

Topographical distributions of gap-related N2 and P3b

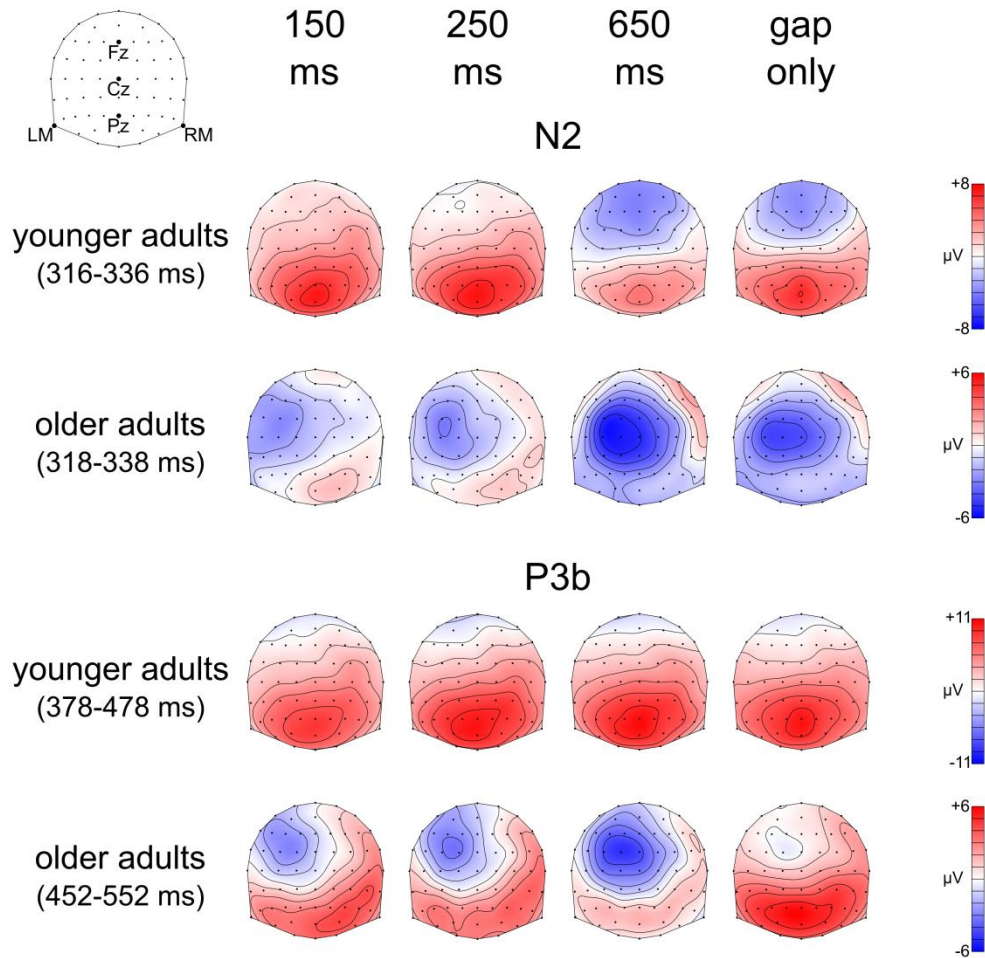


Fig. 7.7. Topographies of the group-mean later gap-related components. N2 is presented in top and P3b is presented in bottom row. The amplitude scales are set to reflect the amplitude differences within each group.

Because the gap-related P2 waveform was not readily observable in older adults (see Fig.7.6), we analyzed the amplitudes without normalizing the data in Group (younger adults / older adults) \times Gap Type (150 ms / 250 ms / 650 ms / gap only) ANOVA. Not only the main effects of Group ($F[1, 30] = 15.922, p < .001, \eta^2_G = .259$) and Gap Type ($F[3, 90] = 4.464, p = .006, \eta^2_G = .048$) were significant, but the Group \times Gap Type interaction as well: $F(3, 90) = 4.253, p = .007, \eta^2_G = .046$. Analyzing the two groups separately, while Gap Type did not affect the amplitudes in the P2 time window in the older adults ($F[3, 45] = .079, p = .97, \eta^2_G = .002$), younger adults exhibited significantly lower amplitudes as glide-gap separation interval decreased ($F[3, 45] = 8.66, p < .001, \eta^2_G = .161$). Following-up the main effect in the younger adult group,

paired t-tests revealed that the amplitudes of 150 ms gaps were significantly lower than 650 ms gaps ($t[15] = -3.041, p = .008$) and gap only trials ($t[15] = -3.096, p = .007$). The amplitudes of 250 ms gaps also differed from 650 ms gaps ($t[15] = -3.346, p = .004$) and from gap only amplitudes ($t[15] = -3.539, p = .003$).

Because of the obvious overlap between the N2 and P3b waveforms (Fig. 7.4 and Fig. 7.7), corrected amplitudes in the N2 time-range were submitted without normalization to a Group (younger / older adults) \times Gap Type (150 ms / 250 ms / 650 ms / gap only) ANOVA. The ANOVA revealed neither a significant Group main effect ($F[1, 30] = 2.326, p = .138, \eta^2_G = .051$), nor a Group \times Gap Type interaction ($F[3, 90] = .838, p = .477, \eta^2_G = .009$). Only a significant Gap Position main effect was found: $F(3, 90) = 9.69, p < .001, \eta^2_G = .09$, showing that glide-gap separation intervals had similar effect on N2 amplitudes in both groups.

The P3b in gap only trials was elicited with significantly higher amplitudes in the younger adult group than in the older adult one ($t[29.211] = 2.615, p = .013$). Analyzing the groups separately, the corrected amplitudes did not differ from each other in the younger adult group ($F[3, 45] = .626, p = .602, \eta^2_G = .014$), whereas in the older adults, the Gap Type main effect was significant: $F(3, 45) = 6.251, p = .001, \eta^2_G = .084$. The amplitude of gap only trials was higher than any other gap types (150 ms gaps: $t[15] = -3.045, p = .008$; 250 ms gaps: $t[15] = -2.344, p = .033$; 650 ms gaps: $t[15] = -4.402, p < .001$) and the difference between 150 ms gaps and 650 ms gaps was also significant ($t[15] = 2.132, p = .05$). Glide-related N1 and P2 amplitudes were compared between older and younger adult groups by Welch's t-test on the same fronto-central cluster as in case of gap-related ERPs. For the N1 no significant difference was found ($t[28.536] = 1.302, p = .203$), however, P2 amplitude was significantly higher in the younger than in the older adult group ($t[29.882] = -4.224, p < .001$).

7.4 Discussion

The goal of the present study was to measure how fast younger and older adults restored task-optimal attention set after distraction occurred. To characterize the duration of the distracted state, N1 amplitudes elicited by gaps were measured in a gap detection task in which the temporal separation between distracters (glides) and targets (gaps) was manipulated. In younger adults, gaps elicited a series of N1, P2, N2 and P3b

waveforms; in older adults, however, P2 was absent. N2 and P3b overlapped partially. Gaps elicited smaller N1s in older than in younger adults; the magnitude of N1 reduction with decreasing glide-gap separation was, however, similar in the two groups. The lack of polarity inversion at the mastoids in the time window of the negative fronto-central N1 peak suggests that the amplitude reduction was not caused by the modulation of the auditory N1 subcomponent, rather, that it was caused by the absence of an additional negativity, presumably a PN reflecting the matching of the auditory event to a task-relevant sensory template. With shorter glide-gap separations accuracy decreased. Whereas older adults responded systematically slower as glide-gap separations got shorter, glide-gap separation did not significantly influence reaction times in younger adults. The distracter glides elicited similar N1s in both groups, but P2 was more pronounced in younger adults.

The lower gap-related N1 amplitudes in the older than in younger adults, are in line with previous studies (Alain et al., 2004; Harris et al., 2012); and the modulation of N1 amplitudes also fits, and extends the literature. The decreased N1 amplitudes at 150 and 250 ms glide-gap separation suggest that the distracted state persisted for at least 250 ms, while the lack of difference between the N1s elicited in the gap only and the 650 ms glide-gap separation trials suggest that attention was restored by 650 ms after distraction occurred. These results are on a par with the results by Schröger (1996), Horváth (2014a) and Horváth and Winkler (2010). The topographical distribution of the N1-effect (no polarity inversion at the mastoids) and its latency (i.e. peaking later than the positive N1 aspect at the mastoids) also support the notion (Horváth, 2014a) that the modulation of the N1 waveform might be not a “genuine” modulation of the auditory N1 subcomponent, but the modulation of the overlapping processing negativity which is characteristically elicited by task-relevant auditory events (Näätänen, 1982).

In contrast to the N1 which was present in both groups, a readily observable P2 was elicited only in the younger adults. In the young adults, however, it was characterized with similar pattern as the N1 modulatory effect: as glide-gap separation decreased, P2 amplitude also became lower. The functional role of P2 waveform is poorly understood. Recent studies show that N1 and P2 are rather independent components (Crowley & Colrain, 2004) and P2 might index processes related to detection threshold mechanisms and stimulus evaluation (Ceponiene, Alku, Westernfield, Torki & Townsend, 2005). The P2 attenuation pattern in younger adults

indicates that the distracting effect of glides also affected stimulus evaluation processes since attention was still captured by glides as demonstrated by Horváth and Winkler (2010) as well: in their study, P2 was attenuated to 150 ms glide-gap separation compared to the gaps presented alone. In the present study, the absence of P2 in the older adults might be explained with the superimposition of earlier negative ERPs, especially the PN: PN might overlap the P2 time interval and cancel that component as suggested by Crowley and Colrain (2004). Also, because Harris and colleagues (2012) found reduced P2 amplitudes to gaps in older adults, the age-related changes in gap detection processes also could lead to this effect.

The pattern of later ERP waveforms supports the interpretation of the N1/PN modulation presented above. When glides and gaps were presented with a longer separation (650 ms and gap only trials), an N2 was elicited. For 150 ms and 250 ms gaps this component was entirely absent in both groups. Since N2 is thought to reflect categorization and decision mechanisms (Folstein & Van Petten, 2008; Patel & Azzam, 2005; Ritter, Simson, Vaughan & Macht, 1982), these results suggest that the disruption of the attentional template also affected these later, endogenous processes, irrespectively of age. The subsequent P3b waveform indexing target detection (Polich, 1997) was also modulated by the presence of distracters: both groups demonstrated amplitude decrease with decreasing glide-gap intervals. One could interpret this effect as disturbance in target identification, however, it is important to note that the N2 at least partly overlaps P3b in the frontal areas. This overlap might modulate P3b amplitudes which might be not identical in different conditions. Moreover, some studies revealed that in tasks requiring sustained attention, a further processing of attended stimuli might be present (Näätänen & Michie, 1979), especially in the older adults, also leading to P3 modulation (Karayanidis, Andrews, Ward & Michie, 1995). The present study does not allow the separation of these contributions, therefore the results on N2 and P3b should be interpreted cautiously.

In order to discuss the effects of attention on gap-related ERPs, it is important to take into consideration glide-related ERPs well. Glides elicited an N1 and a P2 in both groups but N2 and P3b were not present. The N1 and P2 pattern was similar to those observable on gap-related ERPs: while N1 was pronounced in both groups, older adults demonstrated only moderate P2. The latter could be explained with age-related P2

differences in gap processing (Harris et al., 2012) or the partial superimposition with the previous negativity (Crowley & Colrain, 2004).

The behavioral results are in line both with the electrophysiological results and with the literature. The accuracy scores in younger and older participants were affected by different glide-gap separations similarly: both groups detected gaps less accurately when glides preceded them in short time intervals, reflecting the presence of a distraction effect in general (Berti, Grunwald & Schröger, 2013). Lower target detection rates for brief distracter-target separations were also demonstrated in discrete (Horváth & Burgyán, 2011; Schröger, 1996) and in continuous stimulation protocols (Horváth, 2014a; Horváth & Winkler, 2010). Our results regarding the lack of group differences in target detection rate with the change of distraction-target separation interval is at odds with the results of Slawinski and Goddard (2001), who found that while both age groups detected targets following attention capture by 360 ms poorly, the performance of older adults was still impaired at 450 ms. An explanation to the difference between the two studies might be that while Slawinski and Goddard (2001) utilized discrete sinusoidal tone pips in rapid presentation, we presented continuous complex tones which led to lower task difficulty and better performance even at cognitively demanding conditions. It is also important to note that the exclusion of participants with insufficient numbers of responses to gaps could bias gap detection rate results.

Reaction time data differentiated groups more strongly than gap detection rates. Older participants slowed gradually as glides and gaps got closer to each other. In contrast, younger adults could keep their response speed steady between the different glide-gap separations. That is, as task difficulty increased, older adults needed to invest more effort into the task while younger adults could maintain their performance, in other words, older adults had to compensate with enhanced attention (Reuter-Lorenz & Cappell, 2008; Zanto & Gazzaley, 2014). Albeit for the first sight it seems that older adults are more susceptible for distraction, taken accuracy data into consideration, this response pattern might suggest differences not only in cognitive abilities but in task performance strategies as well. On one hand, a trade-off mechanism might be present in older adults favoring high accuracy over speed (Leiva, Andrés & Parmentier, 2015). It was demonstrated that older adults tended to be more cautious than younger adults even when they were instructed to respond as fast as possible, which is also related to age-related structural changes in brain connectivity (Forstmann et al., 2011). On the other

hand, motivational and detection threshold factors could also lead to reaction time differences: while older adults seemed to be motivated to achieve high performance and demonstrated enhanced attention during the whole experiment, younger adults might have not put much effort in responding quickly while they could keep accuracy high (Horváth et al., 2009; Iragui et al., 1993; Leiva, Andrés & Parmentier, 2015). In summary, the present study demonstrated that older adults did not need more time to recover from the sensory effects of distraction than younger adults. This was reflected in the similar modulation of the N1 (presumably mainly the processing negativity) as the glide-gap separation interval shortened which was not influenced by age: from gaps without preceding glides to 150 ms glide-gap separation both groups showed gradual amplitude attenuation. The modulation of N2 and P3b indicated that the disruption of attentional trace caused by glides affected later processes as well, like stimulus categorization and target detection. The behavioral results showed that while both groups kept gap detection accuracy high, older adults slowed down as glide-gap separation decreased in contrast to younger adults whose reaction times were not affected. Taken together, our results suggest that although the distracted state does not last longer in the older than in the younger adults, older subjects were nonetheless more affected by distracters in consecutive processing levels as reflected by reaction times.

7.5 Acknowledgements

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Chapter 8: Age-related processing delay reveals cause of apparent sensory excitability following auditory stimulation¹⁰

8.1 Introduction

When absorbed in a task, task-irrelevant stimuli seem to fade into the background. Moments of such immersion still do not provide a complete isolation from the stimulus environment: sudden changes in the acoustic background still capture our attention, even if they are irrelevant to the ongoing behavior. By “opening up” the sensory system, such involuntary re-allocations of attention (*distraction*) (Escera et al., 1998) allow the acquisition of information that may initiate the re-evaluation of behavioral goal priorities, and thus lead to a change or discontinuation of the ongoing behavior. The sound of an approaching vehicle on the street may compel us to look up from a smartphone screen and take evasive action. Finding proper balance between the ability to focus on one’s immediate behavioral goals, and the ability to be distracted by potentially goal-changing sensory information is crucial for successful adaptation. Older adults are often characterized as being less able to inhibit the processing of task-irrelevant information and therefore more susceptible to distraction than younger adults (Alain & Woods, 1999; Berti, Grunwald & Schröger, 2013; Getzman, Gajewski & Falkenstein, 2013; Healey, Campbell & Hasher, 2008; Woods, 1992). This may be interpreted as a shift in the attention-distraction balance. Distraction, however, is not a unitary phenomenon (Horváth, Winkler & Bendixen, 2008; Schröger & Wolff, 1998a), and impacted performance attributed to higher distractibility may result from changes in various functions contributing to the attention-distraction balance. For example, a lower sensory threshold (Schröger, 1997) that allows intrusions of stimuli with low potential to be behaviorally relevant (a more “open” sensory state) may impact overall performance because distraction-reorienting cycles occur too often. Decreased performance may, however, also result from increased processing times: in older adults more time may be needed for the completion for an involuntary attention switch, whereas re-orienting may take longer in children (Horváth et al., 2009). The goal of the

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present study was to compare the persistence of a more “open” (distracted) sensory state induced by background auditory changes in younger and older adults. The duration of distracted state was measured by probing the capability to process auditory events (as reflected by auditory event-related potentials – ERPs) at several time points after distracter onset.

Rapid changes in auditory stimulation (e.g. sound onsets, pitch changes, or gaps in continuous sounds, referred to as *auditory events* in the following) elicit a sequence of characteristic ERP waveforms, which reflect various stages of auditory information processing (Hillyard et al., 1973; Näätänen & Winkler, 1999). The late part of the auditory ERP, specifically the N1 and P2 waveforms can be utilized to probe the processing capability of the auditory system at a given moment. N1 peaks fronto-centrally at around 100 ms, while P2 exhibits a central peak typically in the 160-200 ms range following the auditory event. Although initially these waveforms were regarded as a unitary phenomenon (the “vertex potential”; Harris, Mills He & Dubno, 2008; Näätänen & Picton, 1987), later studies demonstrated their independence (for a review, see Crowley and Colrain, 2004). Both waveforms are generated (at least in part) in the auditory areas of the temporal cortex (Liegeois-Chauvel, Musolino, Badier, Marquis & Chauvel, 1994; Lütkenhöner & Steinsträter, 1998; Vaughan & Ritter, 1970), and reflect the physical parameters of the stimulation. Whereas there is a consensus on that N1 reflects auditory change detection (Näätänen, 1982; Näätänen & Picton, 1987), the functional role of P2 is poorly understood, with suggestions including stimulus evaluation mechanisms (Crowley & Colrain, 2004), generators related to conscious perception thresholds (Ceponiene et al., 2005) or perceptual learning (Seppänen, Hämäläinen, Pesonen & Tervaniemi, 2012; Tremblay, Ross, Inoue, McClannahan & Collet, 2014).

Importantly, N1 (and possibly P2) amplitude also reflects the readiness of the auditory system to process incoming stimulation. It is well-known, for example, that attentional state influences N1 amplitude: N1 is enhanced when it is elicited by events in the focus of attention (De Chiccis, Carpenter, Cranford & Hymel, 2002; Hillyard et al., 1973; Kauramäki, Jääskeläinen & Sams, 2007; Lange, 2013; Woldorff & Hillyard, 1991), whereas it is attenuated when elicited by events presented during a period of distraction (Horváth, 2014a; Horváth & Winkler, 2010). In the present study, we exploited this to assess the duration of a distracted state by measuring the amplitudes of

N1s elicited by probe-events following distracters at several time points. Although a number of ERPs may overlap P2, several studies found enhanced P2 amplitudes in case when tones were attended actively compared to passive listening conditions (Horváth & Winkler, 2010; Woods, Alho & Algazi, 1992, 1993; but see Hillyard et al., 1973).

The most efficient auditory distracters are rare, unpredictably occurring, or salient events (Berti, 2013; Cherry, 1953; Näätänen, 1990; Schröger, 1997). Such sound events typically elicit enhanced N1s, mismatch negativity (MMN), and P3a. Whereas the negativities reflect auditory change detection processes (Näätänen, 1982; Näätänen & Winkler, 1999), P3a is generally interpreted as a reflection of attentional orienting towards the stimulus (Polich, 2007). To investigate the duration of a distracted state, we adapted the passive version of the continuous stimulation paradigm introduced by Horváth and Winkler (2010). In their paradigm, a continuous tone was presented, which alternated between two pitch levels by occasional, randomly timed, quick glissandos (glides). Short silent periods (gaps) were also randomly inserted into the tone. Whereas gaps occurred frequently (on average once every 2.6 s), glides were rare (on average once every 9.75 s). In the *active* version of the paradigm, participants' task was to respond to gaps by pressing a button. Due to their infrequency and unpredictability, the glides functioned as distracters in these paradigms: Horváth (2014a), Volosin, Grimm, and Horváth (2016) found that rare glides elicited a higher N1 than frequent glides (and possibly an MMN), but no P3a. Importantly, gaps following rare glides in 150 ms elicited lower-amplitude N1s in comparison to gaps following glides by 650 ms (see also Schröger, 1996), or in comparison to gaps without closely preceding glides (Horváth & Winkler, 2010). This impacted auditory processing suggests that 150 ms after the distracter onset the task-optimal attention set for gap-detection was not yet reinstated. Although evidence on duration of allocation of attention in auditory modality is scarce, this is in line with studies suggesting that attention switch occurs between the time range of N1 and P3, starting at about 130 ms and lasting until about 300 ms (Gamble & Luck, 2011; Gamble & Woldorff, 2015).

When the same stimulation was administered to participants who watched a self-selected movie and ignored the tone (*passive* version), gap-related N1 amplitudes showed the opposite pattern: gaps following glides in 150 ms elicited enhanced N1s in comparison to gaps not closely preceded by other events, that is, 150 ms after a glide, auditory processing was enhanced. Horváth and Winkler (2010) suggested that the

enhancement reflected attention capture by the rare glide, which diverted attention from the movie to the auditory stimulation. Whether the enhancement was caused by attentional orienting, or by other mechanisms, is unclear. Similar N1 differences were also reported when identical tones followed each other in short (< 400 ms) time compared to those at longer separations (Budd & Michie, 1994; Loveless, Hari, Hämäläinen & Tiihonen, 1989; McEvoy, Levänen & Loveless, 1997; Todd, Michie, Budd, Rock & Jablensky 2000; Sable, Low, Maclin, Fabiani & Gratton, 2004; Wang, Mouraux, Liang & Iannetti, 2008): tones following in shorter (than 400 ms) intervals elicited higher N1s than those following with larger separations. These results can be interpreted by assuming a short-term facilitatory effect following tone onset (Budd & Michie, 1994), or a more complex interaction of facilitation and inhibition. According to the *latent inhibition* model (McEvoy, Levänen & Loveless, 1997; Sable et al., 2004), tone onsets cause a general facilitation in the auditory cortex, which also spreads to neural structures inhibiting N1-generation. Due to their temporally different unfolding, facilitation dominates till about 400 ms, after which inhibition becomes dominant.

Aging is associated with higher susceptibility to distraction, manifested as a decreased ability to filter sensory input (Fabiani et al., 2006; Lustig, Hasher & Zacks, 2007) and to inhibit the processing of task-irrelevant pieces of information (Andrés, Guerrini, Phillips & Perfect, 2008; Healey, Campbell & Hasher, 2008; Stothart & Kazanina, 2016; Zanto & Gazzaley, 2014). Age-related sensory ERP enhancements are also often attributed to decreased inhibition of incoming stimulation (e.g. Chao and Knight, 1997) which result for example in enhanced slowing in reaction times to distracters (Berti, Grunwald & Schröger, 2013; Woods, 1992). In the present context, we hypothesized that an increased distractibility, or a decreased ability to inhibit the processing of task-irrelevant, background auditory events would be manifested in a longer-lasting enhanced responsiveness to probe events following a distracter. Accordingly, the enhancement of N1 (and possibly P2) would be observable for longer glide-gap separations in older than in younger adults.

To test this hypothesis, in the present study, glide-gap separation was varied in the continuous stimulation paradigm: rare glides could precede gaps in 150, 250 or 650 ms, but gaps without closely preceding glides (“gap only” events), and glides without closely following gaps (“glide only” events) also occurred. By subtracting the “glide only” ERPs from “glide-and-gap” ERPs, the gap-related ERP could be assessed

separately from the preceding glide-related waveform. “Gap only” ERPs served as a baseline for assessing ERP enhancements. In contrast with previous studies which used a procedure relying on the assumption that the range of the between-stimulus jitter was sufficiently large to allow the estimation and subtraction of the ERPs related to the preceding tone (Woldorff, 1993), the present paradigm allowed a simple subtraction of ERPs related to the preceding rare glide. In assessing ERP enhancements, one has to take into account that ERPs may be different between groups per se. Indeed, numerous studies show that in older adults, late auditory ERPs elicited by sound onsets tend to be larger (Amenedo & Díaz, 1998; Anderer, Semlitsch & Saletu, 1996; Ford & Pfefferbaum, 1991) than in younger adults, while gap-related ERPs were found to be smaller in older adults (Alain et al., 2004; Harris et al, 2012). Because of this, ERP enhancements were expressed as amplitude proportions of the respective gap-only ERPs separately in the two age groups.

8.2 Methods

8.2.1 Participants

50 healthy adult women participated in the study, 25 persons in the younger and 25 in the older adult group. Younger adults were recruited by a student part-time job agency; older adults were recruited from the department’s participant database. All of them were compensated by modest amounts of money. Due to excessive amounts of movement artifacts, only the data from 46 participants was used for further analyses. The final sample consisted of 23 younger (3 left-handed) and 23 older (all right handed) adults. The average age was 22.13 years ($SD = 2.01$; from 18 to 26 years) in the younger and 68 years ($SD = 3.71$; from 62 to 76 years) in the older adult group. Participants gave written informed consent. The experiment was conducted in accordance with the Declaration of Helsinki and the protocol was approved by the United Ethical Review Committee for Research in Psychology (Hungary).

All participants reported correct or corrected-to-normal vision and normal hearing. Older adults had higher hearing thresholds than younger adults in the 250-2000 Hz frequency range (as assessed by an SA-6 audiometer, MEDIROLL, Debrecen, Hungary, see Table 1). The threshold difference between the two ears was not higher than 25 dB at any of the frequencies. In order to compensate for potential hearing

differences between participants, the intensity of the sounds presented in the experiment was individually adjusted to 50 dB above the 75% hearing threshold measured by the Single Interval Adjustment Matrix procedure (Kaernbach, 1990); see also Shepherd et al. (2011).

The Hungarian version of Wechsler Intelligence Scale (WAIS-IV; Wechsler, 2008) was administered in a separate session to exclude dementia-related differences between the two age-groups. The mean IQ scores were 119.78 (SD = 18.07; from 85 to 156) in the older, and 106.13 (SD = 18.05; from 81 to 150) in the younger adult group, showing a significant difference ($t[44] = 2.564$, $p = .014$). Moreover, while the IQ scores of younger adults was average ($t[22] = 1.629$, $p = .118$), older adults were characterized with significantly higher IQ than the population average ($t[22] = 5.252$, $p < .001$).

| Group | 250 Hz | 500 Hz | 1000 Hz | 2000 Hz |
|----------------|-------------------------|-------------------------|-------------------------|-------------------------|
| Younger | 13.37 (± 4.6) | 10.11 (± 6.45) | 3.04 (± 5.22) | 4.45 (± 6.69) |
| Older | 19.89 (± 7.99) | 17.93 (± 7.57) | 12.5 (± 8.34) | 20.97 (± 12.96) |
| | $t = 4.80$, $p < .001$ | $t = 5.34$, $p < .001$ | $t = 6.51$, $p < .001$ | $t = 7.78$, $p < .001$ |

Table 8.1. Group mean hearing thresholds (dB SPL) and the corresponding standard deviations in the two groups in the 250-2000 Hz range.

8.2.2 Stimuli and procedure

During the experiment, participants were sitting in an armchair in an electrically shielded and acoustically isolated room, and watched a self-selected movie with subtitles (but without sound) while continuous, 331 s long tones were presented through Sennheiser (HD-600, Sennheiser, Wedemark, Germany) headphones. Participants were instructed to watch the movie and ignore auditory stimuli. The tones were generated using Csound (version 5.17.11, www.csounds.com), with a sampling rate of 44.1 kHz and consisted of three harmonics: the fundamental, second and third harmonics (the first one was missing). Each harmonic was presented with the same amplitude. The tone was alternating between two pitches (characterized by 220 Hz and 277 Hz base frequencies) by quick, 10 ms long glides (*glissandos*). Such glides could occur at fixed timepoints separated by 1300 ms. Glides could occur at these timepoints with a 1/7 probability, with the constraint that consecutive glides had to be separated by at least 3900 ms.

Thus, on average, 36 glides occurred in each continuous tone (i.e. in each recording block). The tones also contained short gaps with a 10 ms silent period and 10-10 ms linear fall and rise times. Such gaps were randomly inserted with a probability of 50% after timepoints at which glides could occur. When a gap was inserted, it followed the potential glide timepoint by 150, 250 or 650 ms (with equal probability). In the following, we refer to gaps following an actual glide in 150, 250, or 650 ms as “150 ms gap”, “250 ms gap”, and “650 ms gap” events (the design is shown in Figure 8.5). Gaps not following a glide within 650 ms (i.e. gaps for which no glide occurred at the preceding timepoint) are referred to as “gap only” events. Glides which were not followed by any gaps in 650 ms, referred as “glide only” events. 14 tones (i.e. blocks) were presented during the experiment, which were separated by short breaks as needed. After the 7th block, a longer break could be taken depending on the participants’ preference.

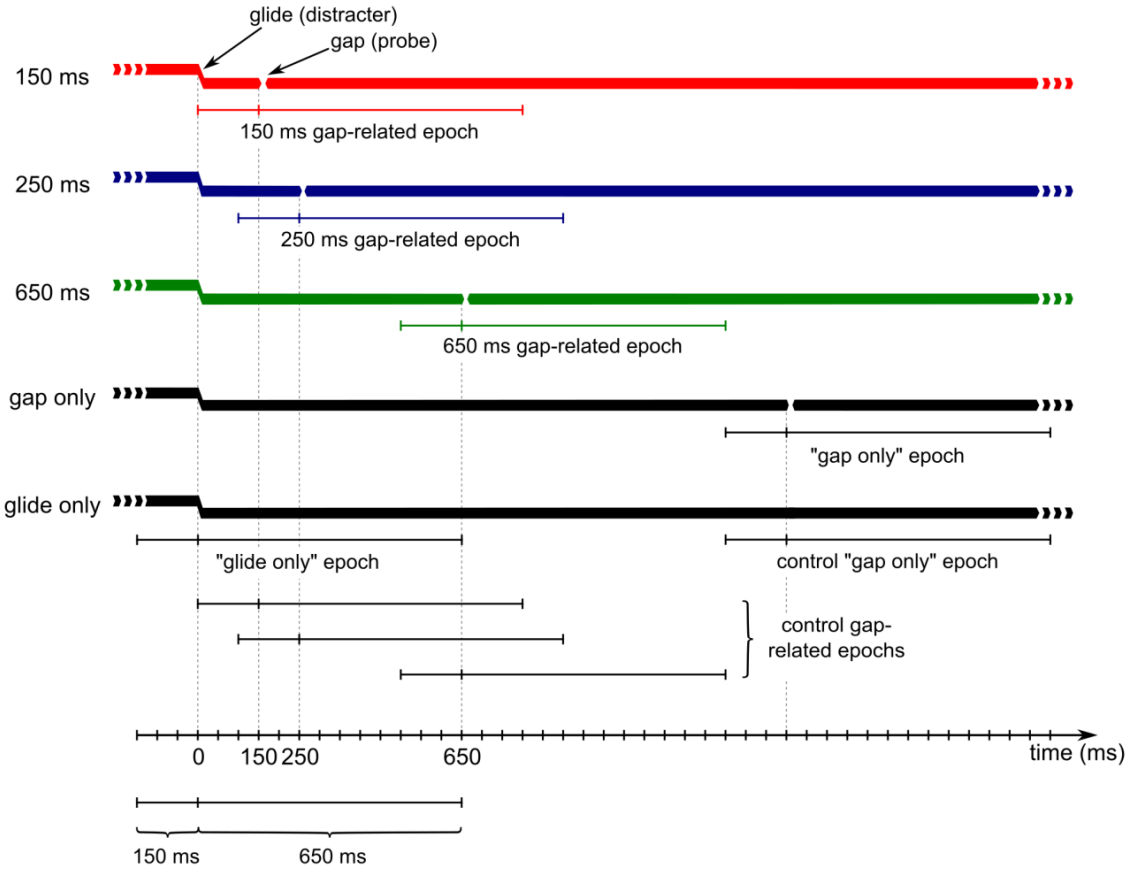


Fig. 8.5 The schematic design of the study. Thick lines represent continuous tones, with vertical displacements indicating glides. Glide- and gap-related (150 ms, 250 ms, 650 ms and “gap only”) epochs and the corresponding control epochs are indicated below the tones by intervals markings.

Before the experiment, 2-3 minutes long EEG-recording was also taken to capture eye-movement-related EEG-activity (with instructions as described by Schlögl et al., 2007).

8.2.3 EEG recording

The continuous EEG was recorded at a sampling rate of 500 Hz using a Neuroscan Synamp 2 (Compumedics Inc., Victoria, Australia) amplifier from 61 Ag/AgCl electrodes were mounted on an EasyCap (EASYCAP GmbH, Herrsching, Germany) arranged by the 10% system (Nuwer et al., 1998). Two additional electrodes were placed at mastoids. The reference and the ground electrodes were placed at the tip of the nose and to the forehead, respectively. Horizontal electro-oculogram was measured by electrodes attached near the outer canthi of the eyes while the vertical electro-oculogram was calculated offline as the difference of Fp1 electrode and an electrode placed under the left eye.

Continuous EEG data was filtered offline using first a 1 Hz highpass filter (Kaiser-windowed sinc finite impulse response filter, beta of 4.53, 2929 coefficients; 0.5 Hz transition bandwidth, stopband attenuation at least 50 dB). After that, an eye movement correction procedure was applied as described by Schlögl and colleagues (2007). Finally, the corrected EEG data was filtered again, using a 30 Hz lowpass filter (Kaiser-windowed sinc finite impulse response filter, beta of 4.53, 2929 coefficients; 0.5 Hz transition bandwidth, stopband attenuation at least 50 dB).

The EEG was segmented into 800 ms long epochs corresponding to the 150 ms gap, 250 ms gap, 650 ms gap, and gap only events, including a 150 ms long pre- and a 650 ms post-stimulus interval. To eliminate non-gap-related ERP-contributions, further EEG segments were extracted in which gaps could potentially occur (i. e. 150 ms, 250 ms and 650 ms after the onset of potential glide timepoints and after the onset of glides which were not followed by any gaps in 650 ms). These segments are referred to control epochs in the following. After discarding epochs with a signal range exceeding 100 μ V on any channel, the control ERPs were subtracted from the corresponding ERPs of the 150 ms, 250 ms and 650 ms gaps and “gap only” events (see Figure 8.5). The results of these subtractions are referred to as *corrected* waveforms. Glide-related ERPs were also investigated for “glide only” events. The datasets generated during and/or analysed

during the current study are available from the corresponding author on reasonable request.

8.2.4 Statistical analysis

The analysis of gap-related ERPs consisted of a hypothesis-driven, and an explorative part. In the hypothesis-driven part, gap-related N1 waveforms were identified for 150 ms, 250 ms, 650 ms gap, and “gap only” events in the group-averaged corrected waveforms, separately in the two groups. Individual ERP amplitudes were calculated in 20 ms long windows centered at the N1 peak latency measured in the group-averaged corrected waveforms for “gap only” events. In order to improve signal-to-noise ratio, statistical analyses were conducted at a fronto-central cluster of electrodes including FCz, Cz, Fz, FC1 and FC2 (referred to as FCz-cluster in the following). The mastoid signals were also averaged, this average signal is labeled M. To assess whether gap-related N1 amplitudes *per se* differed between groups, gap only N1 amplitudes measured in the two groups were compared by Welch’s t-tests. Then N1 amplitudes elicited in the two groups by different Gap Types were submitted separately to repeated measures ANOVAs. To compare the *modulation* of the N1 amplitude by glide-gap separation between groups, the 150 ms, 250 ms and 650 ms gap amplitudes were normalized by the “gap only” N1 amplitudes separately in the two age groups. These normalized amplitudes were submitted to a Group (older / younger) × Gap Type (150 ms / 250 ms / 650 ms) mixed ANOVA. These analyses were also performed for the positive aspect of the N1 measured in the averaged mastoid signal, as well as for the P2 amplitudes measured at the FCz-cluster.

The visual inspection of the ERP waveforms suggested that the amplitude differences found in the hypothesis-driven part of the analysis were not caused by pure modulations of the N1 or P2 waveforms, but by the emergence of a fronto-centrally negative deflection overlapping both of these waveforms. Similarly to N1, its amplitude also seemed to be modulated by the glide-gap separation and its polarity was inverted at the mastoids. Because of these attributes, in the following the deflection is referred to as *delayed auditory response*. Therefore, in the *explorative* part of the analyses, three difference waveforms were calculated by subtracting the ERP to the corrected gap only events from the ERP to the 150, 250 and 650 ms gap events to characterize this deflection. Since the 150 ms – minus – gap only difference waveform showed the highest (negative) amplitude, we normalized the amplitudes of the 250 ms – minus –

“gap only” and 650 ms – minus – “gap only” waveforms separately in each group in a 20 ms window centered at this peak. The mean amplitudes were calculated at FCz cluster, and were submitted to a Group (older / younger) × Gap Type (250 ms / 650 ms) ANOVA.

From the visual inspection of the group-average difference waveforms, it was also apparent that the delayed auditory response emerged later in the older than in the younger adult group. To verify this post-hoc observation, the latencies for the 150 ms gap – minus – “gap only” waveforms in the two groups were compared by Welch’s t-tests following the jackknife procedure combined with a fractional area technique based on Kiesel, Miller, Jolicoeur & Brisson’s (2007) description. The latencies were determined separately for the two groups, using a boundary of $-0.5 \mu\text{V}$ at the FCz-cluster. Since it seemed to be inverted at the mastoid sited, we also measured its positive aspect in the average mastoid signal with a $0.2 \mu\text{V}$ boundary. Latencies were defined as the halving points of the area between 50 and 300 ms in the younger adults and between 50 and 400 ms in the older adults. To further compare the temporal and topographical characteristics of this effect, a Group (younger adults / older adults) × Site (FCz cluster / M cluster) ANOVA was applied.

Finally, N1 and P2 amplitudes elicited by “glide only” events were also compared between the older and the younger adult group. The individual ERPs were averaged in a 20 ms time window centered at the group-mean negative peak, separately for the two age groups. The N1 and P2 amplitudes measured at the FCz-cluster were analyzed in Welch’s t-tests. All statistical tests were calculated in R (version 3.1.0, R Core Team, 2014). Generalized eta squared effect sizes (Bakeman, 2005; Olejnik & Algina, 2003) are also reported.

8.3 Results

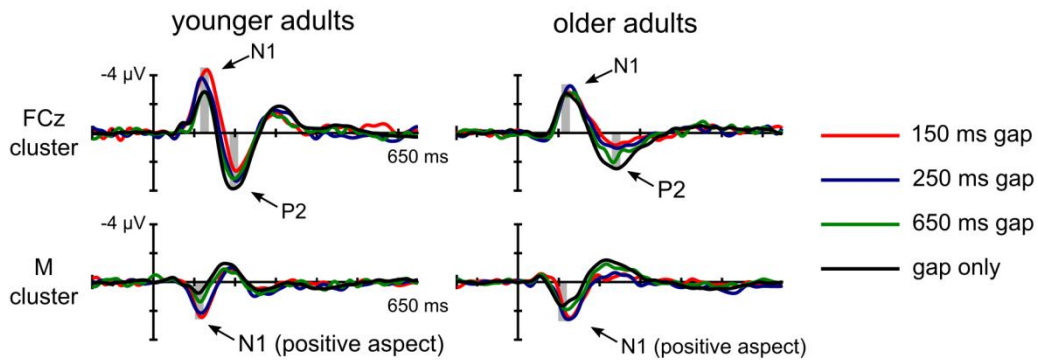
8.3.1 Gap-related ERPs – Hypothesis-driven analysis

Following the exclusion of the artifact-contaminated epochs, individual ERPs were averaged separately for the two groups for each gap position. The mean epoch numbers (and their standard deviations) in the younger adult group for the 150 ms and 650 ms gaps were 81 (SD = 3.21 and 3.47, respectively), for the 250 ms gaps 82 (SD =

2.28) and for gap only events 1427 (SD = 46.31). “Glide only” events included 244 (SD = 7.03) epochs on average. In the older adult group the mean epoch numbers for 150 ms, 250 ms and 650 ms gaps were 81 (SD = 4.24; 3.66 and 4.99, respectively). “Gap only” events were averaged from 1408 (SD = 69.5), “glide only” events from 241 (SD = 12.37) epochs.

The group-averaged corrected waveforms are presented in Fig. 8.1a and their topographic distributions are depicted in Fig. 8.2. All corrected gap-related ERP waveforms showed a negative peak, followed by a positive deflection, which were identified as the frontal aspect of N1 and P2 respectively. For “gap only” events, in the younger adult group, N1 reached its maximum (negative) peak at Cz at 126 ms. P2 peaked at FCz at 194 ms. In older adults, both N1 and P2 peaked at FCz, with 120 and 242 ms latency, respectively. The positive aspect of the N1 peaked at the mastoids slightly earlier than the frontally negative aspect (110 ms in younger and at 106 ms in older adults). The “gap only” N1 amplitudes measured fronto-centrally did not significantly differ between the two groups. The positive aspect of the N1 (i.e. the amplitude measured in the average mastoid signal) was, however, significantly higher (more positive) in the younger adult group ($t[43.965] = 3.939, p < .001$).

Corrected ERP waveforms



Difference of 150 ms, 250 ms, 650 ms gaps and "gap only" events

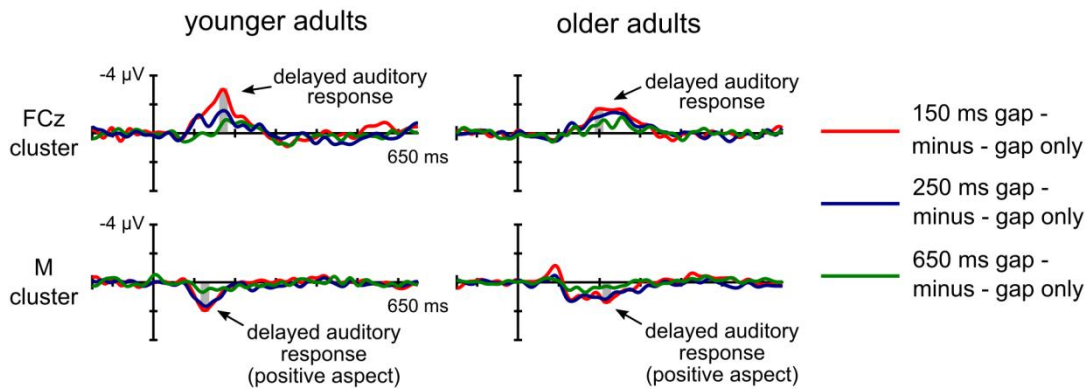


Fig. 8.1 Group-mean gap-related ERPs. Group-mean corrected gap-related ERP waveforms (a) and the difference of 150 ms, 250 ms and 650 ms gaps and “gap only” events (b) measured at the electrode cluster centered on FCz and in the average mastoid signal in the younger and older adult groups. The grey bands indicate the time windows in which the amplitude-related statistical analyses were conducted.

The one-way Gap Type ANOVAs (150, 250, and 650 ms gap trial) of the fronto-centrally measured N1 amplitudes conducted separately in the two groups showed no significant effect in the older adult group; in younger adults, however a significant Gap Type effect was found: $F[3, 66] = 9.531, p < .001, \eta^2_G = .159$. Follow-up paired Student’s t-tests revealed that the amplitudes were higher (more negative) for the 150 ms than for the 650 ms gaps ($t[22] = 4.349, p < .001$) or for the “gap only” events ($t[22] = 4.762, p < .001$); amplitudes for the 250 ms gap were also higher (more negative) than for “gap only” events ($t[22] = 2.419, p = .024$). Similarly, the one-way Gap Type ANOVAs of the mastoid signals showed no significant effect in the older

adult group, but a significant Gap Type effect was present ($F[3,66] = 17.999, p < .001, \eta^2_G = .26$) in the younger adult group. The amplitudes for 150, 250, and 650 ms gaps were significantly higher (more positive) than for gap only events (t -scores > 2.559 , p -values $< .019$). Significant differences were also present between 150 ms and 650 ms gaps ($t[22] = 3.615, p = .002$), as well as between 250 ms and 650 ms gaps ($t[22] = 3.955, p < .001$). For the normalized N1 amplitudes measured fronto-centrally (Figure 8.3a), the Group \times Gap Type (150 ms / 250 ms / 650 ms) ANOVA showed significant Gap Type main effect: $F[2, 88] = 5.54, p = .005, \eta^2_G = .05$; and Group \times Gap Type interaction: $F[2, 88] = 4.24, p = .017, \eta^2_G = .039$. Follow-up t -tests between Gap Types showed no significant differences in the older adult group, but in the younger adult group amplitudes were significantly higher for 150 ms than for 650 ms glide-gap separations ($t[22] = 4.345, p < .001$).

Topographical distributions of gap-related ERPs

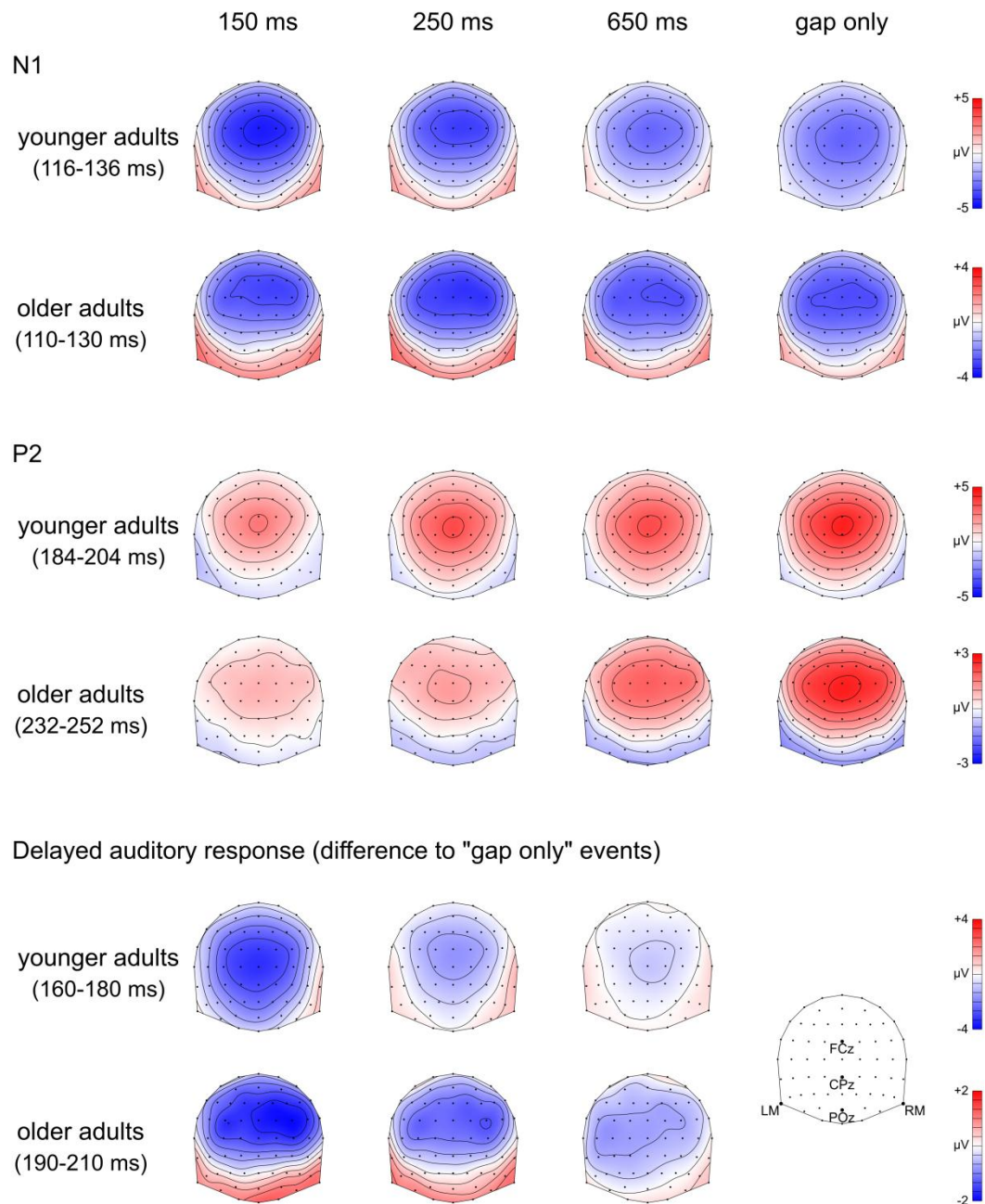


Fig. 8.2 Topographic distributions of the group-mean ERP effects. Topographies of group-mean, corrected gap-related ERPs in the N1 (a) and P2 (b) time windows and the delayed auditory response overlapping them (c). The amplitude scales differ between rows to allow between-group topographical shape comparisons, while allowing the observation of Gap Type amplitude differences for the two groups.

The Group \times Gap Type ANOVA of the normalized amplitudes for the positive aspect of the N1 (measured in the average mastoid signal) (Figure 8.3b) showed a

significant Group main effect: $F[1, 44] = 29.255$, $p < .001$, $\eta^2_G = .29$; a significant Gap Type main effect ($F[2, 88] = 7.6$, $p < .001$, $\eta^2_G = .06$; and a significant Group \times Gap Type interaction: $F[2, 88] = 8.47$, $p < .001$, $\eta^2_G = .07$). Follow-up t-tests revealed that in younger adults both 150 ms and 250 ms gaps elicited higher amplitudes than 650 ms gaps ($t[22] = 3.615$, $p = .002$ and $t[22] = 3.955$, $p < .001$, respectively). In the older adults, however, only one comparison showed a significant difference, and it was in the opposite direction: 150 ms gaps elicited lower amplitudes than 250 ms gaps ($t[22] = 2.2$, $p = .04$).

For the “gap only” events P2 was significantly larger (more positive) in younger, than in older adults (Welch’s $t[43.841] = 2.973$, $p = .005$). The one-way Gap Type ANOVA showed significant effects both in the younger ($F[3, 66] = 6.553$, $p < .001$, $\eta^2_G = .098$) and in the older adult group ($F[3, 66] = 13.672$, $p < .001$, $\eta^2_G = .174$). In the younger adult group, P2 amplitudes to 150 ms gaps were lower than those to 650 ms gaps ($t[22] = 2.61$, $p = .016$) or “gap only” events ($t[22] = 4.472$, $p < .001$). Furthermore, 250 ms gaps also resulted in lower amplitudes than “gap only” events ($t[22] = 2.373$, $p = .027$). In older adults, amplitudes differed between all gap types (t -values > 2.536 , p values $< .017$), except for the 150 and 250 ms gaps.

The Group \times Gap Type ANOVA of the normalized P2 amplitudes (Figure 8.3c) showed a significant Gap Type main effect ($F[2, 88] = 8.21$, $p < .001$, $\eta^2_G = .06$) only. Follow-up t-tests showed (with pooled groups) that the modulation of P2 amplitude was significantly larger at 150 ms ($t[45] = 4.302$, $p < .001$) and 250 ms ($t[45] = 2.058$, $p = .045$) glide-gap separations in comparison to 650 ms gaps.

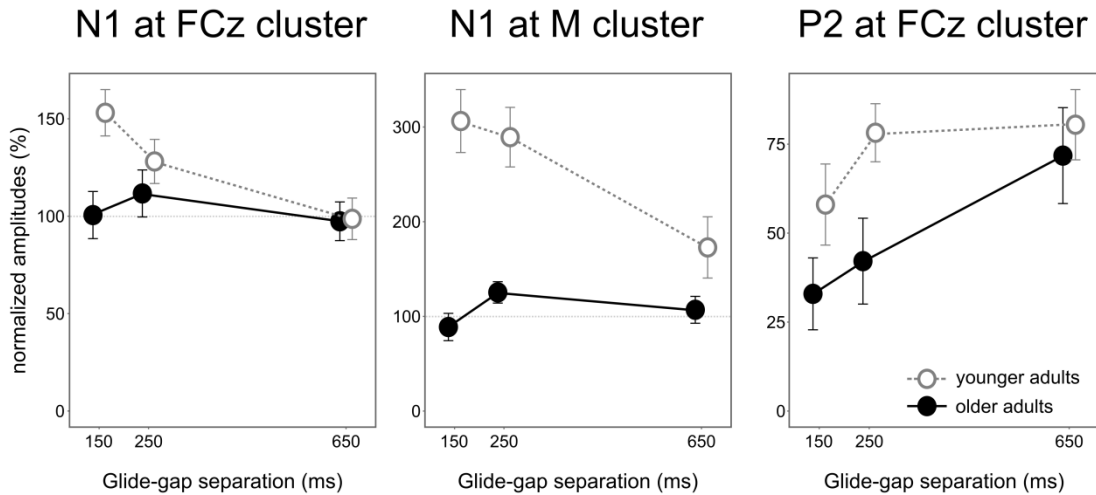


Fig. 8.3 Normalized gap-related ERP amplitudes. Group-mean normalized gap-related ERP amplitudes of measured in the N1 interval at the electrode cluster centered on FCz (a) and in the average mastoid signal (b), and also in the P2 interval at the electrode cluster centered at FCz (c). Whiskers indicate standard errors of means. The basis of the normalization (100% on the vertical axes) refers to the group-mean amplitude in the corresponding corrected “gap only” waveforms.

In summary, the hypothesis-driven analysis revealed that with shorter glide-gap separation, a stronger N1-enhancement was present (i.e. amplitudes were shifted in the negative direction at fronto-central and in the positive direction at mastoid sites) in the younger, but not in the older adult group. Interestingly, P2 (measured fronto-centrally) was reduced (i.e. amplitudes were shifted in the negative direction) as glide-gap separation decreased in both groups.

8.3.2 Gap-related ERPs – Exploratory results

The pattern of results presented above opens up the possibility that the observed effects are not due to the modulation of the N1 or P2 components, but rather, they may reflect an overlapping ERP. Indeed, the visual inspection of the waveforms (Figure 8.1b) suggests that in the younger adult group the fronto-central N1 enhancement and the P2 reduction are caused by a fronto-centrally negative ERP overlapping both components. Similarly, the visual inspection of the group-average older adult ERP suggests that the P2 reduction, that is, the amplitude shift in the negative direction at fronto-central sites, is paralleled by an amplitude shift in the negative direction at the mastoid sites. To better visualize the glide-gap separation effects, the ERP differences between the ERPs to the 150, 250, and 650 ms gaps and the “gap only” ERP were

calculated (Figure 8.1b). The waveforms in these differences, referred to as *delayed auditory responses* in the following, were most prominently observable at 150 and 250 ms glide-gap separations, between 90-260 ms in younger adults and between 110-330 ms in the older adults, peaking at 170 ms at Cz in the younger, and at 200 ms at FC4 in the older adult group at 150 ms glide-gap separation.

To confirm the visual impression that the amplitude of the delayed auditory response was modulated by glide-gap separation, the average amplitudes in a 20 ms time-window centered at the local minima of the “150 ms gap” – minus – “gap only” difference at the FCz cluster were measured separately for both groups. Similarly, because the polarity of the negativity seemed to be inverted at the mastoids, amplitudes were measured in a 20 ms time-window around the positive peak of “150 ms gap” – minus – “gap only” events waveform, separately for the two age groups. Similarly to the hypothesis-driven analysis, the “250 ms gap” – minus “gap only” and 650 ms gaps – minus – “gap only” amplitudes were normalized by the “150 ms gap” – minus – “gap only” amplitudes, then submitted to Group \times Gap Type (250 ms / 650 ms) ANOVAs.

At the FCz cluster, the Group \times Gap Type (250 ms / 650 ms) ANOVA for the normalized amplitudes showed only a significant Gap Type main effect: $F[1, 44] = 6.11, p = .017, \eta^2_G = .04$. , The same type of analysis of the mastoid signals showed a significant Gap Type main effect only: $F[1, 44] = 18.28, p < .001, \eta^2_G = .17$. In both cases the amplitudes were higher (more negative for the FCz, cluster, and more positive at the mastoids) for the 250 than for the 650 ms gaps.

To confirm the visual impression that there was a latency difference between groups, the latencies of the “150 ms gap” – minus – “gap only” waveforms, as measured with a fractional area technique in combination with a jackknife procedure (Kiesel et al., 2007) were submitted to a Welch t-test. This procedure was also used to compare the latencies of the delayed auditory responses at FCz and its positive aspect at the mastoids as well. When defining the latencies at the averaged mastoids, in case of three participants the boundary defined two areas in the younger adults group. In their case, the larger area was selected, which corresponded to the earlier one. Note that in the following the jackknife-adjusted F-, t- and p-values are reported. The degrees of freedom remained unadjusted.

In the “150 ms gap” – minus – “gap only” ERP difference, a significant group-difference was present both at the FCz-cluster ($t[42.405] = 6.823, p < .001$), and at mastoids ($t[24.947] = 4.251, p < .001$). In both cases, the waveform peaked earlier in the younger adult group. The Group (younger adult / older adult) \times Site (FCz cluster / M cluster) ANOVA revealed significant Group ($F[1, 44] = 44.909, p < .001, \eta^2_G = .996$) and Site ($F[1, 44] = 18.071, p < .001, \eta^2_G = .988$) main effects. The Group \times Site interaction was not significant.

8.3.3 Glide-related ERPs

Glides elicited a clear N1 and P2 in both groups (Figure 8.4). In the younger adult group, N1 peaked at 106 ms and P2 peaked 194 ms, both at FCz, in the group-average waveform. In the older adult group, N1 and P2 reached their maximum peaks at FCz as well; at 106 ms and at 218 ms, respectively. Glide-related amplitudes for N1 and P2 were also compared between the two groups by Welch t-tests at the FCz cluster. There was no significant difference in N1 amplitudes, but P2 was elicited with significantly lower amplitudes in the older than in the younger adult group ($t[38.428] = 2.887, p = .006$).

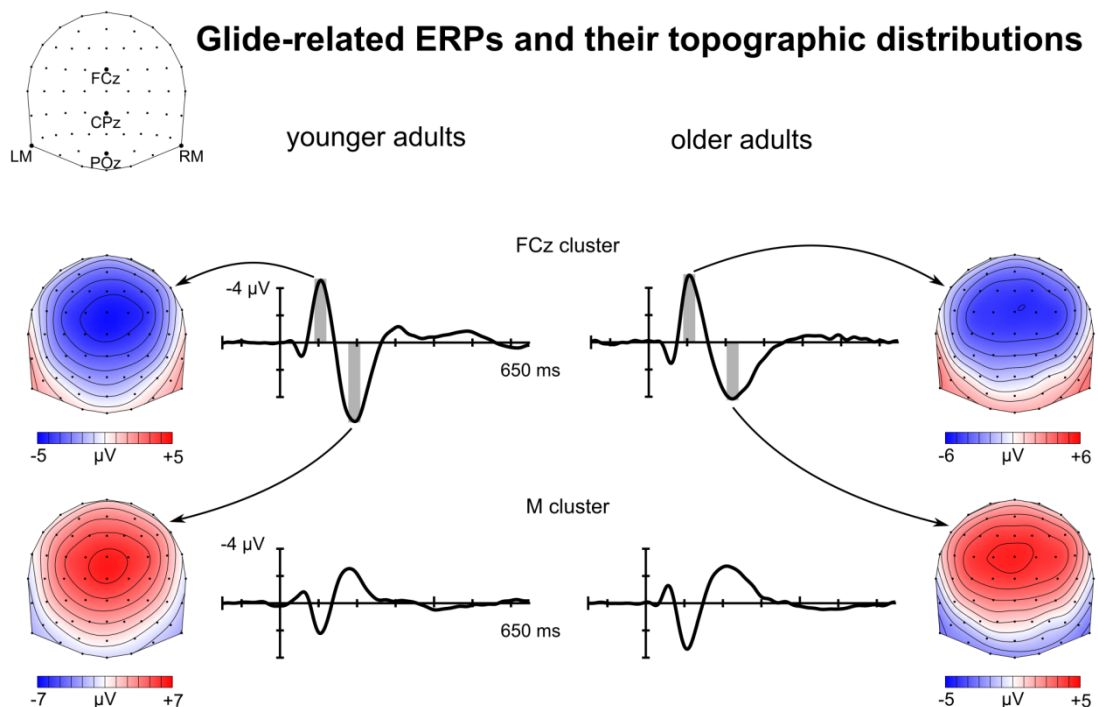


Fig. 8.4 Group-mean glide-related ERPs and the corresponding topographies in the N1 and P2 time ranges in the younger and older adult groups. The grey bands indicate the time windows where the amplitude measurements were performed and for which the topographic

distributions are presented. The amplitude scales differ in order to support the comparison of distribution shape information between groups.

8.4 Discussion

The goal of the present study was to compare the duration of a distracted state induced by randomly occurring rare, background auditory events between younger and older adults. While participants watched a silent movie with subtitles, continuous tones containing rare glides (distracters) and frequent gaps (probes) were presented. Based on previous studies, we hypothesized that gap-related N1 and P2 ERPs would be enhanced when gaps closely followed glides, reflecting an increased readiness of the auditory system to process incoming stimuli. Based on the hypothesis that older adults showed a higher distractibility, and decreased ability to inhibit the processing of task-irrelevant pieces of information, we hypothesized that such ERP enhancements would be present for longer glide-gap separations in older than in younger adults.

Gaps elicited N1 and P2 with higher amplitudes in the younger than in the older adult group (fitting previous results: Alain et al., 2004; Harris et al., 2012; Volosin, Gaál & Horváth, 2017a). Although the results showing an ERP enhancement with decreasing glide-gap separations in the N1 time range in the younger adult group are on a par with previous studies (Budd & Michie, 1994; Horváth & Winkler, 2010; Loveless et al., 1989; McEvoy, Levänen & Loveless, 1997; Todd et al., 2000; Sable et al., 2004; Wang et al., 2008), the attenuated amplitudes in the P2 interval, and the comparison with the older adult group suggests a more economical explanation. Instead of a modulation of the N1 and P2 peaks, the hypothesis-driven analyses of the ERP amplitudes in the N1 and P2 time-intervals revealed a pattern which could be best described as an overlap by a fronto-centrally negative waveform with a polarity reversal at the mastoids. This – presumably – auditory response was delayed in comparison to the N1, which resulted in a virtual enhancement of the N1 and attenuation of the P2 in the younger adult group. Because the overlapping waveform was even more delayed in the older adult group, its presence was manifested only in a marked (but virtual) P2 attenuation. The delayed auditory response showed decreasing amplitudes with increasing glide-gap separations.

This result contradicts our hypothesis that rare glides temporarily raised the responsiveness of the auditory system to process closely following events, and thus invalidates the premise of our initial hypothesis regarding an age-related increase in the

persistence of such ERP enhancements. In addition, neither the distraction-based hypothesis (that a brief, involuntary allocation of attention to the tone lead to enhanced processing), nor the latent inhibition hypothesis (suggesting that a basic excitatory effect preceding the onset of inhibition enhances N1-elcitation) can explain the emergence of an additional gap-related ERP.

The idea that the higher N1 (and lower P2) amplitude for a tone closely preceded by another tone was not a genuine N1- or P2-modulation, but the result of an overlapping negative ERP component has been suggested by Wang and colleagues (2008). They speculated that the overlapping ERP may have been an MMN, which was elicited because of the relatively short (i.e 100, 200 ms) separations from the preceding tone in comparison to the typical inter-stimulus intervals (sampled from an equiprobable 100-1000 ms distribution, with a mean of 500 ms) used in their study (see e.g. Sable et al., 2004). The idea that MMN may contribute to the N1 enhancement was also hinted at by Todd and colleagues (2000) who found that the N1 facilitation to very short (50 ms) inter-tone intervals and the amplitude of the MMN to rare duration deviants (100 ms tones presented among 50 ms tones) were strongly correlated in healthy adults. The present results showing that the delayed auditory response had a polarity inversion at the mastoids also fits the MMN explanation, because – being of supratemporal origin – MMN also often shows a similar inversion (Alho et al., 1993; Maess, Jacobsen, Schröger & Friederici, 2007; Scherg, Vajsar & Picton, 1989).

A further possibility is that the closely following gap is processed *together* with the preceding glide by the auditory system. Indeed, numerous studies suggested that processes underlying MMN generation integrate information over longer intervals (150-300 ms, see e.g. Tervaniemi, Saarinen, Paavilainen, Danilova & Näätänen, 1994; Yabe, Tervaniemi & Reinikainen, 1997; Grimm, Roeber, Trujillo-Barreto & Schröger, 2006). The temporal window of integration seems to be of similar duration between younger and older adults (Horváth et al., 2009). Although the glide probably elicited an enhanced N1 and possibly an MMN (Horváth, 2014a) in itself, the closely following gap may be integrated with the glide, and treated as a single unit of stimulation. Because the glide-and-gap event-combination was as rare as the glide-only event in the present paradigm, an MMN time-locked to the gap may additionally be elicited.

Studies investigating age-related MMN latency differences in conditions of inattention for tones deviating in pitch, duration, or novelty from the frequently presented tones found either no differences (Amenedo & Diaz, 1998; Bertoli, Smurzynski & Probst, 2005; Horváth, Czigler, Winkler & Teder-Sälejärvi, 2007) or age-related delays (Cooper, Todd, McGill & Michie, 2006; Schroeder, Ritter & Vaughan, 1995; a tendency: Gaeta et al., 1998). MMNs elicited by unattended, rare tones with gaps showed age-related delays (Alain et al., 2004; Bertoli, Smurzynski & Probst, 2002). The fact that the delayed auditory response was elicited later in older than in younger adults is therefore also compatible with the notion that the ERP is a gap-related MMN. Although the gap-duration was longer than that used in the studies by Alain and colleagues (2004) and Bertoli, Smurzynski & Probst (2002), and it allowed close-to-perfect gap-detection rates in an active version of the administered paradigm for both younger and older adults (Volosin, Gaál & Horváth, 2017a), the age-related latency-difference may still be the consequence of an age-related deterioration of fine temporal resolution (Humes, Kewley-Port, Fogerty & Kinney, 2010).

In summary, the present results confirmed previous ERP findings showing enhanced ERP responses to auditory events shortly following another auditory event. In contrast to previous studies, by comparing younger and older adults, the present study provided evidence that the enhanced auditory ERP response was not due to the enhancement of the N1, but to an overlapping ERP originating from the auditory cortex, presumably an MMN. The delayed elicitation of this waveform suggests that central auditory processes related to the detection of gaps in continuous tones are slowed in older adults.

Chapter 9: GENERAL DISCUSSION

The aim of the present dissertation was to shed light on the mechanisms contributing to the attention–distraction balance. While Study I and Study II focused on preparatory processes which could play role in preventing distraction and in the establishment of an efficient selective attention set, Study III and Study IV focused on the time course of distraction and its age-related changes.

We demonstrated in Study I and Study II that regularities of the acoustic environment are utilized strongly by the cognitive system in order to prepare for forthcoming relevant events and to suppress the distracting effect of task-irrelevant tones. In Study I (Volosin & Horváth, 2014), the constantly available information on the occurrence of a distracting stimulus lead to decreased P3a amplitudes compared to the condition when participants could not prepare for such events. This result fits to and extends the previous literature in which information on the forthcoming deviant was delivered by cues presented preceding each stimulus. In these experiments (Horváth & Bendixen, 2012; Horváth, Sussman, Winkler & Schröger, 2011; Sussman, Winkler & Schröger, 2003; Wetzel, Widmann & Schröger, 2007), one could speculate only that the decreased distraction-related ERPs like P3a a RON genuinely reflect that participants could shield against distraction and the amplitude modulation was not a mere byproduct of cue processing.

Study I strengthened the assumption that prediction and preparation effects lead to reduced distraction which was also supported in a subsequent experiment of Max, Widmann, Schröger and Sussman (2015). They investigated whether implicit predictability was enough to decrease distraction or explicitly generated top-down processes are necessary. They utilized a duration discrimination oddball task in which every 5th tone was a pitch deviant and conditions differed from each other in the instruction and the amount of information provided to participants. In the informative conditions, participants were informed about the regularity of the sequence structure while in the uninformative condition they did not get any information. P3a amplitudes were significantly reduced in the informative condition, suggesting that beside of predictability provided implicitly by the presentation regularities, explicit knowledge-related top-down processes are essential in generation of P3a and in electrophysiological signs of distraction. However, distraction was present in all

conditions, suggesting that in behavioral terms, the implicit knowledge was as effective as the explicit, and that predictions have a differential effect on electrophysiological and behavioral indices (Max et al., 2015), similarly as shown by our study (Study I).

In Study I, beside of the visual counter presented along with the tones, the constant time interval between stimuli (1.3 sec) also allowed to prepare for the presentation of subsequent tone. This preparation effect is observable at the baseline of ERPs (Fig. 5.1) which exhibit a negative, CNV-like (Walter et al., 1964) going trend before the onset of each tone. Although we did not analyze this baseline part of ERPs, its presence was demonstrated in numerous studies (Berti & Schröger, 2001; Horváth, 2014a; 2016; Horváth, Gaál & Volosin, 2017; Schröger & Wolff, 1998b) utilizing constant SOAs in different oddball tasks. Beside of the regular pace of presentation, a second informative foreperiod also characterized the stimuli in the Study I. Because sounds started to move to the left or right always 200 ms following the onset, participants could prepare not only to the presentation of the tones in general, but the tone onset predicted the beginning of the movement as well. In these terms, although tone onsets were not informative regarding the correct response (left or right), they could be regarded as temporal cues. This second foreperiod effect can further explain the lack of behavioral difference between predictable and random conditions: although participants could not prepare for the pitch deviance which captured their attention, this attention capture and the additional arousal enhancement (e. g. Parmentier et al., 2010), speeded-up response times, leading to null-effect.

While in Study I both the sequence structure and the tone onsets provided predictability, in Study II we changed the stimulation from discrete to continuous, in order to control cue value of the regularities of trial-to trial presentation. Study II (Volosin, Grimm & Horváth, 2016) demonstrated that in case when distracter events predicted the timing of the task-relevant ones (but not their type), attention-related ERPs were observable to the distracters. One of these attention-related components was identified as N2b which often overlaps MMN and reflects the detection of task-relevant events. The elicitation of N2b is in line with previous findings with rare but task-relevant events (Sams et al., 1983; Ritter et al., 1992), implying that in our case, originally task-irrelevant events were incorporated into goal-oriented behavior. Moreover, in the informative condition a significant CNV elicitation was also observable which is one of the first discovered cognitive ERP components (Walter et

al., 1964) reflecting preparation processes. That is, when the constant time interval between distracter and target events was available to be mapped, distracters did not only get enhanced attention but also resulted in preparatory effects, similarly to the negative going baseline amplitudes in Study I. This preparation affected behavioral results as well: decision on gap duration was significantly faster compared to the uninformative condition, however, the accuracy of performance was not impacted, probably because glides were not informative regarding the duration of the forthcoming gaps. Comparable results were found a subsequent study by Herbst and Obleser (2017) in which predictive foreperiods speeded up response times when acoustic events (pitch) were embedded in noise. Unfortunately, the design of Study II did not allow to investigate the ERP correlates of the preparation effects in case of targets. A fair comparison would be to select glide-gap pairs with the same temporal separation than in the informative condition (400 ms) but because the time intervals between distracter and target events varied highly in the uninformative condition, the number of such events would have been extremely low.

In general, Study I and Study II pointed out that human cognitive and auditory system takes advantage on the regularities in the acoustic environment, both in cases when participants are aware of the temporal structure of stimulation and when they are not. Results fit well in the framework of predictive coding as well: the brain constantly creates and updates hypotheses about the forthcoming events based on previous experience and current context, and the system is able in principle to control its learning in a continuous manner (Denham & Winkler, 2017). This process is reflected in our studies both in P3a reduction to predictable deviants in Study I, and the presence of task-relevance (N2b) in Study II and preparation-related (CNV) negativities in both cases. Moreover, Study I solved some questions arose from cuing paradigms: in such studies visual cues are constantly presented in 340-900 ms before targets, cue-related attentional effects might easily overlap with ERPs to the target, leading to the misinterpretation of modulation of different components. That is, the common target-related P3a attenuation in cuing tasks (Horváth & Bendixen, 2012; Horváth, Sussman, Winkler & Schröger, 2011; Sussman, Winkler & Schröger, 2003; Wetzel, Widmann & Schröger, 2007) cannot be regarded as a byproduct of cue processing, and it is more likely that preparation effects shielding against distraction led to this effect as it was

suggested – but not entirely proved in previous studies. Study II also contributed to clarify issues from studies using distracters presented shortly before target events.

The age-related differences in the deviance processing and its effects on detection of subsequent acoustic events were investigated in Study III and Study IV. Both studies applied a continuous stimulation paradigm in which the temporal separation between rare glides and frequent gaps was systematically manipulated. In contrast to Study I and Study II, no temporal relationship was present between glides and gaps, that is, glides served only as distracters. Both Study III and Study IV were based on the assumption that N1 peaks with the largest amplitude the eliciting event is in the focus of attention (Hansen & Hillyard, 1980; Hillyard et al, 1973; Lange, 2013; Okamoto et al, 2007), while attentional disruptions attenuate its amplitude (Horváth & Winkler, 2010; Horváth, 2014a, 2014b). The modulation of N1 amplitude was expected to exhibit an opposite pattern during active and passive registration of the same sound. That is, in the active condition when participants voluntarily listen to the continuous tones, rare glides should disrupt the attention set which is optimal for the detection of the gaps, which results in diminished N1 to closely (150 ms) presented gaps. In contrast, in the passive condition, participants' attention was expected to be engaged in the visual modality (watching the movie), and glides were supposed to orient the attention to the task-irrelevant modality (tones), that is, attention would be allocated to the tone, thus enhancing N1 elicited by closely following gaps. In both experiments, we expected that recovery from the distracted state will take longer in older adults as reflected by the modulation pattern of gap-related N1 amplitudes.

However, only a part of the hypotheses was supported by the results. Fitting previous studies (Alain et al., 2004; Harris et al., 2012), gaps consistently elicited lower N1 amplitudes in older than in younger adults in both studies. Older adults did not differ from the younger group neither in their gap detection performance, nor in the time course of the modulation of N1 amplitude: the attention set of both groups was restored by 650 ms following glides, suggesting that older adults do not need more time to re-orient their attention to the relevant task (Study III). Although at the first sight, it seems like that the N1 amplitudes were changed, it is more possible that not a pure N1 modulation was present: as shown by topographic distributions in the upper two panels in Fig. 7.6 (N1 first time window vs N1 second time window), there is a dissociation between maximum peaks at the mastoid and fronto-central electrodes, suggesting the

presence of an overlapping negativity, probably a PN, reflecting that the gaps matched the task-relevant sensory template (Alho et al, 1986; Alho, 1992; Näätänen, 1982). This matching process occurred probably at very similar times with the elicitation of genuine N1 in the younger adults resulting in one visible peak while the timing of the two components isolated more strongly in time in the older adults. Although no age differences were present in the modulation pattern either of N1 or PN, older adults were nevertheless impacted more by glides, indicated by the enhanced reaction times compared to gap only events in the 150 ms condition while no such speed difference was present in the younger adult group (Study III). Moreover, in the Study III, the active attention to the ongoing tone and task made possible to compensate performance by more focused attention and with the contribution of extra cognitive resources which was more pronounced in the older adults (Getzman, Gajewski & Falkenstein, 2013; Lustig, Hasher and Zacks, 2007; Reuter-Lorenz & Cappell, 2008; Zanto & Gazzaley, 2014). This compensation was reflected both in reaction time pattern (significant slowing in case of 150 ms glide-gap separation) and the negative sustained CNV-like potential which typically elicits in the older population with larger amplitudes and suggests the further processing of a stimulus (Näätänen & Michie, 1979).

A further study of our research group (Horváth, Gaál & Volosin, 2017) demonstrated additional evidence to enhanced cognitive control in the older adults. Participants completed a tone duration discrimination task in discrete tones and every sound was presented with the same pitch (that is, no distracting oddball tones were embedded). We investigated both onset- and offset-related ERP responses and found enhanced N1 amplitudes at tone onsets and no age differences at the offsets at temporal electrodes (T-complex: Wolpaw & Penry, 1975), fitting to the previous literature (onset: Amenedo & Díaz, 1998; Anderer, Semlitsch & Saletu, 1996; Chao & Knight, 1997; offset: Ross et al., 2009). More importantly, older adults exhibited a significant centrally distributed negative deflection, probably an N2 at tone offsets which was absent in the younger adults group, suggesting the presence of additional cognitive control processes (Folstein & Van Petten, 2008).

The results of the passive arrangement in the Study IV also strengthened the assumptions of Study III. When participants had no chance to compensate their performance by more focused attention as in the Study IV, the background processing of gaps preceded by glides shortly was characterized with an overlapping negative

deflection, probably a mismatch negativity. In the older adults, MMN peaked with a significant delay compared to younger adults which is in consonance with previous studies utilizing either discrete tones (Cooper, Todd, McGill & Michie, 2006; Schroeder, Ritter & Vaughan, 1995) or more importantly, gaps embedded into rare tones presented in the background (Alain et al., 2004; Bertoli, Smurzynski & Probst, 2002). A possible explanation for the absence of hypothesized gap-related N1 modulation pattern in the Study IV could be that the MMN which can be characterized with a relatively slow time-course overlapped N1. Besides, the temporal interval in which MMN elicited (between 90-260 ms in younger adults and between 110-330 ms in the older adults) also overlapped with the time-course of P2, explaining why the pattern of P2 modulated in the opposite way compared to N1, that is, its amplitude lineally increased with the glide-gap separation. It is also important to emphasize that the overlapping MMN effects was observable only in case of 150 ms glide-gap separation, and this interval corresponds to the window of temporal integration. That is, a further possibility that in such cases gaps were presented during the temporal integration period of the glide and these two events were represented together (Yabe, Tervaniemi, Sinkkonen, Huotilainen, Ilmoniemi & Näätänen, 1998) and served as a unique type of rare event, leading to MMN elicitation.

However, since the overlapping MMN in Study IV was revealed as an explorative result, its interpretation should be cautious. For further studies, an important step would be to clarify whether it is a real MMN originating from the regularity violations of rare events and not a byproduct of gap processing. This question can be answered easily by switching the role of gaps and glides, that is, to introduce a control condition in which glides are the frequent and gaps are the rare events and compare whether both conditions will elicit similar MMN effects. When both combinations of the events were leading to similar neural responses, it would support the presence of MMN.

The declined processing of fine temporal resolution with aging is also in line with the results from speech processing in background noise. This is a frequently reported symptom in the older population leading to significant frustration, and since the perception of pure tones is usually intact, they remained untreated, decreasing the well-being more strongly (Pichora-Fuller, 2003a, 2003b). The difficulty of following conversations in noisy background despite normal cognitive functioning is a typical

case of a decline in the central auditory system in the synapses between hair cells and cochlear nerve terminals, also known as “hidden hearing loss” (Lieberman, Epstein, Cleveland, Wang & Maison, 2016). Although we measured pure tone audiometry only and adjusted the loudness individually, individual differences in the central auditory processing could still be present. A feasible way to screen such differences – note that hidden hearing loss can also affect younger adults – more complex control tests should have been utilized, for example speech-in-noise tests (Le Prell & Clavier, 2017) which was unfortunately not available in our experiments. Later studies should pay more attention to individual differences regarding the central auditory processing.

When observing the results from Study III and Study IV, one might speculate whether the processing of glides could be modulated with aging in general leading to differences in the default processing of the stimuli presented in the experiments, for example regarding the sensitivity to attention capture. There are studies showing that older adults detected frequency modulation less accurately when it was applied to discrete tones with a lower frequency (500 Hz) compared to higher one (4000 Hz), and similarly when they had to decide whether the two presented tones were the same or different one and also when they had to decide which of the three subsequent tones differed in pitch from the remaining two (He, Dubno & Mills, 1998; He, Mills & Dubno, 2007). However, when frequency modulation was present within the tones (i. e. to glides) presented in the background, older adults were found to be less sensitive to them at 500 Hz compared to 3000 Hz; that is, larger frequency change needed to elicit electrophysiological response (P1-N1-P2 waveform) and delayed latencies were observable as well (Harris, Mills, He & Dubno, 2008). This effect might be explained by the different processing of high and low frequencies: while the discrimination of lower frequencies is based mainly on temporal information and phase-locking cues might contribute, at higher frequencies, temporal information is less useful (Harris et al., 2008; He, Dubno & Mills, 1998). It is important to note that these studies used relatively small frequency differences (from 0 to 8%) and slower glides (150 ms in the study of Harris et al., 2008), and we utilized quicker (10 ms) and more salient frequency changes (cca 25%). The age-related differences to glide-elicited N1 amplitudes were not significant either in active (Study III) or in passive/background presentation (Study IV), suggesting that both older and younger adults were similarly affected by distracting glides or at least they had no difficulties to detect them.

The utilization of glides in Studies II, III and IV arise an additional interesting question on the possible processing differences between the two directions of pitch changes (that is, different perceived saliency of ascending or descending glides). For example, Kalaiah and Shastri (2016) demonstrated that when the pitch of discrete tones changed between two frequencies by 30 ms glides, ascending glides led to the elicitation of N1-P2 with larger amplitudes and shorter latencies compared to the descending glides. This effect might be explained with the evolutionary significance of rising tones: gradual pitch changes are similar to the Doppler frequency shifts to approaching and receding sounds in natural environments serving as important warning cues about the moving direction of a sound – and its source. Because looming objects are more salient and require a more immediate response regarding the planning of goal-oriented behavior, they capture attention in a larger extent (Neuhoff, 1998; Rosenblum, Wuestfeld & Anderson, 1996). In our studies, the rate of ascending and descending glides was 50-50% therefore the two effects might have been averaged, nevertheless it would be informative to compare glides with different directions, especially when they convey information on the forthcoming events like in Study II (Volosin, Grimm & Horváth, 2016).

The perception of the moving sounds should be mentioned in context of the potential alerting effect of higher pitch tones in Study I (Volosin & Horváth, 2014) as well. Based on the Doppler-effect described above, one could speculate that high pitch deviants were more alerting compared to the lower ones and this could lead to null effect in reaction times. We tested this possibility by comparing results of participants who listened to blocks with high deviants and low standards and those who listened to low deviants and high standards. There was no difference between their performance which suggest that perceived pitch and velocity played no or insignificant role in results. That is, although sound movements either in dimension of direction or pitch could lead to general processing differences of stimuli in our experiments, it is not possible that the results would be caused by such asymmetries. First, because we balanced the amount of these factors, and second, the results were based on modulation patterns of different components, in which significant effects were always the results of interaction. Nevertheless, further studies need to handle these factors more carefully and to compare them directly would also result in valuable information on the perception of the dynamical acoustic changes.

When discussing the role and possible effects of glides and moving sounds, one cannot disregard the critical evaluation of the continuous stimulation paradigm either, especially in context whether it was an adequate method to indicate and to investigate distraction. First of all, as mentioned above, its significant advantage is against oddball tasks utilizing discrete tones that in continuous tones no tone onsets are present which could be used as cues during the task. Note that in case of discrete tones, the first task-relevant event is always the onset of the tones and the second one when decision can be made, that is, the offset of short tones. In the gap detection tasks (Study III and IV) gaps serve as offsets of short tones but in the absence of tone onsets – except of preceding glides – no events can predict their presentation therefore its temporal structure makes the rare events more surprising and sudden (Horváth & Winkler, 2010). Second, because it contains less acoustic events compared to classical oddball tasks, gap detection might be an easier task for older adults than duration discrimination. Moreover, the everyday acoustic contexts can be characterized more often with events which are continuously present than with repeating discrete tone patterns. On the other hand, the concept of long tones containing only two kinds of acoustic events can be regarded as a disadvantage as well since the acoustic environment around us is much more complex and contains more variability. Although the main function of experiments created in laboratory settings is to model the regularities and characteristics of the environment (Winkler & Schröger, 2015), the highly strict control of the variables and stimuli can easily lead to low ecological validity. Taken together, despite the potential weaknesses of the continuous stimulation paradigm, it appeared to be an appropriate method to investigate distraction, especially because the elimination of tone onsets as temporal cues led to a higher level of uncertainty during the stimulation.

Altogether, the results of the studies presented above contributed not only to the scientific literature but also might be adequate starting points of future studies. Although they can be regarded as basic research in principle, Study III and Study IV can be strongly connected to applied science as well. As we demonstrated that although healthy aging is accompanied with declined temporal processing, highly functioning older adults can compensate with the recruitment of additional cognitive sources which was observable both in electrophysiological and in behavioral results. It would be interesting to compare whether older adults can experience these compensational strategies in the everyday life; and if yes, how can it be related to the results from the

laboratory. For example, Tomaszewski Farias and colleagues (2018) compared cognitively healthy older adults and those with mild cognitive impairment (MCI) and dementia in their compensation and cognitive abilities. They found that the higher and more effective functioning in daily life was strongly correlated with more frequent use of compensational strategies (for example using reminders, shopping lists, keeping important objects in well-visible places etc): demented participants used significantly lower amount of such strategies than healthy or MCI persons (Tomaszewski Farias et al., 2018). In context of the present doctoral dissertation, it would be interesting and suitable to include older adults with various levels of cognitive impairments in the studied sample and to follow-up how sensory and higher level cognitive processing interact in their case, especially when compensatory mechanisms are required.

Once it is known which functions decline with aging and which strategies can be utilized to compensate them, the development of cognitive trainings strengthening those abilities are crucial (Tomaszewski Farias et al., 2018; Harada, Love & Triebel, 2013). Several studies aimed to find cognitive trainings with reliable transfer effects, during which the improvement by practice in one test can be generalized to other cognitive domains as well. However, results on the long-term benefits in the cognitive performance is mixed: while practicing particular tasks per se did not lead to stable effects (for example Souders, Boot, Blocker, Vitale, Roque & Charness, 2017), the acquisition of different cognitive strategies in general (for reviews: Harada, Love & Triebel, 2013; Schubert, Strobach & Karbach, 2014; Zelinski, 2009) is nevertheless a promising area of psychology and neuroscience which requires further investigations.

Chapter 10: CONCLUSIONS

The aim of the present dissertation was to investigate the mechanisms contributing to the balance of attention and distraction and its changes with healthy aging. The present results support and extend previous results in the literature. Our studies demonstrated that explicitly and continuously provided information on the forthcoming stimulus reduces distraction as reflected in the electrophysiological components. Moreover, we pointed out that the cognitive system is able to detect whether otherwise task-irrelevant distracters can predict the occurrence time of a task-relevant event. This process led to enhanced attention and preparation effects to these distracters, suggesting that these events are incorporated into the goal-oriented behavior.

The third and fourth studies of the thesis aimed to shed light on the duration of the distracted state and its differences with healthy aging. In these studies, the lack of temporal relationship between distracter and target events led to the disruption of the attention set and varying the temporal separation of these two types of events allowed to measure the time required to recover from distraction. Both studies demonstrated that older adults needed similar amount or more time to re-orient their attention to the original task. In the same time, however, older adults were characterized with deteriorated processing of the fine temporal resolution, which was possible to be compensated with enhanced attention and involvement of additional cognitive sources.

In summary, our studies contribute to the current knowledge on how the cognitive system extracts regularities from the acoustic environment and made a step toward understanding how our brain utilizes this information to perceive the world and control our behavior in an optimal way. We also got closer to explore the duration of the distracted state and its changes with aging. In addition, we found evidence for the declined temporal processing in older age, which can be a major cause of poor speech understanding in noise and which often remains hidden by the common method of audiometry. This condition therefore deserves further attention both when investigating and diagnosing age-related changes in hearing abilities.

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