Are Stimuli Representing Increases in Acoustic Intensity Processed Differently? An Event-Related Potential Study

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Abstract

The present thesis employed event-related potentials, the minute responses of the brain, to examine the differences in processing of increases and decreases in auditory intensity. The manner in which intensity was manipulated (i.e., whether it represented *physica*l or *psychological* change) varied across the studies of the thesis.

Study 1 investigated the processing of physical intensity change during wakefulness and natural sleep. An oddball paradigm (80 dB standard, 90 dB increment, 60 dB decrement) was presented to subjects during the waking state and during sleep. The increment elicited a larger deviant-related negativity and P3a than the decrement in the waking state. During sleep, only the increment deviant continued to elicit ERPs related to the detection of change. The waking and sleeping findings support the notion that increases in intensity are more salient to an observer. Studies 2 and 3 of this thesis determined the degree to which this differential salience could be attributed to the fact that intensity increments result in increased activation of the change and transient detection systems while intensity decrements result in greater activation of only the change detection system. In order to address this question, an alternating intensity pattern was employed (HLHLHLHL) with deviants created by the repetition of a tone in the sequence (HLHLH**H**HL) that violated the expectancy for a higher (psychological decrements) or lower intensity tone (psychological increments). Because deviant stimuli were physically identical to preceding standards, this manipulation should not have led to increased output of the transient detection system (N1 enhancement), permitting isolation of the output of the change detection system (Mismatch Negativity, MMN). The findings of these studies indicated that psychological increments resulted in shorter latency and larger amplitude MMNs than psychological

decrements and that these differences could not be explained by the physical differences between deviant stimuli or temporal integration.

This thesis provides convincing evidence that stimuli representing increments in intensity result in faster and more robust change detection. Further, the increased salience of increment stimuli cannot be solely explained by the contribution of transient detector activation, as it persists even when deviance-related processing is isolated to the change detection system.

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Chapter 1

General Introduction

The ability to detect the occurrence of highly relevant, salient changes in the environment and to take appropriate action is crucial to the survival of all mammalian species. In order for this detection to be most effective, it is imperative that it occur even when the observer's focus of interest is directed elsewhere and regardless of the nature and extent of ongoing cognitive activities (i.e., regardless of what the observer "is doing" at the time of the change). The auditory modality is particularly well-suited for the detection of change occurring at some distance from the observer. We are able to hear sounds occurring in front, beside, or behind our ears. On the other hand, visual input is largely restricted to stimuli in front and to some extent peripheral to the eye. The somatosensory modality is particularly effective at detecting unattended input, but critically can do so only for only very-near stimuli (e.g., a light touch occurring behind the observer). The brain is thus equipped with highly sensitive mechanisms capable of rapidly detecting different elements of *acoustic* change. The detection of potentially relevant auditory change is carried out automatically, without the need for attention. If it is determined that an incoming auditory stimulus is indeed highly relevant, ongoing cognitive activities may cease and attention may be switched to the auditory channel (often referred to as "attention capture") allowing the individual to become aware (conscious) of its features.

The notion that salient auditory change can capture the attention of an observer forms the basis of most alarm and emergency systems (e.g., your house is on fire, your car is being stolen, it's time to wake up, etc.). Most of these alarm systems alert the observer by using the presentation of a particularly intense auditory stimulus implicitly employing the common knowledge that increases in intensity tend to be particularly effective in capturing the attention of

an observer. Evolutionary considerations help to explain why this might be the case. While the experience of a decrease in intensity in an organism's auditory environment would suggest the retreat of a possible predator, an increase in intensity would, contrastingly, suggest its approach, and thus represent a set of circumstances with much more urgent implications for survival. It has, in fact, been demonstrated that an increase in stimulus intensity is experienced as "looming" or approaching and may elicit a fear response in animals and a decrease in intensity is experienced as "fading" or retreating (Bach, Schachinger, Neuhoff, Esposito, Salle, Lehmann, et al., 2007; Freiberg, Tually, & Crassini, 2001; Maier & Ghazanfar, 2007).

A variety of models of auditory processing have been developed. A problem with many of these models is that few are able to provide a means of quantifying the extent of processing when subjects are not actively attending to the stimulus channel, making it difficult to examine processes such as attention capture. This thesis will thus place particular emphasis on a model developed by a Finnish neuroscientist, R. Näätänen, which is unique in that it employs event-related potentials (ERPs) to provide a measure of the extent of cognitive processing (Näätänen, 1990). ERPs provide a measure of the changes in the electrical activity of the brain (the electroencephalogram or EEG) that are elicited by a physical stimulus or a psychological event. Before reviewing Näätänen's (1990) model, a brief overview of the event-related potential method will be provided.

1. The ERP Method

1.1 History and development. The first published instance of the use of EEG to measure the electrical activity of the human brain was carried out by Hans Berger in 1929 (Collura, 1993). Through a series of experiments he was able to demonstrate that a continuous measure of neural activity could be recorded via electrodes placed on the scalp. Over the following decades the

EEG measure would prove to be a useful tool, with both scientific and clinical applications, but its utility to the field of cognitive neuroscience became most apparent with the advent of the ERP method. Rather than measuring ongoing spontaneous activity, event-related potentials provide measures of electrophysiological changes in the brain *in response to specific stimuli or events* which are derived from the continuous EEG (Picton, 1995). ERPs were first used in the domain of cognitive neuroscience as a complement to studies measuring speed and accuracy of motor responses (see Luck, 2005 for a historical review). ERPs have two main advantages in this regard. First, ERPs provide a measure of ongoing cognitive processing unavailable with traditional performance measures such as speed and accuracy of behavioural responding, which permits an in depth analysis of the stage of processing affected by a given experimental manipulation (Luck, Woodman, & Vogel, 2000). In the usual cognitive experiment, the subject is asked to make a decision following the presentation of a stimulus. The decision is often made using a button press, providing two dependent measures, the speed of responding (or reaction time, RT) and accuracy of responding. Variation in the dependent measures is then used to *infer* the cognitive processes that led to the response. This approach has been criticized as being unscientific because the cognitive processes can only be inferred from the response pattern and cannot be directly observed. ERPs have the advantage that they can be used to observe processing prior to, at the time of, and following the actual behavioural response. A second major advantage of the use of ERP methods is that they can be used in the study of so-called "automatic" processing, processing that occurs independently of attention and the fact that the subject may not be aware that a stimulus has been presented. Automatic processing does not vary when the subject's attention is, for example, engaged in another task and is asked to ignore the stimulus channel of interest. Because the subject does not respond to the to-be-ignored stimulus,

it is difficult to infer the extent of processing based on the absence of a behavioural response. ERPs offer an exquisite means to monitor the extent of processing during so-called pre-attentive or pre-conscious conditions. Indeed, ERPs have been used to monitor the extent of processing during unconscious states such as natural sleep (Campbell & Colrain, 2002; Colrain and Campbell, 2007).

1.2 Theory of signal averaging. A major limitation of the use of ERPs is that their amplitude is very small relative to the ongoing amplitude of the EEG. ERPs are thus not generally visible within a segment of EEG corresponding to the presentation of a single stimulus or the occurrence of a single event. In the waking adult, the ERP amplitudes vary from less than 1 μV to perhaps as large as 20 μV. On the other hand, the amplitude of the waking EEG varies from about 25 to 100 μV. The ERP "signal" is therefore buried in the background "noise" of the ongoing EEG (Picton, 1995). The breakthrough in ERP methodology came in the 1950s with the advent of computer averaging techniques (Dawson, 1954). The ongoing background EEG (activity not related to the eliciting event) is essentially random. Sometimes it is negative-going; sometimes it is positive-going. If a stimulus is presented an infinite number of times, the summation of the positive and negative-going activity should tend toward zero. Thus, over time, the background noise of the EEG should be reduced and eventually cancel out. On the other hand, it is assumed that the response to the stimulus is constant. Over an infinite number of trials, the average of a constant is the constant itself. Experimental paradigms employing ERPs are thus often designed to elicit the response of interest many times so that individual responses to stimuli can be summated. In this process, the EEG collected from a given subject is divided up into segments time-locked to a specific event (e.g., -100 ms to +400 ms around the onset of an auditory of an eliciting stimulus) and these segments are then averaged together. When a

sufficiently large number of stimuli are presented, surrounding fluctuations in electrical activity are smoothed out (as negative and positive noise cancel each other out), while the non-random ERPs become visible (Luck, 2005).

The number of stimulus presentations sufficient to allow the ERPs to emerge from the background EEG is dependent on the amplitude of the component of interest as well as that of the background noise. The degree to which an ERP component is able to stand out against the background EEG, is referred to as the "signal-to-noise ratio" (S/N ratio) (Picton, 1995). S/N ratios deemed acceptable vary across laboratories, but it has been suggested that a minimal ratio of at least 2:1 is acceptable, although 5:1 (signal amplitude that is 5 times greater than that of the noise) or even 10:1 is preferable (Campbell, 2010). Unfortunately, it may take a considerable amount of stimulus presentations to obtain such a high S/N. This is because according to the "square root rule of averaging" the averaging process will result in a reduction of background EEG noise that is inversely proportional to the square root of the number of repetitions of the stimulus of interest (Picton, 1995). Thus, in order to increase the S/N by two (or half the background noise), one must increase the number of stimulus presentations by a factor of four. For example, given an ERP component with an amplitude of 2.5 μV and background EEG measuring approximately 10 μV, the S/N ratio corresponding to a single stimulus presentation would be 1:4. Averaging together the responses to 4 stimulus presentations would result in the S/N ratio increasing to 1:2, while an average of the responses to 16 stimulus presentations would result in a fourfold increase S/N by 4 resulting in a ratio of 1:1. One would need to present 400 trials in order to achieve the "ideal" 5:1 S/N ratio that would allow this component to be largely visible against the background EEG noise. In this thesis, some of the ERP components of interest

might measure less than 1 μV. These will thus require a considerably large number of stimulus repetitions to attain a satisfactory S/N.

Though the averaging process reduces the amount of background noise, it is impossible to remove this noise entirely. The period prior to the onset of the stimulus can be used as an estimate of noise remaining in the averaged ERP. Because no stimulus has yet been presented, the pre-stimulus period should be reflective of random neural activity not associated with a response to any stimulus (assuming the interval between stimulus presentations is sufficiently long). Thus, this pre-stimulus interval should appear relatively flat, if most of the background noise has been reduced sufficiently through the averaging process. For this reason, the pre-stimulus interval is also used to provide a baseline approximating zero voltage from which the ensuing responses are measured.

1.3 ERP Components.

1.3.1 Classification and labelling of components. The ERPs that emerge from this averaging process are composed of a series of negative and positive deflections referred to as "components" that are thought to reflect different aspects of stimulus processing. Different experimental paradigms will reliably elicit a given set of components, which can be classified with reference to the time between the onset of the stimulus and their maximum peak deflection (i.e., their latency). Short-latency auditory ERP components peak within the first 10 ms of auditory stimulus onset, and are thought to reflect activity in the peripheral auditory nerve and the brainstem relay centers. These short-latency components are often called the brainstem auditory evoked potentials (BAEPs). Mid-latency auditory evoked potential components peak between 10-50 ms and are thought to reflect later processing of auditory stimuli in regions including the thalamus and primary auditory cortex. The presentation of any auditory stimulus

will result in the occurrence of the basic, obligatory processing indexed by these short- and mid-latency components. The cognitive and psychological processes that are of most relevance to this thesis (i.e., change detection, attention capture) are reflected by the so-called long latency components, occurring from 50 to 500 ms following stimulus onset.

ERP components can also be classified as either being exogenous (exo = outside) or endogenous (endo = inside) (Sutton, Braren, Zubin, & John, 1965; Donchin, 1978). Exogenous (or sensory) components are those thought to be reflective of processing of the physical features of incoming stimuli and are relatively unaffected by ongoing psychological processes. The short- and mid-latency components would be classified as largely exogenous. Manipulation of physical features of the stimulus might affect the exogenous component. For example, increasing the intensity of the auditory stimulus or its location of presentation could affect an exogenous component. An exogenous component is also said to be elicited independent of psychological processes. In the example above, attending to or ignoring the auditory stimulus would not affect an exogenous component. In contrast, endogenous components are those thought to index psychological or cognitive processes. These components are not strongly dependent on the precise physical features of particular stimuli, but are rather determined by the significance of the stimuli to the subject and ongoing cognitive activities. The long-latency components described above are often classified as endogenous. As an example, the contingent negative variation (CNV) is a slow negative wave that occurs when two stimuli are paired together such that the occurrence of the first stimulus acts as a "warning" that the second (often requiring some form of behavioural response) is about to occur. The CNV occurs following the presentation of the warning tone and is thought to index the subject's building expectation for the second tone (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV represents an ERP that

indexes an internal process driven by the psychological significance of the eliciting stimulus rather than by its physical features, and thus can be classified as endogenous. As further evidence of its endogenous nature, the CNV occurs independent of the physical (exogenous) features of the stimulus. Indeed, it can be elicited by any paired stimuli in any modality (auditory, visual or somatosensory).

ERP components are typically described with reference to their polarity (i.e., whether they are positive- or negative-going deflections), their latency (the amount of time between the onset of the eliciting stimulus and the peak amplitude of the component), their scalp-distribution (the pattern of electrophysiological activity as it varies across the scalp), and the processes they are thought to index (based on the experimental manipulations that typically lead to their occurrence). Different methods for labelling ERP components have been developed. One commonly-employed method uses polarity and typical latency to label components. In accordance with this system, a positive deflection that has been previously shown to occur approximately 300 ms post-stimulus onset would be referred to as the P300. This system has been criticized, however, on the basis that the latency of components can vary across subjects, experiments, and even conditions within the same experiments (Luck, 2005). Thus, a P300 may actually occur as early as 250 or as late as 600 ms depending on the complexity of classification of a relevant stimulus. The component is still however labelled as "P300" because it describes a common psychological process, the detection of a rare, relevant stimulus (Donchin, 1981). An alternative nomenclature has been developed in which components are labelled according to their polarity and their sequential position within the ERP waveform. For example, the label N1 is used for the first negative peak that occurs following presentation of an auditory stimulus while, P2 would be the label given to the second positive deflection. There are also issues with this

system of nomenclature however, as it becomes difficult to label multiple small deflections superimposed on a larger wave or to label newly discovered components (Picton, 1995). For example, P300 was also labelled, by some labs, as "P3" representing the third positive peak in the sequence. Later studies however noted that there may be two sub-components within the P3. These were subsequently labelled as the P3a and the P3b, to reflect the fact that under certain experimental conditions the third positive deflection in an ERP waveform reflected a composite of two differing processes that overlapped temporally but differed in terms of their psychological function and scalp distribution (Polich & Criado, 2006). More recently, positive peaks that can precede and follow the P3a component have also been identified (Wetzel, Widmann, & Schröger, 2011). Rather than updating the labeling system to reflect the new sequential order brought about by the discovery of these additional positive deflections (e.g., by renaming the P3a, the P4a, and shifting the labels of the following peaks accordingly), the terms *early P3a*, *late P3a,* and even *post-P3a* have been suggested for these components. A third nomenclature has also been employed in which components are labelled with reference to their functional significance (Picton, 1995). The "contingent negative variation" (CNV) described previously is an example of a component labelled in this way, as it is named to reflect the subject's expectation of the upcoming stimulus given their awareness of the *contingency* existing between stimulus presentations. In this thesis, a "mismatch negativity" (MMN) will be described. This label refers to a negative component that purportedly reflects a detection of a *mismatch* between the features of an incoming stimulus and that which would be predicted to occur based on the recent auditory past (Näätänen, 1990; Winkler, 2007).

A consistent nomenclature has yet to be established within the ERP methodology. Indeed, most authors use labels stemming from more than one of the above described systems within the

same article, varying in accordance with the particular ERP component being discussed and the label that is most commonly used to connote that component within the extant literature. It has been suggested that the most useful system of nomenclature would involve some reference to both the hypothesized underlying process and the source of the ERP component (Picton, 1995).

1.3.2 Independence of ERP components. ERP 'components' have been defined in different ways. Donchin, Ritter, and McCallum (1978) proposed that a component is a

> source of controlled, observable variability… we try to dissect [the] morphology of the wave in terms of the manipulated variables. Different neuronal aggregates might be activated at different times to different extents in different forms by different values of our critical variables. …ERP data are presumed to represent the activity of intracranial neuronal aggregates. Through careful experimental dissection of the waveforms... it should be possible to partition the observed variance of the ERP waveform into sources of controlled variance we call components. (p. 354)

This definition emphasizes the fact that independence of an ERP component can be determined through its response to the manipulation of independent variables. Thus, a given experimental manipulation might affect one component but not a second component. In turn, the second component might be affected by a different experimental manipulation. Thus, the two components are functionally independent, reflecting different cognitive processes.

A second definition put forth by Näätänen and Picton (1987) emphasizes that independent components are generated in different neuronal populations within the brain. According to this definition a component is

> the contribution to the recorded waveform of a particular generator process, such as

> the activation of a localized area of cerebral cortex by a specific pattern of input ...Whereas the peaks and deflections of an EP can be directly measured from the average waveform, the components contributing to these peaks can usually be inferred only from the results of experimental manipulation. (p. 376)

Both of these definitions acknowledge that a given experimental manipulation will be reliably associated with activation of a particular pattern of neuronal activation as reflected in the different components of an ERP waveform, but place differing emphasis on the degree to which these factors are critical in the definition of these components. The Donchin et al. (1978) definition places more emphasis on the independent functioning of components in response to experimental manipulation, while the Näätänen and Picton (1987) definition stresses the intracranial generator source in the definition of a component.

The scalp distribution of a peak deflection can be used to model the intra-cranial sources of a component (Scherg & Von Cramon, 1986). This is called the "inverse problem." The solution to the inverse problem is not easily solved. This is because a given scalp distribution can occur as a result of the activity of an infinite number of source configurations. On the other hand, the "forward problem", predicting the scalp distribution when the intra-cranial sources are known is solvable. It thus follows that a means to distinguish ERP components is on the basis of their scalp distribution. Components having different scalp distributions must have different intracranial sources (Picton & Stuss, 1980).

The determination of the underlying sources of a component does require the EEG to be recorded from a large number of electrodes, varying anywhere from 32 to 256 different channels. Note, however, that the independence of an ERP component does not require knowledge of the actual intra-cranial source. In accordance with the "forward problem," only the scalp distribution

needs to be shown to vary. A large number of electrodes is however not necessary to make this decision. The recent use of large numbers of EEG channels has, in fact, been questioned, particularly when the scalp distribution of the component of interest has been well established. It has been suggested that in most ERP studies large numbers of electrodes do not provide a significant advantage (Luck, 2005).

The P3a and P3b deflections described earlier can be used as an example of the how the two definitions can be used to delineate the independence of the components. When a subject is asked to attend to a sequence and signal the detection of a rarely occurring stimulus, both a P3a and P3b are elicited. When the subject is now asked to ignore the sequence, the P3b is no longer elicited, but the P3a continues to be elicited. This fits Donchin et al. (1978) definition of component independence. The experimental manipulation (varying the direction of attention in this case) affects P3a and P3b differently. The P3a and P3b also have different scalp distributions. P3a is maximum over centro-frontal areas of the scalp while P3b is maximum over more parietal regions of the scalp. Because the scalp distribution of P3a and P3b is different, they must have different underlying intra-cranial sources. The fact that P3a and P3b have different sources fits the Näätänen and Picton (1987) definition of component independence.

In the Näätänen model, different auditory ERP components are claimed to reflect different aspects of auditory processing. These components can be separated both on the basis of their differential scalp topography and differential responses to experimental manipulations.

2. Näätänen's Model of Auditory Processing

The model of auditory processing put forth by Näätänen (1990) posits that the processing of all encoded auditory stimulus input, whether attended to or not, initially enters a permanent feature detection system that extracts basic features of the stimulus, such as its frequency,

intensity, duration and location. These encoded features are stored in a short-lasting sensory memory (or "buffer"). They are also simultaneously forwarded to three different specialized systems, the temporary feature detector, transient detector, and change detector systems, which differ in the degree to which their activation requires the active attention of the observer. A description of these three systems will follow.

The operations of the first system to be discussed, the temporary feature detection system, require active (or selective) attention. The present thesis is, however, concerned with passive attention and attention-capture. Thus, only a brief discussion of the temporary feature detection system will follow.

Temporary feature detection involves the activities of the central executive and working memory systems. The central executive has a limited capacity to process information. As such, it must selectively choose which of the many stimulus inputs to process and which should be prevented (or gated) from further processing. This selection process involves top down processing. The central executive determines what is relevant depending on present goals. The features of relevant stimuli are stored in a working memory, which is maintained by active rehearsal and as such uses valuable, but limited, central resources. The maintenance of working memory thus requires cognitive effort, vigilance and concentration. Incoming features are compared to those that exist in working memory. If they match, further processing is warranted; if they fail to match, further processing is not warranted and the observer will not become conscious of this information (or at least will not become conscious of it through this route). An example of an activity that might activate this temporary feature detection system would be attempting to identify the sound of a friend's voice within a room of talking people. One would first have to identify the features of the voice in question (e.g., usual range of frequencies). These

features must then be held in working memory in order to allow for a comparison with incoming auditory stimuli. The voice corresponding to the features actively held in the temporary feature detection system will become the focus of the subject's attention. Of course, the recognition of a voice and its specific content (the "conversation") employs a cognitive system considerably more complex than working memory, but it does require working memory. Active attention is dependent on the availability of sufficient cognitive resources. If these resources are used by other current task demands, then the operations of this system will diminish. Näätänen (1990) thus calls this "task dependent processing."

The observer must become aware of auditory stimulus input that is critical for survival, even if their attention is focussed on another extremely resource-demanding task and not attending to the auditory channel. Näätänen's model (1990) thus posits two passive routes (i.e., not requiring active attention) through which interruption of the central executive (controlling the allocation of attentional/cognitive resources) and subsequent attention capture can be initiated. These involve the operations of a transient detector and a change detection system.

2.1 The transient detection system. According to the Näätänen (1990) model, the transient detection system, as its name implies, is uniquely responsible for the detection of changes in transient energy. It is thus activated by changes in stimulus intensity, with its output varying directly with the transient energy of the auditory stimulus. This activation is indexed by a frontro-centrally maximal negative-going ERP, referred to as N1, which peaks approximately 100 ms following stimulus onset (see Näätänen and Picton, 1987 for an extensive review). Accordingly, the amplitude of N1 varies with the intensity and rate of presentation of the eliciting stimulus, with louder, infrequently presented stimuli eliciting larger N1s. Any perceptible auditory stimulus will elicit an N1, even if the subject is not actively attending to it, its amplitude

dependent on only the exogenous, physical features of the stimulus, particularly its intensity and how often it is presented. The N1 is typically immediately followed by a P2, a positivity thought to reflect basic sensory processing. In fact, these two ERPs are often referred to jointly as the N1-P2 complex because they generally occur together in the waking state. In actual fact, the manipulations that affect P2 remain poorly understood (see review by Crowley and Colrain, 2004).

An acoustic signal does not always need to be loud to capture our attention. The second route through which attention capture can be initiated involves a change detector system, which provides a means by which non-obtrusive input can also interrupt the central executive, providing it signals sufficient change from the immediate acoustic past.

2.2 The change detection system. The detection of auditory change requires that the homogenous, repetitive and non-changing acoustic past be stored in memory. This requires the sensory buffer. In the Näätänen model (1990), encoded stimulus features are forwarded and stored in a sensory memory where integration of the features takes place. The features of an incoming, but encoded stimulus are compared to those of the representation stored in sensory memory. If the features match, the representation is strengthened and processing ceases. If, however, the features fail to match, change is detected and the change detection system is activated. Sensory memory is different from working memory in many ways. Critical for this thesis is that sensory memory operates passively and thus does not require active effort for the memory to be maintained. Because it does not require attention, it does not use central resources. Detection of change also does not require attention to be directed to the auditory channel, occurring passively and prior to the time at which the subject becomes conscious of change

(Näätänen, 1990). Thus, like the transient detector system, the change detection system also operates pre-attentively (or pre-consciously).

The operations of the change detection system are often studied by use of the so-called oddball paradigm. In this paradigm, the subject is presented with a frequently occurring and repetitive "standard" stimulus. The standard stimulus will activate the transient detector system and thus an N1 will be elicited. At rare and unpredictable times, a feature of the standard is changed. This "deviant" stimulus, like the standard, will activate the transient detector system and thus an N1 will be elicited. The N1 elicited by the standard and the deviant will however be essentially identical, if both are physically similar. However, because at least one feature of the deviant is different, it does signal change from the past features of the repetitive standard, and it will thus activate the change detector system.

In the Näätänen (1990) model, output of the change detection system can be monitored by a small amplitude (1-2 μV) negativity referred to as the Mismatch Negativity (MMN) that occurs 100-250 ms following stimulus onset. The MMN is maximum over fronto-central areas of the scalp and inverts in polarity at the mastoid and other inferior/lateral areas of the scalp when a nose reference is employed. This scalp topography has been explained by intra-cranial sources located in the auditory cortex of the temporal lobe although contributions from the frontal lobe have also been reported (Rinne, Alho, Ilmoniemi, Virtanen, & Näätänen, 2000). Because the MMN is so small (often less than 1 μV) relative to the background EEG, several hundred stimulus repetitions trials are require to be presented in order to allow the MMN to emerge. The standard and deviant stimuli in an oddball paradigm however need to be presented rapidly, often as frequently as 2 to 4 times per s. The fast rate of stimulus presentation is required because sensory memory fades rapidly, estimates varying between 2 and 10 s (Cowan, 1984; Sams, Hari,

Rif, & Knuutila, 1993). If stimuli are presented slowly, the memory for the standard will have time to fade prior to the presentation of the deviant. Therefore, even though several hundred stimulus presentations may be required to observe the MMN, this can be achieved in a relatively short period of time when a rapid rate of presentation is used.

The MMN is best observed in a difference wave constructed by subtracting the ERPs elicited by the standard from those of the deviant. The subtraction process is illustrated in Figure 1. This subtraction process removes obligatory, exogenous processing that is common to both the standard and deviant (e.g., the N1-P2 complex) isolating the endogenous components unique to the deviant (the MMN and possible subsequent ERPs, elicited as a result of the detection of change).

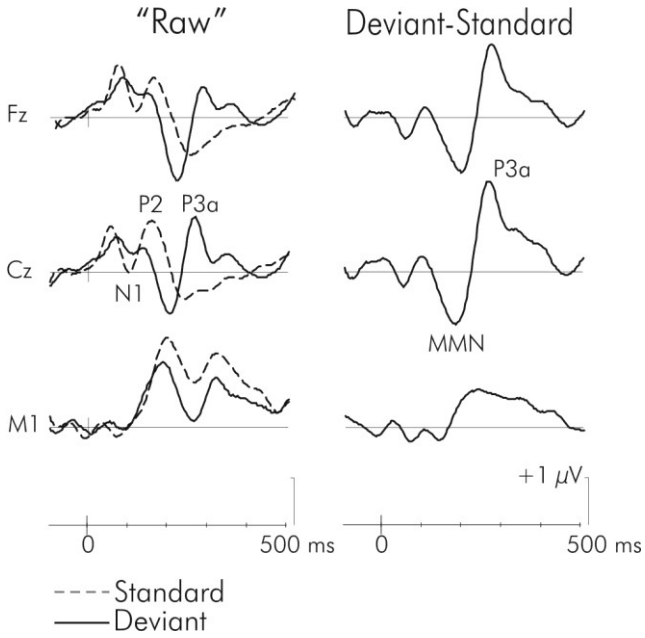

Figure 1. Computing the MMN difference wave. In this example, the subject was presented with a frequently occurring standard stimulus, a 1000 Hz pure tone. In the left column, the "raw" standard waveform is illustrated. The standard elicited an N1 (at about 100 ms) and a later P2, at about 180 ms. On 15% of trials, the frequency of the standard was changed to 2000 Hz. This deviant stimulus also elicited an N1. An additional negativity that overlaps with the P2 is apparent in the deviant "raw" waveform. This is the MMN. The MMN is however best observed in the deviant-standard waveform (right column). The subtraction process removes processing that is common to both the standard and the deviant. The MMN is maximum over fronto-central areas of the scalp but inverts in polarity (recorded as a positive potential) at the mastoid. In this example, a later positivity, the P3a, is also apparent following presentation of the deviant.

3. Fresh Afferents and the Separability of the MMN and N1

Care must be taken ensure that the standard and deviant stimuli are essentially physically identical except for a small change in a specific feature, in order to properly isolate the endogenous components associated with the change detection process (Deacon, Gomes, Manette Nousak, Ritter, & Javitt, 2000). For this reason, the N1-P2 complex following presentation of both the standard and deviant should be essentially identical (Deacon et al., 2000). Many studies have however shown that the amplitude of the MMN increases when the extent of change between the standard and deviant increases. In these instances, the standard and deviant may be physically very different. In some of these instances, the deviant will elicit a larger N1 than the standard. For example, critical to this thesis will be the detection of a change in stimulus intensity. A deviant that is constructed by increasing its intensity relative to the standard will indeed elicit an MMN because it represents stimulus change. However because this deviant contains more energy (i.e., is more intense) than the standard, it will also elicit an N1 that is larger in amplitude than that elicited by the standard. N1 occurs at about the same time as the MMN and has a similar fronto-central scalp topography. A large negativity will be apparent in the difference wave. This negativity could be reflective of the increase in the amplitude of N1 following presentation of the deviant (it is more intense). It could however be reflective of the MMN (the deviant signals change). The composite N1 and MMN is sometimes called a deviance-related negativity (DRN) in which the relative contribution of the change and transient detection systems is unclear. Deviants that are physically very different in features from the standard may also result in greater activation of the transient detector system. As an example, the auditory system is organized in a tonotopic manner (Hudspeth & Konishi, 2000). At various levels in the auditory system, neuronal populations selectively respond to specific frequency

ranges. Thus, the detection of a change in frequency does not necessarily require a memory comparison system. Because the standard tone is presented frequently, the neurons of the afferent neuronal population responding to the frequency of the standard will tend to be in a refractory state. Thus, the output of the transient detector system and thus the amplitude of N1 will be reduced. The neurons of the afferent population responding to the deviant will, however, remain "fresh," and the output from the transient detector system will be greater. Thus, the amplitude of N1 will be larger. The "fresh afferent theory" posits that the negativity seen in a deviant-standard waveform reflects the differences in the amplitude of the N1s elicited by the two stimuli, rather than the memory-comparison-based MMN. According to this interpretation, there is no need for a separate "change detection system" as differences in deviant and standard processing can be entirely explained by differential activation of the transient detection system (May & Tiitinen, 2010). In Figure 1, the frequency of the standard was 1000 Hz and that of the deviant, 2000 Hz. This frequency difference is quite large and thus the deviant will activate a neuronal population different from that of the standard. Thus, the negativity that is labelled as an MMN in the figure could also reflect an enhanced N1, as the rarely presented deviant would activate a fresh neuronal population.

On the other hand, there is, ample evidence refuting the fresh afferent theory and supporting the separability of the MMN and N1 responses. For example, studies have demonstrated differences in the latency (N1 occurs earlier than the MMN) and loci of generation for the MMN and N1 components (see Näätänen, Jacobsen, &Winkler, 2005 and Näätänen, Kujala, & Winkler, 2011 for a review). Additional evidence for the separability of these two ERP components comes from studies demonstrating that the MMN can be elicited in situations in which an N1 response is absent, such as in response to the omission of a tone from a pre-

established sequence (Tervaniemi, Saarinen, Paavilainen, Danilova, & Näätänen, 1994). Nonetheless, the activation of fresh neuronal populations and consequent increased activation of the transient detection system complicates the disentanglement of the resulting DRN into the N1 and MMN components elicited in the traditional oddball paradigm, particularly when the extent of difference between standard and deviant stimuli is particularly large. The fresh afferent theory is also only applicable to situations in which specific neuronal populations have been demonstrated to respond to different features of the stimulus. Of interest to this thesis, although there is considerable evidence for tonotopic frequency-specific neuronal populations, there is far less evidence for ampliotopic specific populations. Thus, when the deviant is created by decreasing the intensity of the standard, this should result in reduced activation of the transient detection system compared to the standard. In this case, the amplitude of N1 will be smaller for the deviant than the standard. The larger negativity that is apparent upon presentation of the deviant can thus only be attributed to increased activation of the change detection system and thus, the MMN.

4. Factors Affecting the MMN

Initial studies in the 1980s and 1990s investigated the many factors that affect the amplitude and latency of the MMN. These studies largely employed the oddball paradigm. Almost any type of stimulus change relative to the standard stimulus, including its frequency (Näätänen, Gaillard, & Mäntysalo, 1978), intensity (Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1989), location (Schröger & Wolff, 1996) and duration (Näätänen, Paavilainen, & Reinikainen, 1989) were found to elicit the MMN. Importantly, the amplitude of the MMN was shown to vary directly with the extent of stimulus change; the greater the extent of change, the larger the MMN, and the latency of the MMN was shown to be shorter when the extent of

change is large (Tiitinen, May, Reinikainen, & Näätänen, 1994). A number of studies have also examined the effect of stimulus probability on the MMN. Most indicated that the amplitude of the MMN increases as probability of the occurrence of the deviant decreases (Imada, Hari, Loveless, McEvoy, & Sams, 1993; Javitt, Grochowski, Shelley, & Ritter, 1998; Sonnadara, Alain, & Trainor, 2006). The concept of probability can however be thought of in two different ways. When referring to the deviant, sequential probability is the term used to denote the probability that a deviant will occur within a sequence of tones and is equal to the ratio the number of deviant tones to the total number of tones presented. Alternatively, the term temporal probability has been used to refer to the amount time separating presentations of the deviant. If the sequential probability of deviants to standards is 1:10 and a stimulus is presented every 0.5 s, the temporal probability of occurrence is 1 deviant every 5 s. However, if a stimulus is now presented every 2 s and the sequential probability remains the same (i.e., 1:10), a deviant now occurs much less often (every 40 s). Sabri and Campbell (2001) examined the effects of sequential and temporal probability on the MMN. When sequential probability was held constant, they noted that the amplitude of MMNs elicited by a change in stimulus frequency was larger when stimuli were presented with a longer stimulus onset asynchrony (SOA). Similarly, when the temporal probability was held constant, lower sequential probability was associated with larger MMN amplitudes.

Sculthorpe and Campbell (2011) noted that previous studies finding an effect of deviant probability had generally employed oddball paradigms, using frequency deviants. Frequency deviants do risk the confound of also activating fresh afferents. The effect of probability seen in these studies might thus actually reflect differences in activity of the transient rather than the change detection system as the relatively lower probability of occurrence of the deviant stimulus

would also be associated with reduced refractoriness of the neuronal populations associated with the N1 response to this stimulus. Sculthorpe et al. (2011) tested this hypothesis by employing a concrete pattern with stimuli alternating in frequency (ABABABAB, A=841 Hz, B=1189 Hz) in which deviance was created via the occasional repetition of a stimulus (ABABABA**A**ABA) or (ABABABAB**B**BA). Because the A and B tones served as both the standard and the deviant, the degree of refractoriness of neuronal populations activated by deviants and standards could not vary (as standard and deviant stimuli are physically identical). In addition, because the deviant was physically identical to the preceding standard, a *decrease* in the amplitude of N1 amplitude would have been expected as a result of its repetition. The authors failed to find an effect of deviant probability on the amplitude of the MMN. Previous studies indicating an effect of deviant probability on the MMN amplitude thus might well be explained by an effect on the transient rather than the change detection system.

5. Updating the Classic Model of Change Detection

The Sculthorpe et al. (2011) study provides a strong example of the difficulties associated with interpreting the results of studies employing the oddball paradigm to examine change detection. The initial, "classic" Näätänen model of auditory processing was largely based on the findings of studies employing this paradigm. Recent studies have begun to examine the processing of auditory change that involve violations of more complex concrete and abstract patterns (Alain, Woods, & Ogawa , 1994; Bendixen, Schröger, & Winkler, 2009; Bendixen, SanMiguel, & Schröger, 2012; Horváth, Czigler, Sussman, & Winkler, 2001; Nordby, Roth, & Pfefferbaum, 1988; Paavilainen, Jaramillo, & Näätänen, 1998; Paavilainen, Degerman, Takegata, & Winkler, 2003; Sculthorpe, Collin, and Campbell, 2008; Todd, Myers, Pirillo, & Drysdale, 2010). In many of these studies, a frequently occurring pattern forms a standard sequence and

deviants are created by the violation of the pattern. For example, in the sequence A, B, C, D, E, the frequency of the stimulus gradually increases from A to E. This pattern could be broken by a decrease in frequency (A, B, C, B, E) which would serve as the deviant. Alain et al. (1994) and Sculthorpe et al. (2008) employed simple, concrete patterns of equally probable tones alternating in frequency. Deviants were created by the repetition of a physically identical stimulus (ABABABA**A**AB), and were successful in eliciting an MMN. In the visual domain, visual MMNs have also been elicited by similar alternating (ABABAB) patterns (Czigler, Weisz, &Winkler, 2006; Stefanics, Kimura, & Czigler, 2011).

The findings of studies such as these challenge the early interpretation of the MMN as representing the detection of a change in the *physical* parameters of an auditory stimulus relative to preceding stimuli, as the deviant in many cases is, in fact, physically identical to the sound directly preceding it. In response to issues such as these, attempts have been made to update the interpretation of the process indexed by the MMN. For example, in a review Winkler (2007) suggested that, rather than signalling a mismatch between the physical parameters of an incoming stimulus and those encoded in a trace stored in sensory memory, the MMN signalled more of a *psychological* mismatch between the parameters of incoming stimuli from that which would be predicted based on regularities extracted from the preceding auditory stimulation. The usual oddball paradigm (AAAAABAAA) can also be considered to be a special patterned sequence. The frequently occurring standard establishes a rule, A follows A, and this rule is violated by the presentation of the deviant. The elicitation of the MMN can thus be considered to be because of physical change (B is physically different from A) or psychological change (B violates the expectation of A). According to Winkler's (2007) interpretation, the "trace" that would lead to MMN generation would consist of a predictive model made up of representations

of regularities extracted from the preceding auditory stimulation which could produce extrapolations to future sound events. These representations would include a rule(s) corresponding to regularities extracted from analysis of the recent auditory past (e.g., a high frequency tone will be followed by a low frequency tone), sensory information regarding the particular tones embedded within the regularity, and an ongoing representation of the most recent sound presented (sensory buffer). By expanding the notion of the "trace" being violated to include a model of the relation between stimuli presented, Winkler's (2007) interpretation of MMN generation helps to account for the findings of studies employing abstract patterns as well as concrete patterns that are more complex than the oddball pattern. Indeed, Näätänen has recently updated his model of auditory processing to reflect these changes in the interpretation of the change detection process indexed by the MMN (Näätänen et al., 2011).

6. Intrusion into Consciousness

In the classic Näätänen model (1990) and also in the updated model (Näätänen et al., 2011), both the operations of the transient and change detection systems are claimed to be carried out prior to awareness (or consciousness) that the auditory stimulus has occurred. Thus, these systems are said to operate at the level of the pre-conscious. They are also said to operate independent of attention (i.e., pre-attentively). Thus, even if the subject is engaged in another cognitive task, change in an unattended auditory sequence will still be detected. The effects of attention and consciousness on the MMN have been studied extensively and will be discussed in further detail in a later section of this thesis.

Critically, when the output of the either the transient or change detection system reaches a certain variable threshold, ongoing cognitive activity controlled by the central executive will be interrupted. Attention may then be switched to the auditory channel and the contents of sensory

memory will be probed, allowing for the conscious perception of the auditory experience. As referred to above this is often called attention capture. It is also referred to as an "intrusion into consciousness". The switching of attention to stimuli deemed salient by these systems is thought to be indexed by a different later ERP, the P3a, a centro-frontally maximal positivity, peaking around 250-350 ms (Escera, Alho, Winkler, & Näätänen, 1998). The centro-frontal topography of this response may reflect the interruption of the frontally located central executive which controls the allocation of attentional resources (Escera, Alho, Schröger, & Winkler, 2000). During instances of involuntary attention capture, the content of sensory memory, representing the immediate acoustic past, become available to the limited capacity attentional system and is evaluated for its relevance. In most cases, this information is not deemed to be sufficiently urgent or significant to the organism. It is thus not processed further and attention is redirected back to the ongoing task. If however, the contents of sensory memory contain information that is highly relevant to the organism, this information is likely to be consciously perceived and evaluated further.

Independent, behavioural evidence for the attention-capture function underlying the P3a was first provided by studies employing a paradigm created by Schröger and Wolff (1998). In this paradigm, subjects were presented with equiprobable tones of short and long duration and the frequency of the tones was varied between a high-probability standard frequency and a low-probability deviant frequency. Subjects were asked to behaviourally discriminate the duration of the tones (e.g., through pressing a button) and thus were presumably not actively attending to the frequency of the tones. Even though the frequency deviant stimuli were not relevant to the task, they did result in deterioration of performance. Accuracy decreased and RTs increased. This thus provided convincing evidence of the fact that acoustic change resulted in "distraction." In

addition, the deviant stimuli elicited an MMN, reflecting the automatic detection of acoustic change. They also elicited a large P3a in accordance with attention capture and thus distraction away from the demands of the primary task (Schröger, Giard, & Wolff, 2000). Results such as these have been viewed as providing evidence for the long-prevailing view that the P3a serves as an index of the distraction or "attention capture" process.

6.1 Attention capture and intensity change. Increases in stimulus intensity are particularly obtrusive. This is probably because a deviant created by increasing the intensity of the standard (i.e., an increment deviant) results in greater activation of both the transient and the change detector systems. On the other hand, a decrease in intensity (decrement deviant) will activate only the change detector system. In the Näätänen model, attention capture and the associated P3a can result from sufficient activation of either the transient or change detection systems. The nature of the types of intensity change capable of eliciting the P3a and initiating the attention capture process has been a subject of recent investigation. In a study conducted by Rinne, Särkkä, Degerman, Schröger, and Alho (2006), participants were presented with an oddball task in which the intensity of a frequently occurring standard was set at 60 dB HL (about 75-80 dB SPL). The intensity of a rarely presented deviant either decreased by 3, 6 or 9 dB or increased by 3, 6, or 9 dB. The pitch of the stimuli (i.e., both standards and deviants) was set at random to either 186 or 196 Hz, with equal probability of occurrence. As in the Schröger and Wolfe (1998) study, subjects were asked to press one button upon detection of the low frequency and another button upon detection of the high frequency stimulus. The intensity of the deviant was thus irrelevant to the task. The intensity increment elicited a P3a. The intensity decrement did not. In spite of the absence of a P3a following presentation of the decrements, both the increments *and* the decrements caused a deterioration in performance on the discrimination task.

Larger intensity changes, whether increments or decrements, resulted in lower hit rates and longer reaction times. Hit rates were nevertheless significantly lower in response to large intensity increments than to large intensity decrements, indicating that intensity increments were more distracting than intensity decrements. Still, there was evidence of behavioral distraction following the presentation of the decrement, yet a P3a was not elicited. The authors interpreted these findings as an indication that the attention capture process and the P3a response can only be triggered via the transient detector route. The attention capture process cannot be activated by the change detection system alone. There are issues with this interpretation. Because the dB scale is logarithmic (i.e., not linear), a 9 dB increase represents a much larger change in stimulus energy than a 9 dB decrease in intensity. Thus, differences in response to the increment and decrement stimuli might have resulted from the larger extent of change from the standard in the case of the increment deviants. Had much larger decrements been employed, they may also have sufficiently activated the change detector system to result in the interruption of the central executive and the subsequent elicitation of the P3a.

Researchers employing larger intensity decrements have, in fact, reported that these deviants do indeed elicit a P3a. For example, Muller-Gass, Stelmack, and Campbell (2006) presented subjects with 80 dB SPL, 1000 Hz standard tones that were occasionally replaced by a large frequency deviant (80 dB, 1050 Hz,) or a small intensity decrement (70 dB, 1000 Hz) in one condition and by small frequency deviant (80 dB, 1016 Hz) or a large intensity decrement (60 dB, 1000 Hz) in a second condition. While both the large intensity decrement and the large frequency deviant elicited a P3a, the small decrement and small frequency deviant did not. Thus, deviants representing large, but not small, degrees of deviance did elicit a P3a. Muller-Gass, Macdonald, & Campbell (2007) examined the issue of the direction of stimulus intensity change

in more detail. They employed an oddball paradigm in which a to-be-ignored auditory sequence consisted of an 80 dB SPL standard and either a +10 dB increment or a -20 dB decrement in intensity (i.e., 90 dB SPL and 60 dB SPL deviants respectively). Both elicited a P3a, although the P3a was significantly larger for the increment.

6.2 Attention capture and the P3a. Recent research has questioned the original notion that P3a reflects the actual switching of attention to a potentially more relevant channel. As alluded to previously, Wetzel et al. (2011) discussed the possible presence of early and later P3a components, with early components proposed to index processing related to preparation for a possible attentional switch, and later components reflecting the switch itself. In a very recent study, Wetzel, Schröger, and Widmann (2013) had participants engage in a primary visual task in which they were asked to sort targets according to different categories via a button press and presented an irrelevant, "to-be-ignored" auditory oddball sequence in the background. In one condition, the timing between the presentation of auditory and visual stimuli was synchronized such that the irrelevant auditory tones were always followed by presentation of the to-be-attended visual targets. In a second condition the time between the two types of stimuli was varied and did not follow any set pattern. The visual targets only followed the auditory tones on 50% of trials. In the first condition, the auditory tones, although irrelevant, could act as cues to the subsequent presentation of the visual task stimuli. This was not the case in the second condition. Auditory deviants in both conditions were successful in eliciting a P3a and in the classical interpretation of this component, should have resulted in a switch of attention away from the visual task with a resulting deterioration in performance. This was the case in the first condition; the presentation of the deviant auditory stimulus did lead to increased reaction times to visual targets, providing evidence that attention was diverted to the irrelevant auditory channel, distracting attention away

from the relevant visual task. The presentation of the auditory deviant did not have an effect on performance in the second condition, however, even though it did elicit a P3a. The authors interpreted these findings as indicating that the process indexed by the P3a does not reflect the actual switching of attention (attention capture) per se, given that the two (i.e., distraction and the P3a) appeared separable. They suggested that the P3a may be a necessary, but not sufficient, step in the attention capture process that represents an evaluation of the relevance of incoming stimuli, and that this evaluation does not employ any of the attentional resources required for completion of the primary task. Further, they posited that distraction may be more likely to occur in cases in which distracting stimuli provide information relevant to the ongoing task. Wetzel et al. (2013) did not however speculate about the possible role of an early and late P3a in this context. The exact nature of the P3a is thus currently a subject of debate. While all appear to agree that there is strong evidence of the P3a's relation to attention capture and distraction, further research will be needed to clarify the precise nature of its underlying processes.

7. Automaticity of Auditory Processing

In order for the transient and change detection processes to be most protective to an organism, they need to operate regardless of the nature and extent of other ongoing cognitive activities. In cognitive psychology such processes would be claimed to occur *automatically*, independent of the direction or the strength of attention. Importantly, as alluded to earlier, Näätänen's model of auditory processing proposes that all auditory stimuli are analyzed for their sensory content and represented in sensory memory, whether the channel in which they occur is attended to or not (Näätänen, 1990). Further, this model holds that attention does not affect the quality or decay of this information within sensory memory. Thus, according to this model, the amplitude and morphology of the MMN should not vary according to the direction of the

subjects' attention. Thus, "what the subject is doing" will have little effect on the MMN. Näätänen (1990) does however concede that the threshold for the interruption of the central executive can vary, depending on a number of factors such as ongoing task demands and individual differences.

Näätänen's view of basic sensory processing and the change detection process has been referred to as a *strong-automaticity theory* (Hackley, 1993). This view can be contrasted with what Näätänen (1986) referred to as *gain theories*, which posit that sensory processing of attended stimuli is facilitated (resulting in enhanced stimulus representations) and the processing of unattended stimuli is suppressed (resulting in degraded stimulus representations) (Hackley, 1993; Woldorff, Hansen, & Hillyard, 1987).

The effects of attention and task demands have been studied extensively over the past 25 years, typically through the manipulation of selective attention. Attention requires the subject to choose between competing inputs. The subject must thus selectively choose which channel should be attended and thus merits additional processing and which channel should be ignored and thus further processing should cease. In selective attention paradigms, subjects are therefore presented with two (or more) stimulus input channels concurrently and are asked to restrict their attentional focus to only one of these. Subjects are often required to respond behaviourally to target stimuli presented within the "attended" channel, with this overt response serving as evidence that subjects' attention was indeed directed toward the intended channel. Selective attention paradigms in which the "to-be-attended" and "to-be-ignored" channels are presented within the same modality (e.g., audition) are referred to as *intramodal* paradigms. Early studies examining the effects of attention on stimulus processing often employed an intramodal dichotic listening task, in which subjects are instructed to attend to stimuli presented in one ear while

ignoring stimulus input presented to the other ear. Woldorff and Hillyard (1991) employed a paradigm in which frequently occurring standards and rarely presented deviants were presented in both ears, while the subject was asked to detect the deviant in the attended ear. The MMN was larger when the deviant was attended compared to when the deviant occurring in the same ear was ignored. Other labs using different paradigms have since reported similar results, a larger MMN when the deviant was attended compared to ignored (Alain & Woods, 1997; Arnott & Alain, 2002). Näätänen (1991, 2005, 2011) has however insisted that the enhanced MMN in intramodal studies can be explained by the effects of attention on another negativity, the N2b, which overlaps both spatially and temporally with the MMN. The N2b typically peaks approximately 200-300 ms following stimulus onset and is thought to reflect detection of deviants or "target" stimuli in the attended channel. The N2b does not occur (or is much reduced) when the deviant occurs in a to-be-ignored channel. (Sams, Alho, & Näätänen, 1984; Sams, Paavilainen, Alho, & Näätänen, 1985). Thus, the larger apparent MMN occurring in the attended channel was also claimed to be another example of a DRN, in this case a composite MMN+N2b. Researchers have attempted to circumvent the problem of the overlapping N2b by investigating the effects of attention on the change detection process using *intermodal* selective attention paradigms. Subjects are asked to direct their attention to a primary task carried out in a different modality (often the visual modality) and ignore the stimulus sequence occurring in the auditory channel. Because the auditory sequence is to-be-ignored, the occurrence of the deviant stimulus should elicit an MMN, assuming it is not affected by attention. It should not however elicit an N2b, because this does not occur when the auditory sequence is ignored. In these studies, the difficulty of the relevant, to-be-attended visual task is manipulated with the rationale that an easy visual task would make minimal demands on cognitive resources, and allow some to be available

to also sample (or eavesdrop on) the auditory channel. A difficult task would, on the other hand, make such large demands on available central resources that few would be available to sample the auditory channel. A large number of intermodal studies have been carried out. Most of these studies failed to find an effect of visual task difficulty on the MMN elicited by the irrelevant auditory deviant (e.g., Alho, Woods, Algazi, & Näätänen, 1992; Harmony et al., 2000; Kathmann, Frodl-Bauch, & Hegerl, 1999; Otten, Alain, & Picton, 2000). Many of these studies could however be criticized because the difference in performance between the easy and difficult tasks did not vary sufficiently or the rate of presentation of the visual stimuli was so slow that subjects could have sampled the auditory channel between stimulus presentations. Muller-Gass et al. (2006) carefully controlled for many of these possible confounds. The difficulty of the visual task did not affect the morphology of the MMN, suggesting that it was elicited automatically, independent of the availability of attentional resources. The amplitude of the P3a, did, however, vary with the extent of task demands, with more difficult tasks associated with a reduction in the amplitude of the P3a.

The Muller-Gass et al. (2006) study employed an oddball paradigm in which both discrete visual and auditory stimuli were presented rapidly within a sequence. Because the visual stimuli were presented discretely, it might still have been possible for subjects to also sample and process the auditory stimuli between presentations of the visual stimuli. To test this possibility, they asked subjects to divide their attention between the auditory and visual channels and thus detect changes in either modality. Presumably they should have been less able to detect the changes in the visual targets when attention was divided between the visual and auditory channels than when attention was focused only on the visual channel. This would have been particularly the case when the visual task was very difficult. The results did not support this

assumption. Subjects were able to detect both the visual and auditory deviants with a high degree of accuracy. This provided strong evidence that subjects were capable of sampling the auditory channel even if they were not required to do so.

In an attempt to overcome the possibility redirection of attention during the time between presentation of the visual stimuli, Sculthorpe et al. (2008) employed a continuous, rather than a discrete, visual task. Subjects were engaged in a continuous visual multiple object tracking task (MOT) in which objects moved at random around a computer monitor. Some of the objects were designated to be targets and an equal number to be nontargets. The targets and nontargets were physically identical and at the beginning of the task, the targets were cued. Subjects were asked to button-press upon detection of a colour-change in the targets, but to withhold responding to identical colour changes in nontargets. An irrelevant auditory pattern ABABAB (in which A and B were different tones varying in frequency) was presented in the background. In different conditions, the two tones were separated by a small (one semitone) or by a large (6 semitones) degree of deviance. The difficulty of the visual task was manipulated by varying the number of objects to be tracked. Presumably again, a difficult visual task would allow fewer attentional resources to be available for the co-processing of the auditory stimuli than an easy visual task. Importantly, because a continuous visual task was employed, subjects would not have been able to sample the auditory channel between stimulus presentations, particularly during the difficult visual task. Both auditory deviants elicited an MMN, its amplitude varying with the extent of separation between the standard and the deviant. The difficulty of the visual task did not however affect the amplitude of the MMN. Other studies have also employed continuous visual tasks to study the effects the effects of visual load on the MMN. Most of these studies have presented auditory oddball sequences in the background. The results are inconsistent; some studies have

found a reduction in MMN amplitude when subjects are carrying out difficult as compared to easy continuous visual tasks (Yucel, Petty, McCarthy, & Belger, 2005a, 2005b), while others have found an increase in MMN amplitude during more difficult tasks (Restuccia, Della Marca, Marra, Rubino, & Valeriani, 2005; Zhang, Chen, Yuan, Zhang, & He, 2006). In many of these studies, the features of the auditory standard and deviant stimuli widely differed. In some cases, the standards were pure tones while the deviants were very novel, environmental sounds. Thus, the deviants were also more likely to activate the transient detector system than the standards, bringing into question whether the effects observed were specific to the change detection system and the MMN.

Almost all cognitive tasks require the subject to sustain attention. The memory comparison operation reflected by the MMN is an exception; it can be elicited independent of attention and task demands. For this reason, the MMN provides is an excellent tool in both the clinical and applied fields in which the ability of patients or other groups (e.g. children, the elderly) to sustain attention might compromise the results of more traditional cognitive tasks. Its use in these settings has been extensively reviewed by Näätänen, Paavilainen , Rinne, and Alho, (2007) and Näätänen et al. (2012). For example, the MMN has been used to examine change detection in studies of ageing (e.g., Alain & Woods, 1999; Cooper, Todd, McGill, & Michie, 2006; Czigler, Csibra, & Csontos, 1992), neurological populations (e.g., Schroeder, Ritter, & Vaughan, 1995; Yokoyama, Nakashima, Shimoyama, Urakami, & Takahashi, 1995) and psychiatric populations (e.g., Fisher, Labelle, & Knott, 2010; He et al,. 2010; Todd, Michie, Schall, Ward, & Catts, 2012). It has also been used in the applied setting, for example in the study of the effects of drugs (e.g., Hirvonen, Jääskeläinen, Näätänen, & Sillanaukee, 2000; Knott et al., 2009; Murakami et al., 2002), individual differences in mental abilities (e.g., Beauchamp

& Stelmack, 2006; Houlihan & Stelmack, 2012) and personality (e.g., Franken, Nijs, & Van Strien, 2005; Matsubayashi et al., 2008).

8. The Present Thesis

The primary question addressed by this thesis is whether an increase in stimulus intensity is indeed more salient and biologically relevant than a decrease in intensity. This thesis consists of 4 experiments described in 3 articles. Each examines the differences in processing of deviant stimuli that represent higher as compared to lower intensity than would be predicted based on the recent auditory past. The way in which deviance is achieved varies across the studies of the thesis, with some deviants representing a physical change relative to the immediately preceding stimuli (LLLLL**H**LLL), and others representing a psychological change created by violation of a more complex pattern (LHLHLH**H**HL).

The general questions asked in this thesis are:

Study 1

- Is a physical increase in intensity processed differently than a decrease in intensity?
- Will this differential processing continue during an unconscious state, natural sleep?

Study 2

- Will differential processing of increment and decrement stimuli continue when deviance-related processing is isolated to the change detection system?
- Will varying the extent of difference between standard and deviant tones in a concrete alternating pattern (designed to isolate deviance-related processing to the change detection system) have an effect on the amplitude and morphology of the MMN?

Study 3

- Can the physical differences between the deviants themselves (63 dB vs 90 dB) account for the differential processing of psychological increments and psychological decrements in an alternating intensity pattern found in Study 2?
- Can temporal integration account for the differences observed in the processing of psychological increment and psychological decrement stimuli?

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Chapter 2

Study 1. P3a measures of the intrusion of central executive functioning during natural sleep

Rationale. A stimulus of higher biological relevance should presumably be able to intrude into consciousness and capture the attention of an organism more readily. The Muller-Gass, Macdonald, Schröger, Sculthorpe, and Campbell (2007) described earlier investigated the influence of visual task demands on the processing of increment and decrement deviants in an oddball task. The increment elicited a large amplitude negativity, probably a DRN, a result of the summation of both N1 and MMN processes (activation of both the transient detector and change detector systems). The decrement also elicited a smaller amplitude negativity. As mentioned previously, both deviants elicited a P3a, which was not however affected by the demands of the continuous visual task. The P3a was however much larger to the increment than to the decrement. Thus, so relevant is an increase in the intensity of a stimulus that it will result in a very robust switching of attention even when the ongoing to-be-attended cognitive task requires continual vigilance and even when this task is extremely demanding.

The purpose of selective attention is to allow the observer to become conscious of that which is deemed to be relevant. At the same time, the observer should not become conscious of that which is deemed to be irrelevant. Unfortunately, during the waking state, the observer is almost never completely unaware of their external environment. In the typical MMN study, if asked, the observer will almost always report at least partial awareness of the auditory channel and more importantly, awareness of the occurrence of the deviant. Thus, in spite of the very clever designs of studies of selective attention, none have been able to prevent at least partial awareness of information in the unattended channel. A major premise of most theories of auditory processing is that a good portion of the processing takes place in the pre-conscious. To test this assumption requires a period of time at which consciousness of the external environment

approaches a zero level. This may only be possible during unconscious states such as coma, general anesthesia and natural sleep.

In order to sleep, the processing of almost all stimulus input must be inhibited. Nevertheless, this inhibition cannot be complete as this would place the sleeping organism in a state of extreme vulnerability to its external environment. Mechanisms must allow for sleep to be reversed upon presentation of highly relevant input, such as those that result in a switch of attention in the waking state and result in the elicitation of a P3a. The effect of sleep on the mechanisms responsible for detection and awareness of changes in auditory intensity were thus examined in the initial study.

The purpose of Study 1 of this thesis was determine whether increments in stimulus intensity would be more disruptive to sleep than decrements in intensity. A problem with the Muller-Gass et al. (2007) study was that subject might have still been able to sample the auditory channel in spite of the demands of the visual task. This would not be possible during an unconscious state, natural sleep.

Study 1 was published in *Neuroreport* in 2008, and is formatted in accordance with the requirements of that journal.

Macdonald, M., Jamshidi, P., & Campbell, K. (2008). Infrequent increases in stimulus intensity may interrupt central executive functioning during Rapid Eye Movement sleep. *Neuroreport*, 1*9*, 309–13.

1. Introduction

The purpose of this study is to examine the extent to which an observer can potentially become aware of an increase or decrease in the intensity of a frequently occurring acoustic stimulus during an unconscious state, natural sleep. The extent of information processing to acoustic stimuli was determined by the recording of event-related potentials (ERPs) during all-night sleep.

Näätänen [1] has developed an elegant model to explain how unattended stimuli can reach and "intrude" into consciousness. A positive-going ERP component, P3a, peaking at about 250-300 ms appears to be intimately related to stimulus evaluation and awareness that an irrelevant and unattended auditory stimulus has been presented [2]. P3a is maximum over centro-frontal areas of the scalp, perhaps reflecting an intrusion into the frontal central executive controlling consciousness. It is often elicited in the so-called oddball task. A subject is presented with a frequently occurring "standard" stimulus. At rare and unpredictable times, a physical feature of the standard is changed. This deviant may elicit a P3a if it is particularly obtrusive (for example, very intense) or if the extent of change is particularly large. The deviant also elicits an earlier N1 and/or mismatch negativity (MMN) components, the former reflecting the detection of transients (such as the onset or offset of a stimulus), the latter reflecting the detection of stimulus change.

In the Näätänen model, both N1 and the MMN are said to occur in the pre-conscious, relatively independent of attention and ongoing task demands (see [3] for a review). If the output of the transient or change detection systems is sufficiently high, ongoing cognitive activities may be interrupted, and the P3a will be elicited. Näätänen does however emphasize that the success of the interrupt is much affected by the extent to which the limited capacity

central executive is already engaged. Thus, the amplitude of P3a is dependent on the strength of output of the transient and/or change detection systems but also on the availability of cognitive resources. The P3a elicited by an irrelevant acoustic deviant has been demonstrated to be affected by the demands of a primary visual task. The auditory P3a is attenuated when the visual task is difficult compared to when it is easy [3-5] although not all studies have reported these effects [6-8].

Sleep marks the transition from a conscious to a largely unconscious state. Waking ERPs undergo remarkable changes during the sleep onset period (see [9,10] for reviews). During non-REM (NREM) sleep, the amplitude of N1 is near baseline level while the amplitude of P2 may increase relative to the waking state [11]. This has been explained by the removal of a long-lasting attention-related waking negativity that overlaps and summates to N1 and P2. The MMN elicited by both frequency and intensity deviants is also very difficult to record during NREM [12-15]. There is also good evidence that the frontal lobe is largely deactivated during NREM sleep. The absence of the N1 or MMN and the deactivation of the frontal central executive may explain why a P3a cannot be recorded during NREM. Cote et al. [16] presented an oddball paradigm in which the rare deviant stimulus was either a large frequency change (1000 vs 2000 Hz) or large intensity increment (80 vs 100 dB SPL). Neither deviant elicited a P3a during NREM sleep. Stimuli were however presented relatively slowly (every 1-2 s). Memory for previous stimulus presentations may thus have faded prior to the presentation of the obtrusive deviant [15]. On the other hand, a large amplitude negative ERP, peaking at 350 ms was visible, especially following presentation of the increment. N350 can only be elicited during sleep and may be related to the need to inhibit processing of stimulus input, thus protecting sleep [17].

Sleep is not a unique state. REM sleep is marked by cortical arousal. Both N1 and the

frequency-elicited MMN can be recorded during REM although their amplitude is much attenuated [12, 13, 18]. Cote and Campbell indicated that a deviant that represented a very large 20 dB increase in stimulus intensity did elicit a P3a-like wave [18], although again stimuli were presented slowly. A similar P3a was reported by Atienza et al. if stimuli were presented very slowly [19]. In both cases, the interrupt indexed by the P3a was probably a result of activation of the refractory-based N1 transient detector system. There is some controversy about whether sufficient output from the MMN change detector system can also elicit a P3a in the waking state [20]. Muller-Gass et al. [3] has reported that a large 20 dB decrement in the intensity of rapidly presented standard stimuli will indeed elicit a P3a and this can only be attributed to activation of the change detector system. Loewy et al. employed rapidly presented 70 dB SPL standards and rare 80 dB increments and 60 dB decrements [21]. Neither deviant however elicited a P3a in either the waking state or in REM sleep. More recently, Muller-Gass et al. [6] presented a sequence of 80 dB standards, rare 90 dB increments and 60 dB decrements. Both the increments and decrements did elicit a P3a even though the subject was engaged in a very difficult continuous visual tracking task.

The +10 dB increment and -20 dB decrement used by Muller-Gass et al. [6] represent much larger physical changes in acoustic energy than those used by Loewy et al. [21].[1] For this reason, the present study employed a similar stimulus sequence, optimized to elicit a P3a through activation of both the transient and change detector systems during all-night sleep.

2. Methods

2.1 Subjects: Nine self-reported good sleepers (4 females) between the ages of 18 and 27 years (mean = 21.4 years, SD = 3.0 years) spent a single night in the sleep lab. None had a history of

[1] Although both studies employed a 10 dB increment, the extent of energy change from 80 to 90 dB is much larger than from 70 to 80 dB. The dB scale is logarithmic.

neurological or psychiatric disorder. Subjects signed a consent form and received an honorarium for participation in this study. The study was conducted according to the guidelines of the Canadian Tri-Council (Health, Natural and Social Sciences) on ethical conduct involving human subjects.

2.2 Procedure and stimuli: EEG was recorded and stimuli were delivered during relaxed wakefulness while subjects read a book (i.e. instructed to ignore stimuli and divert attention to reading). Subjects were then permitted to fall asleep. Presentation of auditory stimuli began 10 minutes after uninterrupted stage 2 sleep and continued throughout the night. EEG and EOG signals were recorded using silver-silver chloride electrodes, filled with electrolytic paste, and affixed to the skin by surgical tape and to the scalp by gauze. The EEG was recorded from midline frontal, central, and parietal sites and the left mastoid (i.e., Fz, Cz, Pz, M1), which were referenced to the nose. A vertical EOG was recorded from electrodes placed at the supra- and infra-orbital ridges of the left eye. A horizontal EOG was recorded from electrodes placed at the outer canthus of each eye. The high frequency filter was set at 35 Hz and the time constant was set at 2 s. EEG and EOG signals were sampled continuously at a rate of 256 Hz and stored on hard disk.

Auditory stimuli were delivered to the subject's right ear via EAR 3A insert earphones to ensure constancy of stimulus input during sleep. A frequently occurring 80 dB SPL 1000 Hz "standard" auditory tone burst having a total duration of 55 ms (5 ms rise/fall time) was presented on 90% of trials. An intensity increment (+10 dB) and decrement (-20 dB) deviant were each presented at random on 5% of the trials. The 10 dB increment and -20 dB decrement represent approximately equivalent changes in acoustic energy. The time between stimulus presentations (onset-to-onset) varied between 450 and 550 ms. This rate of presentation was

similar to that used by Loewy et al. [21] but somewhat slower than that used by Muller-Gass et al [6].The standard and deviant stimuli were presented in pseudo-random order such that deviants were separated by at least 3 standards. The stimuli were presented in blocks of 1220 trials. A minimum of two blocks of trials was presented during waking, stage 2 and REM. The decrement stimulus did not elicit the MMN for one subject during the waking state. This subject was therefore removed from further analyses. Another subject did not have a sufficient amount of REM sleep to allow presentation of a sufficient number of trials.

2.3 Data Analysis and Scoring: Offline, the continuous data were divided into 500 ms discrete trials or sweeps, including a 100 ms pre-stimulus interval. During the waking state, trials in which either EOG or EEG exceeded ± 100 μV were rejected from further analysis. Sleep staging was performed by two experienced raters using standard procedures [22], with the exception that a 16 s epoch was employed rather than the usual 30 s in order to increase scoring precision. In cases of sleep stage changes or scoring ambiguity, the entire block of data was rejected. Single trial data were then sorted and averaged on the basis of stage of sleep and stimulus type (standard, decrement, increment). An inverse FFT high digital filter with a 2-15 Hz bandpass was subsequently applied to the averaged data.

The deviant ERPs are best observed in a difference wave computed by subtracting point-by-point, the standard from the deviant waveforms at each electrode site in the same condition. The subtraction routine thus removes processing that is common to both the standard and deviant stimuli. During the waking state, the difference waves consisted of distinctive negative (N1 and/or MMN) and positive (P3a) deflections. The N1 and MMN components were often difficult to identify in NREM sleep. The ERPs were therefore quantified using data averaging procedures [23]. The 400 ms post-stimulus sweep was divided into eight 50 ms intervals beginning at

stimulus onset. Within each of these intervals, the average of all data points was computed, yielding an average amplitude measure. Confidence intervals were then computed for each of the 8 latency intervals to determine if the presence of a significant MMN-like negativity or P3a positivity.[2]

3. Results

3.1 Increment deviance: During wakefulness, the standard tones elicited a small amplitude N1-P2 complex at approximately 100 and 160 ms, respectively. The grand average increment deviant difference (deviant minus standard) waveforms are presented in Figure 1. A significant ($p < .01$) large fronto-central negativity peaking at approximately 160 ms was evident in the difference wave, and coincided with a small polarity inversion at the mastoid. This is a composite N1 (because of the increase in intensity of the deviant) and MMN (because it signaled stimulus change). This negativity was followed by a central maximal significant ($p<.05$) positivity, the P3a, peaking approximately 265 ms following stimulus onset.

During REM sleep, a much attenuated early fronto-central negativity peaking at 115 ms was observed in the difference waveform. It showed a small inversion in polarity at the mastoids. The negativity did not, however, reach statistical significance ($p > .05$ for either the 100-150 or 150-200 ms intervals). This was followed by a significant early (192 ms) fronto-central positivity ($p < .05$ at Fz and Cz), probably a P2 reflecting the exogenous increase in stimulus intensity. A later (270 ms) central maximal positivity corresponding to the waking P3a was also significant ($p< .05$ at Fz and Cz). Although the stage REM P3a was reduced relative to that elicited in the

[2] An alternative to the use of confidence intervals would be to compare ERP differences between the waking state and the various stages of sleep. However, a significant decrease in the sleep state cannot be used as evidence of the presence of an ERP component during sleep.

waking state, the difference at Cz was not significant, $t(6)= 1.01$, $p > .05$. The increment also elicited a later (350-400 ms) large fronto-central negativity ($p < .05$).

During stage 2 sleep, the negativities that were apparent during wakefulness and stage REM sleep were near baseline level ($p > .05$ in the 50-200 ms intervals). A large amplitude positivity peaking at 210 ms was apparent; the average of data in this interval was significantly different from the pre-stimulus baseline level ($p < .01$). This P2 was significantly larger in stage 2 compared to REM, $t(6) = 7.29$ $p < 0.01$. A later 250-300 ms positivity, corresponding to the P3a, was not apparent. The increment deviant elicited a very large amplitude N350 ($p < .01$ at Fz and Cz).

3.2 Decrement deviance: The grand average decrement deviant difference waveforms are presented in Figure 2. In the waking state, a significant ($p < .05$) fronto-central MMN in the 200-250 ms range was elicited by the decrement. The MMN inverted in polarity at the mastoid. The decrement also elicited a significant ($p < .05$) later (300 ms) central maximal P3a. This was, however, significantly reduced compared to the waking increment P3a, $t(7) = 2.23$, $p < .05$. During stage REM, an MMN-like negativity was apparent in the 150-200 ms latency interval. It was however maximal over centro-parietal regions ($p <.05$ at both Cz and Pz) and did not invert in polarity at the mastoid. A later P3a was not apparent and no positivities in the 200-350 ms intervals were statistically significant. During stage 2 sleep, an early (80 ms) fronto-central negativity was apparent, but this was not significantly different from baseline level. A 250 ms MMN-like negativity was however significant at Fz. It did not however invert in polarity at the mastoid. A P3a was not apparent and, again, none of the 250-350 ms intervals were significantly different from the zero baseline.

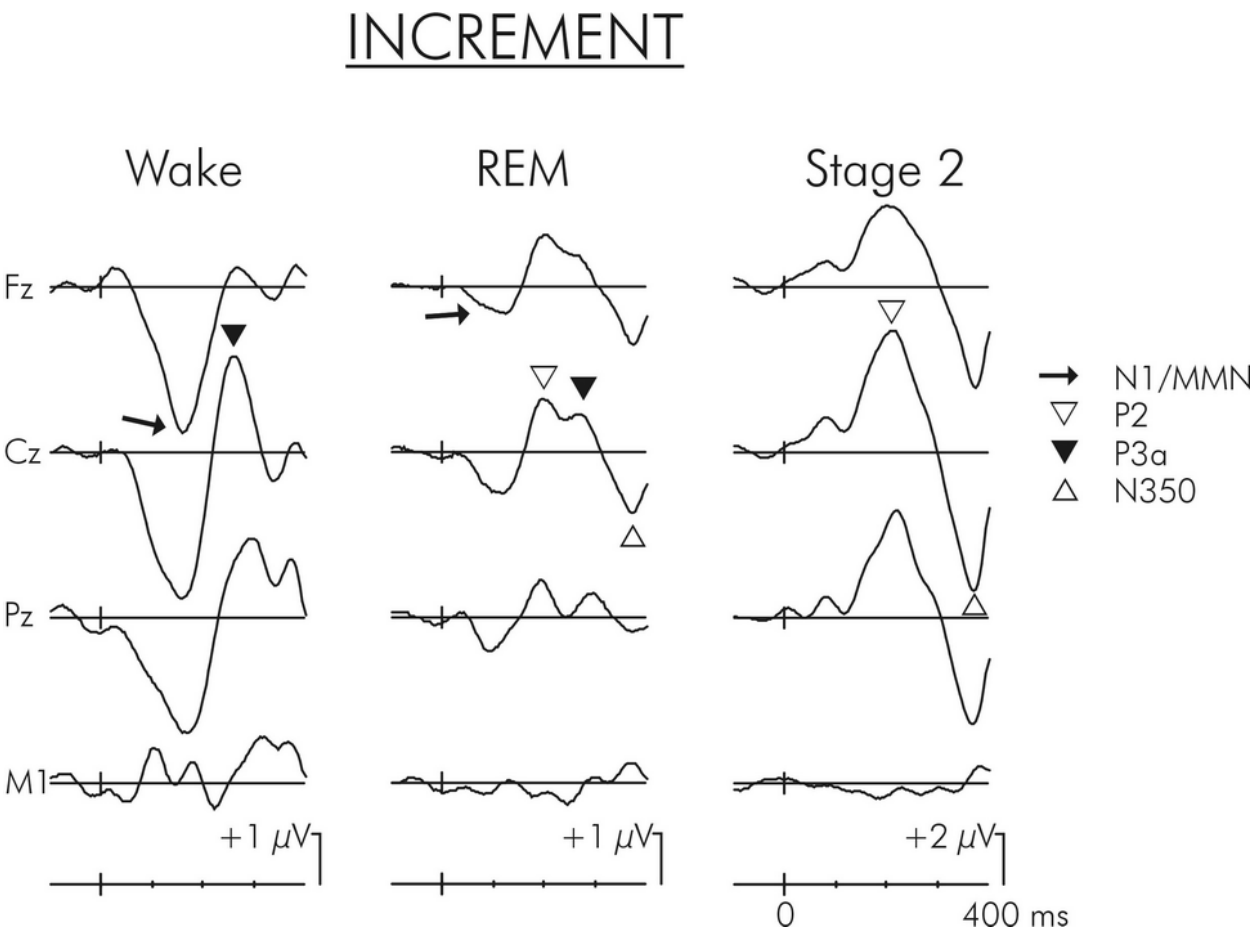

Figure 1. Grand average difference waveforms computed by subtracting the standard from increment deviant ERPs. In the left column, subjects were awake and reading a book (thus ignoring the auditory stimuli). The increment elicited a large negativity peaking at about 160 ms. This is a composite N1 and MMN. A large positivity peaking at about 265 ms is also apparent at Cz. This is the P3a. During stage 2 sleep (right column), neither the N1/MMN nor the later P3a were visible. An earlier P2, peaking at about 200 ms was however quite prominent. During stage REM (middle column), the N1/MMN was apparent but was not statistically significant. An attenuated P3a remained statistically larger than the pre-stimulus baseline level.

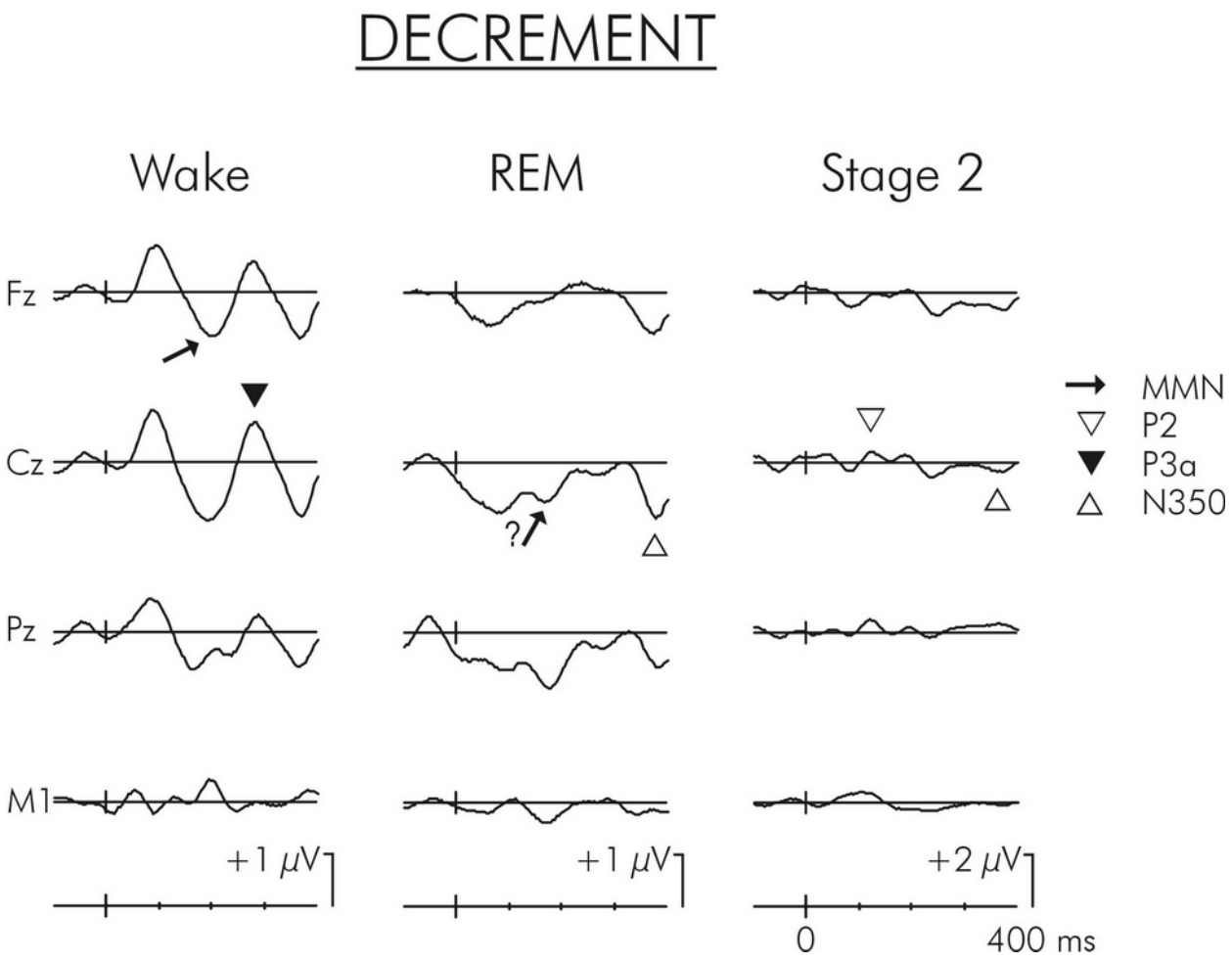

Figure 2. Grand average decrement difference waveform. The decrement elicited a significant MMN and P3a in the waking state. Neither the MMN nor the P3a were visible during stage 2 or in stage REM.

4. Discussion

The waking data closely replicated the recent findings of Muller-Gass et al. [6]. Thus, the increment elicited a large negativity consisting of a composite N1/MMN followed by a large amplitude central maximum P3a. The decrement elicited a "true" MMN but also importantly, a P3a, although it was reduced in amplitude. This adds further support to the notion that the P3a process, reflecting interruption of the frontal central executive, is not elicited exclusively by the activation of the N1 refractory-based transient detector system [20] but can also be a consequence of activation of the change detector system [3,6].

During REM sleep, a P3a was apparent following presentation of the increment deviant. This thus suggests that interruption of the frontal central executive controlling cognitive resources is possible during this stage of sleep. A P3a was not apparent following the decrement. This is consistent with other studies indicating that P3-like ERPs (either a P3a or P3b) can only be elicited during REM following activation of the transient detector system [16, 18, 19]. The physical increase in intensity does, however, need to be relatively large. Loewy et al. [21] have noted that smaller increments that were also presented rapidly do not elicit the P3a in REM sleep. The authors also indicated that small 10 dB intensity decrements do not elicit a P3a during REM sleep. The present study indicated that even a very large 20 dB decrement will not elicit a P3a. This may be a result of an insufficient activation of the change detection system. The large decrement did not elicit an MMN during REM sleep. The presentation of intensity change per se may thus not provide sufficient activation to result in interruption of the central executive, unless change also activates the refractory transient detection system.

As expected, a large change to the waking ERPs was apparent during stage 2 sleep. The waking N1 and MMN were at baseline level. The increment did elicit a later large positivity. Its

peak latency (around 200 ms) and centro-parietal scalp distribution suggest this was a sensory P2 rather than the later endogenous centro-frontal P3a. The absence of the N1 and MMN but the enhancement of the P2 is consistent with the removal of a long-lasting negativity that overlaps and summates with these components during the waking state [9]. P2 is thus larger during NREM sleep [11]. It also increases in amplitude with increasing stimulus intensity. This would explain why P2 as was larger following presentation of the increment than the standard. Consistent with this, when the intensity of the standard was louder than that of the deviant (i.e., the decrement), P2 was not apparent in the difference wave during stage 2 sleep.

Conclusions. During REM sleep, a relatively small increase in the intensity of a rapidly presented acoustic stimulus will elicit a P3a, presumed to reflect the interruption of the central executive resulting in potential awareness of stimulus input. Activation of the central executive is probably a consequence of the output of the auditory transient detector rather than the change detector system. A large decrement in stimulus intensity, that would presumably only activate the change detection system, did not elicit the P3a. During stage 2, neither the decrement nor the increment was able to elicit N1, MMN or P3a potentials. This is consistent with a deactivation of the frontal executive control system and a profound state of unconsciousness.

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Chapter 3

Study 2. Effects of a violation of an expected increase or decrease in intensity on detection of change within an auditory pattern

Rationale. In Study 1, the increment stimulus elicited a fronto-centrally maximum negativity and a subsequent P3a-like ERP during REM sleep, while the decrement failed to produce any evidence of change detection. The findings of this study thus supported the hypothesis that a stimulus increment was indeed more disruptive than a stimulus decrement. The increased disruptiveness attributed to the increment might be a result of the fact that it activates both of the transient and change detector systems.

The issue of activation of both systems was overcome in Study 2 by presenting participants with an alternating patterned auditory paradigm in which deviants are created by the repetition of a previous stimulus (ABABAB**B**BA). This type of paradigm has been shown to elicit large MMNs when variation occurs in the frequency domain (Alain, Woods, & Ogawa, 1994; Sculthorpe, Collin, & Campbell, 2008). Study 2 employed a pattern alternating between high and low intensity stimuli. "Increment" deviants were created by violating the expectancy of a decrement by repeating a high intensity tone (LHLHLH**H**HL), while "decrement" deviants were created by violating the expectancy of an increment by repeating a low intensity tone (HLHLHL**L**LH). Importantly, because deviants are created by the repetition of a tone, an enhancement of the N1 response will not occur, thus allowing isolation of the MMN and the activity of the change detection system. The degree of separation between the stimuli comprising the alternating pairs was also varied in order to determine whether deviants in alternating paradigms with a greater degree of intensity separation would result in larger MMNs.

Study 2 was published in *Brain & Cognition* and is formatted according to the requirements of the journal.

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1. Introduction

Detection of auditory change in the environment is crucial for both the survival and communication of most mammalian species. The brain is equipped with mechanisms capable of rapidly detecting acoustic change and taking appropriate action should the need arise. The detection of change in the intensity of an auditory stimulus, particularly an increase in intensity, is especially critical in forming the basis of many alarm systems, due to the effectiveness of intensity increments in capturing the attention of an otherwise engaged observer. This may, in part, be due to the differential implications of the occurrence of intensity increases and decreases in the auditory environment. An increase in stimulus intensity is experienced as "looming" or approaching and may elicit a fear response in animals, while a decrease in intensity is experienced as "fading" or retreating (Bach, Schachinger, Neuhoff, Esposito, Di Salle, Lehmann, et al., 2007; Freiberg, Tually, & Crassini, 2001; Maier & Ghazanfar, 2007). In the elaborate Näätänen (1990) model of auditory processing, an increase in stimulus intensity is detected in parallel by both a transient and a memory-comparison-based change detector system. The transient detector system, as its name implies, detects changes in transient energy (such as the onset or offset of a stimulus). The output of this system, as monitored by a negative event-related component, N1, peaking about 100 ms after stimulus onset, varies directly with the intensity of the stimulus. A stimulus increment would therefore result in an increase in the output of the transient detector and thus an increase in the amplitude of N1. By contrast, a stimulus decrement would result in a decrease in the output of the transient detector system and thus a decrease in the amplitude of N1. A change in the intensity of the stimulus is however also detected by a different system, the change detection system, by which a change in any stimulus feature, including pitch, location, duration or intensity, is detected. The basic encoded features of a stimulus are stored as

a representation in a very brief-lasting sensory memory where feature and temporal integration take place. The change detection system compares the encoded features of an incoming stimulus to those that exist in sensory memory. If they match, the sensory memory is strengthened, but further processing is deemed to be redundant and thus ceases. If they fail to match, a feature of the deviant stimulus is detected as being different acoustic change is detected. The output of this memory comparison-based change detection system can be monitored by a different negativity, called the Mismatch Negativity (MMN). The MMN is often recorded in the so-called oddball paradigm in which the subject is presented with a string of frequently occurring, homogenous "standard" stimuli. At rare and unpredictable times, a feature of the standard is changed. It is this deviant that elicits the MMN. A more recent model maintains that the MMN is elicited by a mismatch between the current auditory input and the predictions formed on the basis of the trends or rules that are automatically detected in recent auditory stimulation (Näätänen , Kujala & Winkler, 2011; Winkler, 2007; Winkler, Denham, & Nelken, 2009), the repeating, homogenous standard stimulus in the oddball paradigm thus being a special case of acoustic regularity. Thus, a rule is formed that a standard follows a standard and the occurrence of a deviant violates this rule. A rare increment or a decrement in intensity will result in increased activation of the change detection system because both signal stimulus change (or a violation of the standard acoustic regularity). The MMN peaks approximately 100-250 ms following the onset of a deviant stimulus. Its latency varies according to the perceptibility of change between standard and deviant stimuli, with less perceptible changes resulting in longer latencies (Näätänen, 1990).

In the classic Näätänen model (1990), the output of both the transient and change detector systems is forwarded to the central executive, controlling the allocation of attentional and

cognitive resources. When the output reaches a critical threshold, attention to ongoing cognitive tasks is interrupted and switched to the auditory channel, a process called "attention capture." The contents of sensory memory are then probed for further possible perceptual processing. This switching of attention is thought to be reflected by another ERP component, the P3a, peaking 250-350 ms after stimulus onset (Escera, Alho, Winkler, & Näätänen, 1998). Rinne, Särkkä, Degerman, Schröger, and Alho (2006) have however demonstrated that a deviant formed by decreasing the intensity of a standard by 9 dB can produce behavioural evidence of a switch of attention yet not elicit a P3a. They asked subjects to determine whether the duration of auditory stimuli was either short or long. At rare and unpredictable times, the intensity of the stimulus was decreased or increased by as much as 9 dB. The decrement and increment both resulted in a prolongation of reaction time to the auditory stimuli. However, only the increment elicited a P3a. The decrement did not. On the other hand, Muller-Gass, Macdonald, Schröger, Sculthorpe, and Campbell (2007) also employed an oddball paradigm in which subjects were presented with a frequently occurring 80 dB auditory standard and either a 90 or 60 dB deviant (equated for perceptibility), while attention was engaged in a continuous visual multiple moving object task. The decrement did elicit an MMN and a small amplitude P3a, probably because the decrease in intensity was much larger than that used by Rinne et al. (2006). The increment elicited a much larger deviant-related negativity (DRN), likely reflecting the summation of both an N1 and MMN (because of increased activation of both the transient and change detector systems), followed by a large P3a. The larger amplitude of the P3a elicited in response to the increment in this study lends support to the notion that increases in stimulus intensity are more disruptive than decreases. Macdonald, Jamshidi, and Campbell (2008) have noted that an increment will continue to elicit a DRN and a small P3a during REM sleep while a decrement will not. Thus, it

appears that only with sufficient activation of the transient detector system will the P3a be elicited during REM sleep.

As noted, a problem with the usual oddball paradigm is that the standard is physically different from the deviant. This may result in the activation of the refractory-based transient detector system, more so for the rarely presented deviant than the frequently presented standard (see also May and Tiitinen, 2010). To overcome this problem, Jacobson, Horenkamp and Schröger (2003) designed an elegant study in which a 55 dB SPL test tone served as either a 10 dB increment deviant, a 10 dB decrement deviant or as a standard in different oddball conditions (thus reversing the standard and deviant stimuli). They also employed a control condition in which the 55 dB tone was presented with the same probability as the deviants in the oddball blocks among 6 other equiprobable tones varying in intensity from 25 to 85 dB SPL in 10 dB steps. Two alternate estimations of the "true" MMN were isolated in each oddball condition by subtracting the ERPs elicited by the 55 dB tone either in the control condition or and when it acted as a standard in the oddball conditions, from the ERPs elicited by the 55 dB tone when it acted as a deviant. They reported that the amplitude of the MMN elicited by the 55 dB tone when it acted an increment deviant did not differ in amplitude from when it acted as a decrement deviant. Surprisingly, the increment did not elicit a P3a, even when they subtracted ERPs elicited by the standard from the physically more intense deviants, contrary to the findings of Rinne et al. (2006), Muller-Gass et al. (2007) and Macdonald et al. (2008). Their increase in intensity (from 45 to 55 or from 55 to 65 dB SPL) however represents a much smaller change in physical energy than that used by Rinne et al. (as large as 60 to 69 dB HL, approximately 75 to 84 dB SPL) and Muller-Gass et al. and Macdonald et al. (80 to 90 dB SPL). It is therefore possible that differences in the processing of increments and decrements do not emerge until rare

intensity increases become quite obtrusive and elicit a P3a.

An MMN can also also be elicited by sounds violating more abstract or rule-based patterns. Alain, Woods, and Ogawa (1994) employed an alternating low-high frequency pattern paradigm (ABABAB). Violations of the pattern were created by repeating the A or B tone (e.g., ABABA**A**AB). The advantage of this paradigm is that the deviant and the preceding standard are physically identical (A followed by A in the example), overcoming the problems associated with physically different standard and deviant stimuli. An MMN response was elicited by the deviant stimulus, with the amplitude of the MMN varying directly with the extent of separation (1, 6 or 12 semitones) between the tone pairs. Sculthorpe, Collin, and Campbell (2008) tested the automaticity of this pattern-elicited MMN by varying the difficulty of a visual task in which subjects were engaged. Similar to the Alain et al. (1994) results, the violation of the alternating pitch pattern elicited a robust MMN whose amplitude was dependent on the extent of separation between the alternating stimuli. Importantly, the difficulty of the visual task had little effect on the MMN. This is consistent with the classic Näätänen (1990) claim that the operations of the change detection system function relatively independently of attention and task demands. Other labs have employed more complex and at times very abstract rule-based predictive patterns to elicit the MMN (Bendixen, Schröger, & Winkler, 2009; Horváth, Czigler, Sussman, & Winkler, 2001; Nordby, Roth, & Pfefferbaum, 1988; Paavilainen, Jaramillo, & Näätänen, 1998; Paavilainen, Degerman, Takegata, & Winkler, 2003; Todd, Myers, Pirillo, & Drysdale, 2010). Paavilainen et al. (2003) investigated the effects of the violation of an intensity pattern. In this study, brief-duration tone pips were presented in pairs separated by 50 ms followed by a 500 ms pause. In the ascending condition, the standard pattern followed the rule that the intensity of the second tone in the pair was 7 dB higher than the first. Deviation in the sequence occurred when

the second tone descended in intensity. In a second descending condition, the presentation of the descending pairs now became the standard pattern that was sporadically interrupted by an ascending deviant pair. The violation of the abstract intensity rule did elicit an MMN. Unfortunately, the authors did not examine differences between the ERPs elicited in response to the violation of the expectancy of an increment and a decrement. The amplitude of their MMN was nevertheless much smaller compared to that reported by Alain et al. (1994) and Sculthorpe et al. (2008). It is unlikely that this is because Paavilainen et al. (2003) used a more abstract pattern while Alain et al. (1994) and Sculthorpe et al. (2008) employed a fixed, concrete pattern. Schröger, Bendixen, Trujillo-Barreto, and Roeber (2007) noted that both a concrete and an abstract rule-based violation of a frequency pattern can elicit MMNs that do not differ. It is possible that the small 7 dB separation used in the Paavilainen et al. (2003) was not easily perceived and thus resulted in a small-amplitude MMN.

The present study employed a concrete alternating low-high intensity (LHLHLH) pattern analogous to the alternating pitch pattern employed by Alain et al. (1994) and Sculthorpe et al. (2008). Again, the deviant was created by repeating the same physical stimulus (e.g., LHLHLLLH). The repetition of the low intensity tone violates the "local" rule, H follows L. Because the local rule leads to the expectation of a higher intensity stimulus following the presentation of the low intensity stimulus, the repetition of the low intensity tone acts as a *psychological* decrement. Note however that the presentation of the low intensity deviant is not actually physically lower in intensity than the stimulus that preceded it. Similarly, the repetition of the high intensity tone violates the local rule, L follows H. Because the rule leads to the expectation of a lower intensity stimulus, the presentation of the high intensity tone acts as a *psychological* increment. Again, note that the presentation of the high intensity deviant is not an

actual physical increase in intensity from the standard stimulus that preceded it. The physical intensity of the psychological decrement and increment and that of the preceding standard are thus identical. Thus, the presentation of both the decrements and increments should result in increased activation of only the memory comparison-based change detection system, the output of which is reflected by the amplitude of the MMN. Critically, the presentation of the psychological increment should not result in increased activation of the transient detector system compared to the standard (because they are physically identical). There is some evidence that a P3a is largely elicited by sufficient activation of the transient detector system (Rinne et al., 2006). If this is the case, then neither the psychological decrement nor the psychological increment should elicit a P3a.

The MMN elicited by a violation of an alternating pitch pattern varies directly with the extent of separation between the alternating stimuli (Alain et al., 1994; Sculthorpe et al., 2008). The present study thus also examines the effects of the extent of separation in intensity between the alternating stimuli. In different conditions, the intensity separation will either be small, medium or large.

2. Materials and methods

2.1. Subjects

Ten subjects (4 females) between the ages of 24 and 29 years (M= 26.1, SD= 1.5 years) took part in the study. Subjects signed a consent form and received an honourarium for participation in this study. None reported a history of neurological or psychiatric disorder. The study was conducted according to the guidelines of the Canadian Tri-Council (Medical, Natural and Social Sciences) on ethical conduct involving human subjects.

2.2. Stimuli

Auditory stimuli were presented binaurally through EAR 3A insert earphones while the subject sat in a sound-attenuated room watching a silent sub-titled video. The subjects were asked to ignore the auditory stimuli. The auditory pattern consisted of two different 1000 Hz pure tones, with a duration of 100 ms, including a 10 ms rise/fall time. The tones alternated between low and high intensities, following a fixed LHLHLH intensity pattern. The stimulus onset asynchrony (SOA) between the auditory stimuli was held constant at 500 ms. The extent of the intensity separation between the L and H pairs was manipulated in three different conditions, small (75-78), medium (72-81), and large (63-90 dB SPL) separation. Deviants within this alternating standard pattern were created by repeating either the low or high intensity tone. Two different pattern violations were thus possible (LHLHL**L**LH or LHLH**H**HLH). The repetition of the lower intensity tone (L-L), the psychological "decrement" deviant, thus represented a 3, 9, or 27 dB violation of the expected intensity increment (L-H) rule, while the high intensity repetition (H-H), the psychological "increment" deviant represented a 3, 9, or 27 dB violation of the expected intensity decrement (H-L) rule. The L-L decrement and H-H increment deviant patterns each occurred 50 times within a block of 600 stimulus pairings, making the total probability of a deviant repetitive pair approximately .17. The standard:deviant proportion was identical to that employed by Alain et al. (1994) and Sculthorpe et al. (2008) using a frequency pattern that resulted in large amplitude MMNs. The deviant pattern was presented pseudo-randomly with the constraint that it followed a minimum of 4 and a maximum of 20 standard (L-H) stimulus pairs. Three blocks of the small, medium and large intensity pairs were presented (i.e., a total of nine blocks) in random order. Thus, a total of 5400 stimulus pairings were presented consisting of 4500 standard pairs and 450 L-L and 450 H-H deviant

repetitions. The three blocks were compared for each individual subject following the initial averaging process to assure repeatability of the effects.

2.3. Performance Task

The amplitude of the MMN is affected by perceptibility of the deviant. A second group of 10 subjects (8 of whom had participated in the physiological testing) later performed a behavioural discrimination task. The stimuli were the same as those used in the physiological recording sessions. A single small, medium and large separation condition was run. Subjects were instructed to press a keyboard button as quickly and accurately as possible upon detection of a violation of the standard L-H pattern (i.e., a repetition of the same stimulus). Both accuracy of detection ("hits") and reaction time (RT) were recorded. A response had to be made within 1000 ms after stimulus onset in order to be considered a hit.

2.4. Physiological Recording

The EEG was recorded from 10 scalp sites representing frontal (F3, Fz, F4), central (Cz, C3, C4) , parietal (Pz), temporal (T7, T8) and occipital (Oz) areas of the scalp using silver/silver chloride electrodes attached to an electrode cap (Electro-Cap International Inc., Eaton, OH). Two additional channels were recorded from individual electrodes placed on the left and right mastoids (M1, M2). The nose served as a reference. Vertical eye movements and blinks were recorded from electrodes placed at the infra- and supra-orbital ridges of the left eye. A horizontal EOG was recorded from electrodes placed at the outer canthus of each eye. The ground electrode was located between the Fz and FPz sites. Inter-electrode impedances were kept below 5 kΩ.

The physiological signals were digitized continuously at a 256 Hz sampling rate and stored on hard disk. The high frequency filter was set at 35 Hz and the time constant at 2 s. Offline, an inverse FFT high digital filter set at 15 Hz was applied to the data. Eye movements

and blinks were corrected using an algorithm operating in the time and frequency domains (Woestenburg, Verbaten, & Slangen, 1983). The subjects' continuous data were partitioned into 500 ms epochs, which included a 50 ms pre-stimulus baseline period. Epochs containing EEG that exceeded ±100 μV were considered to be artefact and excluded from further analyses. Individual subject's data were then averaged according to electrode site and stimulus type (standard, increment deviant (H-H), decrement deviant (L-L)). The second stimulus within a pair of repetitive stimuli was considered to be the deviant within a condition. The 4 stimuli presented immediately following the deviants were omitted from averaging to allow reformation of the memory for the standard required to elicit an MMN. Similarly, the first 4 stimuli in each condition were also omitted from averaging (a memory for the standard would not yet have been formed).

2.5. Quantification of the MMN

The MMN is best observed in a difference wave representing the difference in processing between the standard and the deviant. Difference waves were computed by subtracting point-by-point the auditory standard from the deviant ERPs at each electrode site. In this experiment, the physical features of the standard and deviant were identical. Thus, the subtraction process removed the exogenous, sensory processing that was common to the standard and deviant isolating the endogenous differential response unique to the processing of the deviant pattern. It was expected that only a small amplitude MMN would be elicited, especially in the small separation condition. Further, it is unknown whether a P3a can be elicited in an alternating intensity pattern paradigm involving psychological increments and decrements. The usual maximum peak amplitude scoring procedures are inappropriate when the amplitude of an ERP component is very small or absent. In such cases, residual noise might be mistakenly scored as a

true “peak”. A scoring method described by Alho, Sams, Paavilainen, Reinikainen, and Näätänen (1989) can be used to overcome this problem. The average of all data points in the 50 ms pre-stimulus period served as a zero amplitude baseline from which all amplitudes were measured. The post-stimulus sweep period was subdivided into seven 50 ms intervals, beginning at 50 ms (50-100, 100-150... 350-400 ms). Within each of these intervals, the average of all data points was computed, yielding an average amplitude measure.

2.6. Statistical analyses.

The statistical analysis of small amplitude or absent ERPs is also problematic. The usual method is to compare the effects of the experimental manipulations employing an ANOVA procedure. In the present experiment, the ANOVA would determine if ERPs differed as a result of the extent of Separation (low, medium high corresponding to 3, 9 and 27 dB respectively) between the intensities or as a result of the Direction of change (the psychological increment or decrement). A significant difference does not however necessarily imply that an ERP component was, in fact, elicited (i.e., if the component significantly differed in amplitude from the zero amplitude pre-stimulus baseline level). Confidence intervals were therefore initially computed within each window. This procedure determined the probability that the mean MMN amplitude value fell within an upper or lower range of zero. Thus, when the lower limit of a confidence interval was significantly less than 0 μV, (i.e., was negative-going), the interval was considered to contain a significant negativity (thus, a possible MMN) and when the upper limit was significantly greater than 0 μV (i.e., was positive-going, a significant positivity (thus, a possible P3a). This procedure is equivalent to computing a *t*-test between the standard and deviant waveforms (Winer, 1971). Because a negative directionality was predicted in the 100-250 ms time intervals corresponding to the latency of the MMN and a positive directionality was

predicted in the 250-350 ms intervals corresponding to the P3a, one-tailed tests of significance ($p<0.05$) were applied to these confidence intervals. To restrict the likelihood of chance findings, the negativity had to conform to the usual latency and scalp distribution (fronto-central maximum and an inversion in polarity at the mastoids) of the MMN, while the positivity had to conform to the usual latency and scalp distribution (centro-frontal maximum) of the P3a.

The method used to quantify the different ERP deflections, the averaging of all data points within time windows does tend to "smear" (underestimate) the amplitude of a peak spanning across intervals. Thus, when the confidence interval testing revealed a significant deflection from the zero voltage baseline, the maximum peak amplitude of the MMN and P3a and their peak latency were measured manually.

Performance data (i.e., hit rates, reaction times) were analyzed using an ANOVA with repeated measures on extent of Separation (low, medium, high corresponding to 3, 9 and 27 dB respectively) and Direction of change (psychological increment, decrement). The statistical procedures employed for the physiological data were however dependent on the results of the initial confidence interval testing. If a peak deflection did not significantly differ from the zero baseline, then no further statistical procedures were carried out. The initial MMN analyses were run on the Fz data where the MMN is maximum. Possible hemispheric differences were run on the F3 and F4 data. Again, the factors entered into the statistical procedure were dependent on whether significant peak deflections were found using the confidence interval testing procedures.

3. Results

3.1. Physiological Data

It was expected that the MMN would vary directly in amplitude with the extent of separation between the low and high intensity pairs. Figure 1 illustrates the grand averaged "raw" standard

and deviant ERPs in the large intensity separation condition (63-90 dB). Note that the same 63 dB stimulus served as both the standard and as the psychological decrement deviant within this condition. Similarly the 90 dB stimulus also served both as the standard and as the psychological increment deviant. Processing until the time of the N1 deflection was very similar for the standard and deviant 63 and 90 dB stimuli. An additional negativity was elicited following presentation of the deviants. This is the MMN. The MMN is best observed in the deviant-standard difference wave. This difference wave is also illustrated in Figure 1.

Figure 2 illustrates the scalp distribution of the difference waves in the large intensity separation (63-90 dB) condition. A large fronto-central negativity, beginning at about 100 ms was apparent in the difference wave following the presentation of the psychological increment (repetition of the 90 dB tone). Confidence interval testing performed on the difference waves revealed that this negative wave was significant ($p<0.05$) in the 150-200 ms interval at frontal and central sites. A significant ($p<0.05$) polarity inversion was also observed at the mastoids in this time period. A later (about 200 ms) large fronto-central negativity was also apparent in the difference wave following the presentation of the psychological decrement stimulus (repetition of the 63 dB tone). Confidence interval testing of the various time intervals revealed that this negativity was significantly different from the baseline level in the 200-250 ms period. This negativity inverted in polarity at the mastoids but the amplitude of this inversion did not significantly differ from the pre-stimulus baseline zero voltage. A central maximum 300-400 ms small amplitude positivity was also visible in the grand averages when the psychological increment was presented. Confidence interval testing failed however to reveal significant positivities in any of the intervals between 200 and 400 ms following the presentation of the psychological increment. Similarly, no significant positivities were revealed in any of the

intervals between 250 and 400 ms following presentation of the psychological decrement. Thus neither deviant in the large intensity separation condition was successful in eliciting a P3a.

Figure 3 illustrates the difference waves in the medium intensity separation (72-81 dB) condition. Confidence interval testing failed to reveal a significant fronto-central negativity (the MMN) in any of the 50 ms intervals in the 50-300 ms latency range in response to either the psychological increment or decrement deviants. Similarly, no significant later positive deflections, corresponding to the P3a, were found within the 250-400 ms intervals.

Figure 4 illustrates the difference wave in the small intensity separation condition (75-78 dB). When a psychological increment was presented, confidence interval testing performed on the difference waves revealed a significant negativity at fronto-central scalp sites during the 150-200 ms time period, ($p < .05$). This negativity was, however, maximum in amplitude at Pz. This is not characteristic of a true MMN. Moreover, no inversion of polarity was apparent at the mastoids. The repetition of the lower intensity 75 dB tone (thus the psychological decrement) did not produce any significant deviations from baseline in any of the 50 ms time intervals. Again, a significant later positivity (the P3a) was not revealed within the 250-400 ms intervals. Thus, no significant deviations from baseline conforming to the criteria associated with the MMN or P3a were elicited in this condition.

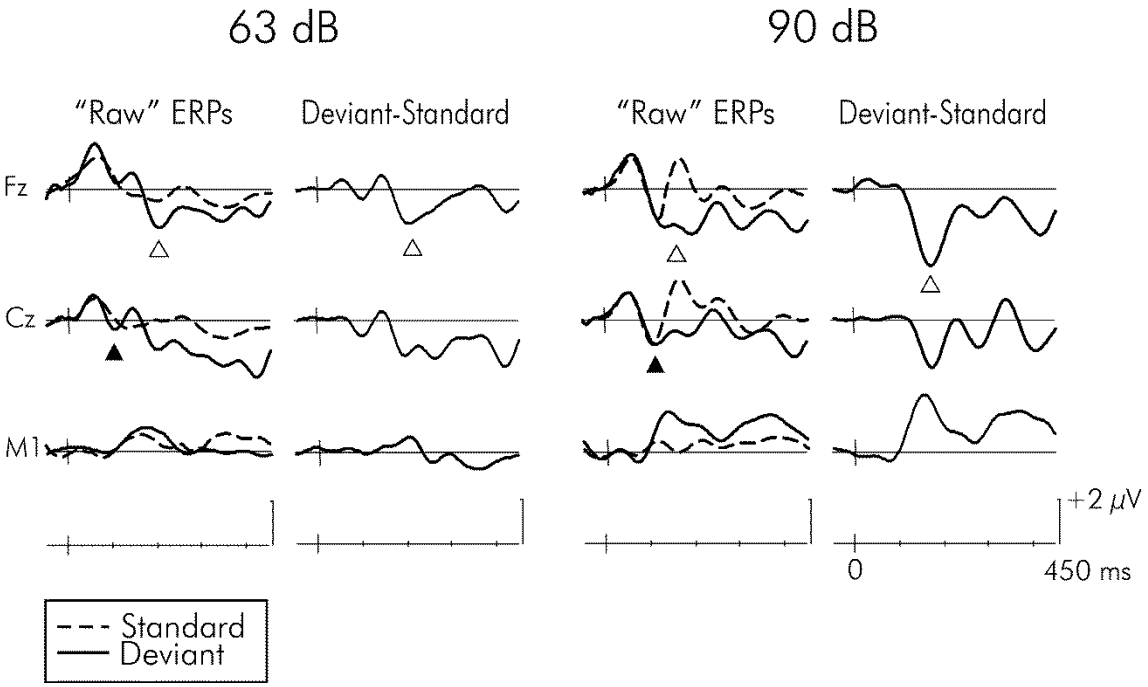

Figure 1. Grand average "raw" ERPs elicited by the standard and deviant stimuli in the large intensity separation condition. In this and all other figures, positivity at the scalp relative to the reference is indicated by an upward deflection. In the large separation condition, subjects were presented with an alternating 63-90-63-90 dB SPL sequence pattern. The pattern was violated by the repetition of either the low intensity 63 dB stimulus (left portion of the Figure) or the high intensity 90 dB stimulus (right portion of the Figure). The intensity of the deviant (either the 63 or 90 dB stimulus) was thus identical to the preceding standard. The ERPs to the standard and deviant are superimposed. The morphology of the standard and deviant waveforms are very similar until the time of N1 (indicated by the closed triangle) at about 100 ms. An additional negative deflection is apparent following the presentation of the deviant stimuli (indicated by the open triangle). This is the MMN. The MMN is best observed in the deviant-standard "difference" wave.

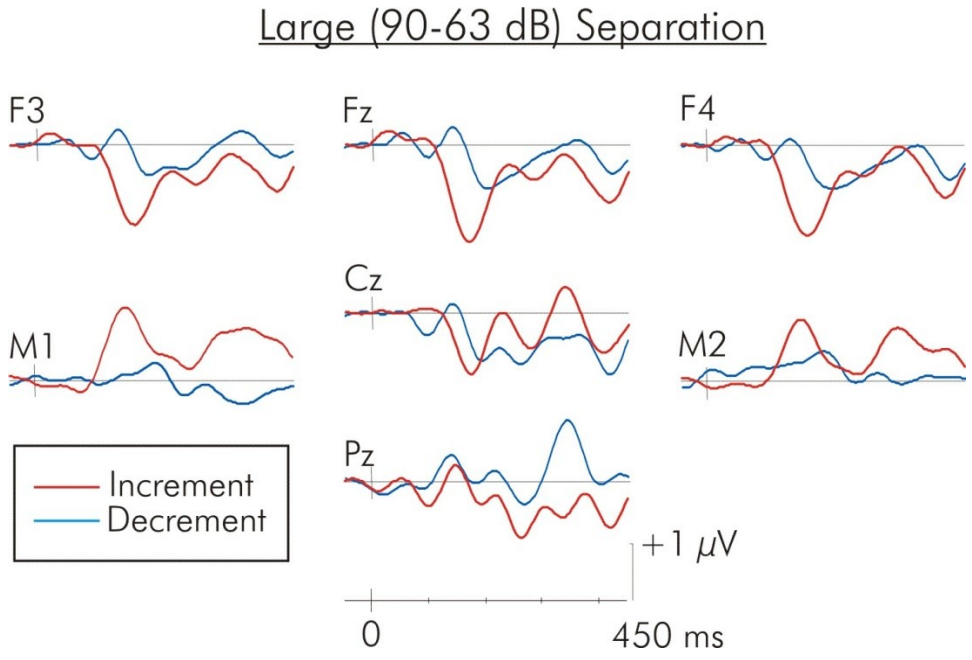

Figure 2. Grand average difference waves in the large intensity separation condition. A large amplitude MMN was evident over fronto-central areas of the scalp between 150 and 200 ms following presentation of the increment. This MMN inverted in polarity at the mastoids. A smaller and delayed MMN was elicited by the decrement. The inversion at the mastoids did not however attain significance. A later positivity, the P3a, typically peaking between 250 and 300 ms was not apparent following presentation of either the increment or decrement.

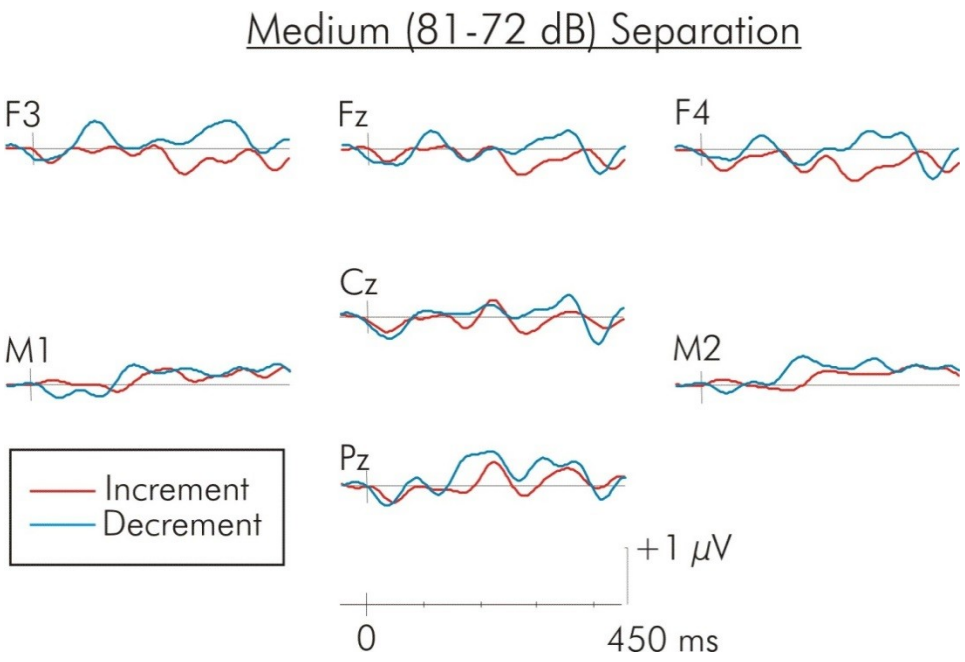

Figure 3. Grand average difference waves in the medium intensity separation condition. Again, there was no evidence of an MMN following presentation of either the increment or decrement.

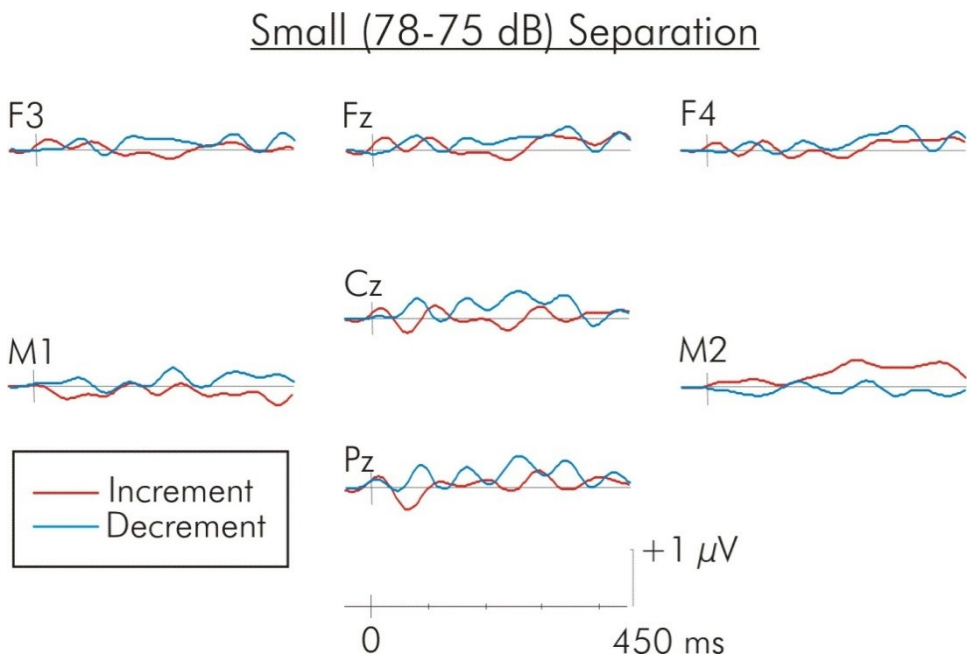

Figure 4. Grand average difference waves in the small separation condition. No negativity corresponding to the MMN was evident following presentation of either the psychological increment or decrement deviant.

The initial confidence interval testing revealed significant negativities corresponding to the MMNs only in the large separation condition. The deflections in this condition were thus also scored using maximum peak deflection methods. In Figure 2, it is apparent that both the latency and amplitude of the MMN varied as a function of whether the deviant represented a psychological increment or and decrement. A one-way ANOVA with repeated measures on Direction of change (increment, decrement) was thus run on the peak latency and amplitude data in the large intensity separation condition. The MMN peaked at 175 ms (SD = 31 ms) following presentation of the psychological increment. Its latency was significantly delayed to 206 ms (SD = 25 ms) following presentation of the psychological decrement, $F(1,10) = 16.69$, $p < .01$. The mean amplitude of the MMN at Fz was -3.81 μV (SD= 1.98 μV) and –1.81 μV (SD = 2.00 μV) following presentation of the psychological increment and decrement, respectively. Again, this difference was significant, $F(1,10) = 9.04$, $p < .01$. Two-way ANOVAs were run on the large intensity separation difference waves to compare Hemispheric differences at F3 and F4 and the influence of the Direction of change. The MMN was slightly larger (by about 0.5 μV) at F4 than at F3 following the presentation of both types of deviants, but the difference failed to reach significance, $F(1,10) = 2.13$, $p > .05$. The interaction of Hemisphere and Direction of change was not significant, $F<1$.

3.2. Performance data

A significant MMN was only elicited in the large intensity separation condition. It is possible that subjects could not detect the change in acoustic regularity in the medium and small separation conditions. A second study was therefore run to determine the perceptibility of the violation of the alternating low and high intensity pattern in the small, medium, and large intensity separation conditions. The mean performance data (hit rates, reaction time (RT)) are

presented in Tables 1 and 2 respectively. The main effect of the Direction of intensity change on subjects' accuracy failed to reach significance, $F<1$. Thus, hit rates did not significantly differ for the psychological increment or decrement deviants. The main effect of the extent of intensity Separation on accuracy of detection was found to be significant, $F(2, 18) = 100.27$, $p < .01$. Post-hoc analyses revealed that hit rates were significantly higher when the intensity separation was large (27 dB) or medium (9 dB) compared to when it was small (3 dB). Indeed, hit rates were only slightly above chance level in the small separation condition. Accuracy of detection did not significantly vary between the large and medium conditions. Similar trends were found for RT. Thus, RT did not differ following presentation of the psychological increment and decrement deviants, $F < 1$, while significant variation was found as a function of the extent of intensity Separation $F(2, 18)=7.47$, $p<.01$. Again, RT was significantly faster in the large and medium separation conditions compared to the small separation condition. Although RT was about 43 ms faster in the large than in the medium condition, the difference was not significant. No significant interaction between Direction of intensity change and intensity Separation was found for either hit rates or reaction times, $F < 1$in both cases.

	Intensity Separation		
	Small (3 dB)	Medium (9 dB)	Large (27 dB)
Decrement	0.26 (0.19)	0.81 (0.20)	0.85 (0.22)
Increment	0.26 (0.22)	0.84 (0.18)	0.85 (0.21)

Table 1. Mean hit rates (SD in parentheses) following presentation of decrement and increment deviants in the low, medium and high intensity separation conditions (i.e. violation of expectancy of an increment and decrement, respectively).

	Intensity Separation		
	Small (3 dB)	Medium (9 dB)	Large (27 dB)
Decrement	700 (144)	523 (87)	484 (56)
Increment	597 (255)	524 (86)	477 (62)

Table 2. Mean reaction times (in ms) (SD in parentheses) following presentation of low and high intensity deviants (i.e. violation of expectancy of an increment and decrement, respectively*).*

4. Discussion

The repetition of both the low and high intensity tones, the psychological decrement and increments, respectively, was successful in eliciting relatively large amplitude MMNs, but only in the large intensity separation condition. Because the intensities of the deviant and standard stimuli were physically identical, this should not have resulted in greater activation of the transient detector system by the deviant. The raw ERP waveforms to the standards and the deviants were thus quite similar up to the time of occurrence of N1 at approximately 100 ms following presentation of the stimuli. The MMN following violation of the alternating pattern was maximum over fronto-central areas of the scalp and inverted in amplitude at the mastoids. It was also larger over right than left frontal regions of the scalp, although the difference was not significant. The scalp distribution of this MMN is thus very similar to that elicited in the usual oddball paradigm. The elicitation of a large MMN by a violation of a concrete rule-based alternating intensity pattern is consistent with the findings of Alain et al. (1994) and Sculthorpe et al. (2008) who employed a similar alternating low-high tonal frequency pattern.

Previous studies in our lab have indicated that a 10 dB increase in the intensity of a relatively loud 80 dB SPL standard will elicit a large composite N1+MMN negativity followed by a large amplitude P3a. By contrast, a 20 dB decrement will elicit a smaller amplitude MMN and P3a (Muller-Gass et al., 2007; Macdonald et al., 2008). In the classic Näätänen model, the physical increment activates two different systems, the transient and change detector systems. There is evidence that it is largely (or only) the transient detector system that will elicit a P3a (Rinne et al., 2006), often claimed to reflect the interruption of the central executive controlling the allocation of cognitive resources (but note that Rinne et al. did find evidence of a deterioration in performance following presentation of a decrement, in the absence of a P3a).

The major question asked by the present study was whether a psychological (rather than a physical) increment, one that did not represent an actual physical increase in intensity, would continue to be processed differently from a psychological decrement. The psychological increment was created by repeating the high intensity stimulus within the alternating high-low intensity sequence, violating the expectation of a low intensity stimulus. The psychological decrement was created by repeating the low intensity stimulus, violating the expectation of a high intensity stimulus. The decrements and increments were thus *psychological* rather than physical because they represented violations of an expectation of intensity change rather than an actual physical intensity change; the physical intensities of the standard and deviant were, in fact, identical. Critically, the psychological increment did nevertheless elicit a significantly shorter latency and larger fronto-central amplitude MMN than that elicited by the psychological decrement. In addition, a significant inversion in polarity of this negativity was observed at the mastoids following presentation of the psychological increment whereas the inversion at the mastoids was not significant following presentation of the psychological decrement. The finding of differences between the MMNs elicited by the two deviants in this study contrasts with the results of the Alain et al. (1994) and Sculthorpe et al. (2008) studies, which indicated that violations of an alternating low-high frequency pattern will result in identical MMNs, whether elicited by a repetition of the low or the high frequency tone. An increase in the frequency of an acoustic sound does not however have the same salience as an actual (physical) increase or the violation of an expected (psychological) decrease in its intensity. The larger MMN observed following presentation of the psychological increment in the present study cannot be attributed to greater perceptibility compared to the psychological decrement. There was no significant difference in either accuracy or speed of detection of the psychological increments and

decrements. The perception of an increment does therefore appear to be much more salient than the perception of a decrement, whether this is a physical increment, reflecting an actual physical increase in intensity or this is a psychological increment, reflecting the violation of the expectation for a decrease in intensity.

A significant MMN could not be elicited when the intensity separation between the low and high tones was reduced to 3 or even 9 dB. This is also consistent with the Alain et al. and Sculthorpe et al. findings that the amplitude of the alternating frequency pattern MMN varies with the extent of frequency separation between the low and high tones. They did however observe a significant, but much reduced MMN, when their alternating frequencies were separated by as little as 1 semitone. The amplitude of the MMN does vary directly with the perceptibility of change (e.g., Pakarinen, Takaegata, Rinne, Huotilainen & Näätänen, 2007). In the present study, detection of the psychological increments and decrements declined with decreasing intensity separation between the low and high intensity stimuli. When the two tones were separated by only 3 dB, subjects were able to only detect about 25% of the violations in the acoustic pattern and RTs were very long. The absence of an MMN in this condition might thus be explained by the subjects' limited ability to perceive the difference between the low and high intensity tones, and hence to detect a deviation from the alternating intensity pattern. Subjects were however able to detect more than 80% of the deviants in the 9 dB separation condition, at rates approaching those observed in the large 27 dB condition, yet a significant MMN was still not elicited. The presentation of the deviants in the medium separation condition was thus quite perceptible. Perceptibility of a violation in a rule-based pattern appears to be a necessary but not sufficient condition for the elicitation of the MMN (see also Sussman, Winkler, Huotilainen, Ritter, & Näätänen, 2002; Winkler et al., 2005).

The failure to observe an MMN in the 9 dB separation condition is difficult to explain. The standard alternating High-Low pattern may be represented in sensory memory by two levels of rules: as mentioned previously, a local rule describing the relationships between adjacent tones (e.g., L follows H, H follows L) but also a global rule describing general regularities in the overall sequence (e.g., every second tone is H, or every second tone is L) (Bregman, 1990; Horváth et al., 2001; Winkler et al., 2007). The present study employed a "double deviant" sequence (HLHLLLHL or HLHLHHHL). Deviants were followed by another repetition. This second repetition preserves the global rule of the sequence (e.g., every second tone is H). The perception of the global rule creates two sound streams (H_H_H and L_L_L). Although the perception of a streaming sequence is most often triggered by differences in frequency, Moore and Gockel (2002) indicate that streaming can be triggered by other detectable differences such as those in intensity. Violation of the global rule assumes a buildup of streaming (every other tone is H or every other tone is L). Streaming best occurs when there is a large difference between features and when stimuli are presented rapidly (Bregman, 1990; Bregman, Ahad, Crum & O'Reilly, 2000; Snyder & Alain, 2007; Sussman, Ritter & Vaughan, 1998; Winkler et al,. 2005). In the large condition, the 27 dB separation between the high and low intensity stimuli might have been sufficient to permit automatic streaming in spite of the relatively slow rate of presentation. It is thus possible that subjects were perceiving the two separate streams and thus violation of the global rather than the local rule. The 9 dB separation may however have been insufficient to allow for the automatic segregation of the stimuli into separate streams and subjects thus failed to passively detect the violation of the global rule. Such a relatively small separation and slow rate of presentation might require active attention to perceive the streaming sequence. In the present study, subjects were able to perceive the occurrence of both the

psychological increments and decrements when actively asked to do so. Sussman et al. (2002) have demonstrated that for the MMN to be elicited, the subject must be aware of the rules of the pattern. They had subjects attend to one of two auditory sequences. A violation of their frequency pattern occurring in the unattended channel did not elicit an MMN unless subjects were previously made aware of the rule of the pattern. In the present study, subjects ignored the auditory channel and were not informed about the rule of the pattern. A large MMN was nevertheless elicited in the large intensity separation condition, suggesting that they had automatically become aware of either the local alternating pattern or the global streaming rule. Regardless of the mode of perception, the extent of separation in the medium condition might not have been sufficient to allow subjects to become passively aware of the rule.

5. Conclusions

In summary, a large MMN was elicited by a violation of an alternating concrete rule-based low-high intensity pattern (LHLHLH) but only when the separation between the intensities was 27 dB. Importantly the deviant was created by a repetition of a stimulus. The repetition of the high intensity tone (the psychological increment) violated the local rule-based expectation for the presentation of a lower intensity tone and elicited a large amplitude MMN. The repetition of the low intensity (the psychological decrement) also elicited an MMN but its amplitude was significantly reduced compared to that elicited by the psychological increment. Importantly, the larger amplitude MMN following the psychological increment cannot be explained by the fact that the deviant was physically more intense than the standard; their intensities were identical. The absence of an MMN when the stimuli were separated by 9 dB is difficult to explain. In a separate behavioural condition, subjects were able to accurately detect the occurrence of the repetition. The alternating sequence might also establish two global-rule based streaming

sequences (L_L_L and H-H-H). The automatic perception of streaming does however require a large difference among features and also a rapid rate of stimulus presentation. The streaming mode might have been perceived when the stimuli were separated by 27 dB but not by 9 dB. Thus, although subjects could detect the occurrence of a violation of the medium separation sequence when actively asked to do so, this may not have been possible when the auditory stimuli were ignored.

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Chapter 4

Study 3 (Experiments 3 and 4). Event-Related Potential Measures of a Violation of an Expected Increase and Decrease in Intensity

Rationale. In Study 2, the deviants created by repetition of high or low intensity stimuli in the large separation condition, repetition of the high intensity stimuli produced significantly larger-amplitude and shorter-latency MMNs than did the repetition of the lower intensity tones. Neither the repetition of the high nor low intensity stimuli were successful in eliciting a significant P3a, although the repetition of the high intensity deviant did result in a non-significant P3a-like ERP. These results lend support to the notion that increments in intensity are, in fact, more disruptive, even when eliminating the possibility of increased activation of the transient detector system. Such an interpretation is confounded, however, by the fact that the deviants representing the repetition of the high and low intensity stimuli were physically different (i.e., 63 dB, 90 dB). Differences in the MMN could thus be attributed to these physical differences rather than to the differential psychological relevance of the deviants.

The third study of this series thus consisted of two separate experiments controlled for the confounding issue of physically different deviants. This was achieved in both experiments by presenting participants with two separate conditions comprised of the stimuli employed in Study 1 (60, 80, and 90 dB tones). Deviants in both the increment and decrement conditions were created by repeating the identical 80 dB tone, thus eliminating the physical differences between deviants that confounded interpretation of the previous study. In these experiments, both standards and the increment and decrement deviants were thus physically identical. Any differences that were found could thus only be attributed to psychological processing.

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1.Introduction

Detection of salient auditory change in the environment plays a critical role in the survival of mammalian species, providing information regarding the presence and position of potential predators or mating partners. Changes in the intensity of stimuli within the environment have been suggested to have particular significance in this regard, with a an increase in the intensity of auditory input signalling the potentially critical approach of an organism and, on the other hand, a decrease in intensity signalling the retreat of an organism. In support of this notion, studies have shown that an increase in stimulus intensity is experienced as "looming" or approaching and may elicit a fear response in animals and a decrease in intensity is experienced as "fading" or retreating [1-3]. The brain has evolved a set of mechanisms to detect such change and redirect attention away from ongoing cognitive activity and toward potentially critical auditory input.

The classic Näätänen [4] model describes the types of processing required to detect a change in the features of an acoustic signal. The model has undergone revision recently [5], while other models including a regulatory extraction model [6] and a predictive coding model [7] have also been developed. There is a good deal of overlap among the models and most assume an encoding and memory storage of the regularities in previous "standard" stimulation and a comparison of the features of an incoming stimulus with those stored in memory. In the Näätänen model, if these features match, further processing is deemed redundant and thus ceases. If any feature (e.g., frequency, intensity, duration) fails to match, the change detection system is activated. Unique to this model is the use of event-related potentials (ERPs) to provide a means to monitor the extent of processing when the subject is not actively attending to the auditory channel. The detection of a stimulus regularity that signals change from the past is reflected by a

fronto-centrally maximum negative-going ERP, the mismatch negativity (MMN) occurring approximately 150-250 ms following the onset of the deviant auditory stimulus. The output of this system varies in proportion to the extent of change. If the magnitude of change reaches a certain variable threshold, an interrupt is sent to the central executive controlling the allocation of cognitive resources, resulting in a halting of ongoing activities and a switching of attention to the auditory channel. This process of redirection has been called "attention capture" and is indexed by a different and later ERP, the P3a, a centro-frontally maximum positivity occurring 200-300 ms following the onset of a deviant auditory stimulus [8].

The MMN is often recorded using the so-called "oddball" paradigm. This paradigm consists of a series of physically identical frequently occurring repetitive "standard" stimuli that are periodically changed to a "deviant" stimulus whose physical features differ in some way from the preceding standard series. Muller-Gass, Macdonald, Schröger, Sculthorpe, and Campbell [9] employed an oddball paradigm to examine the influence of a change in auditory intensity on attention capture. Participants were presented with a frequently occurring 80 dB SPL auditory "standard" on 85% of trials and either a 90 dB increment or 60 dB decrement "deviant" on the remaining trials. The 90 dB and 60 dB deviants represent approximately equivalent changes in acoustic energy relative to the 80 dB standard. Subjects' attention was diverted to a continuous visual multiple moving object task and thus the auditory stimuli were irrelevant and to-be-ignored. The MMN is best observed in a difference wave computed by subtracting the ERPs elicited by the standard from those elicited by the deviant. The subtraction procedure isolates processing that is unique to the deviant by removing processing that is common to both the standard and deviant. An MMN and a small amplitude P3a were evident in the decrement difference wave in this study, while a much larger negativity, followed by a large P3a were

observed in the increment difference wave. The larger amplitude of the P3a elicited in response to the increment in this study lends support to the notion that increases in stimulus intensity are more disruptive than decreases.

The large negativity that was evident in the difference wave following presentation of the increment was probably not an unambiguous MMN, however. This is because in the Näätänen model [4] increments in intensity also result in increased activation of a second, different system, the transient detection system, in addition to the change detection system. The output of the transient detection system, as indexed by the N1 ERP, varies in proportion with the energy (or intensity) of the stimulus. A deviant, whose intensity is higher than that of the standard, will therefore elicit a larger N1 than the standard and also an MMN; the N1 and MMN thus summate both temporally and spatially. Because the negativity that is observed on the scalp recording is a composite N1+MMN, it is called a deviant-related negativity (DRN). By contrast, a deviant whose intensity is lower than the standard will elicit a smaller N1 but also again, an MMN, because it also signals change. Thus, the additional negativity elicited by a decrement deviant can only be attributed to increased activation of the change detection system.

The obtrusiveness of an intensity increment can even be observed in an unconscious state, natural sleep. Macdonald, Jamshidi, and Campbell [10] employed an oddball paradigm to examine the differences in the processing of intensity increments and decrements during the waking and sleeping states. Subjects were presented with a similar oddball sequence consisting of frequently occurring 80 dB standard tones and rare 90 dB increment or 60 dB decrement deviants. The results observed during the waking state mirrored those of the Muller-Gass et al. study [9], with the increment resulting in a larger negativity than the decrement, and both deviants successfully eliciting a P3a. The increment deviant was successful in eliciting a

negativity corresponding to the latency and scalp distribution of a DRN and a P3a during the REM stage of sleep. The decrement deviant failed to elicit either of these ERPs. During non-REM sleep, neither the increment nor decrement elicited a DRN. The findings from both studies appear to indicate that increments in intensity are much more salient than decrements of equal magnitude, and are more likely to passively capture the attention of an observer.

Recently, researchers have begun to use more complex patterns rather than simple oddball paradigms to study the change detection process [11]. The change detection system has been shown to be sensitive to violations in both concrete and abstract rule-based acoustic patterns [12-18]. Alain, Woods, and Ogawa [19] and Sculthorpe, Collin, and Campbell [20] employed a concrete rule-based pattern consisting of high and low frequency alternating tones (A-B-A-B-A-B-A-B), with deviants created by the repetition of a tone within the sequence (A-B-A-B-A-B-**B**-B-A). The deviant in this paradigm was thus physically identical to the stimulus preceding it (i.e., the standard). A highly consistent finding in the neurophysiological literature is that the repetition of the same, identical rapidly-presented stimulus will result in a reduction of the response because of refractory and possibly habituation processes. This was not the case in the Alain et al. and Sculthorpe et al. studies. The deviants in both studies elicited a larger negativity, the MMN, than the physically identical standard stimulus that preceded it. This is because the deviant violates the *expectancy* for a high or low frequency tone; it thus signals a psychological rather than a physical change.

Macdonald and Campbell [21] employed an alternating pattern with the intensity of the auditory tones alternating rather than their frequency. A sequence of 1000 Hz tones followed a standard, rule-based alternating high-low intensity pattern (H-L-H-L-H-L). This standard pattern was periodically interrupted by a deviant created by repeating one of the stimuli in the sequence

(e.g., H-L-H-L-**L**-L-H). The repetition of the high intensity stimulus represented what Macdonald and Campbell [21] called a relative, *psychological* increment compared to what the alternating rule would have predicted (the low intensity). Because the deviant was created by the repetition of a physically identical stimulus (the high intensity) that did not differ in intensity relative to the preceding standard, it should not have resulted in increased activation of the transient detector system. Similarly, the repetition of the low intensity stimulus acted as a relative, *psychological* decrement compared to what the alternating rule would have predicted (the high intensity). Thus, the alternating pattern paradigm employed in this study allowed for direct comparison of the processing of increment and decrement stimuli within the change detection system, circumventing additional activation of transient detector activation and the overlapping N1 component. In different conditions, the intensity difference between the low and high intensity tones was 3 dB (75 dB and 78 dB), 9 dB (72 dB and 81 dB) or 27 dB (63 dB and 90 dB). The repetition of the lower intensity tone (L-L), the psychological "decrement" deviant, thus represented a 3, 9, or 27 dB violation of the expected intensity increment (L-H) rule, while the high intensity repetition (H-H), the psychological "increment" deviant, represented a 3, 9, or 27 dB violation of the expected intensity decrement (H-L) rule. A large MMN was elicited only when the separation between the low and high intensities was 27 dB. Importantly, this MMN peaked significantly earlier and its amplitude was significantly larger following presentation of the psychological increment. The results of this study would seem to indicate that psychological increments are still more salient than decrements even though the repetition of the high intensity stimulus (the deviant) would result in less activation of the refractory-based transient detector system.

There remains a problem with this conclusion. Jacobsen, Horenkamp, and Schröger [22] suggest that in the ideal study, all standards and deviants should be physically identical. In the Macdonald and Campbell study [21], while the standard and psychological increment deviant (both 90 dB) and the standard and psychological decrement deviant (both 63 dB) were physically identical, the two deviants were nevertheless physically different (90 vs 63 dB). The repetition of a 63 dB stimulus (the psychological decrement) may not be experienced in the same way as the repetition of a 90 dB stimulus (the psychological increment). In order to address this issue, the present study consists of two experiments again employing an alternating high and low intensity pattern, but now, the standards and also the increment and decrement deviants will be physically identical.

2. Experiment 1: Alternating Paired Pattern

The MMN can also be elicited in a somewhat different "paired" pattern to examine the influence of psychological intensity change. Paavilainen et al. [17] presented two brief duration tones separated by 50 ms followed by a 500 ms pause. In an ascending condition, the standard pattern followed the rule that the intensity of the second tone in the pair was 7 dB higher than the first. Deviation in the sequence occurred when the second tone descended in intensity. The presentation of the lower intensity deviant violated the rule that the second stimulus is higher in intensity than the first, thus also representing a psychological decrement in intensity. However, the deviant was physically lower in intensity. In a second descending condition, the presentation of descending pairs was the standard pattern that was sporadically interrupted by an ascending deviant pair. Again, this represented both a psychological and a physical increment in intensity. Both the increment and decrement deviants were successful in eliciting DRNs. Unfortunately, the authors did not examine differences between the ERPs elicited in response to the increment

and decrement deviants. In the decrement condition the DRN was probably only an MMN, solely reflecting increased activation of the change detection system. The DRN elicited by the increment deviant, however, may have reflected a composite DRN, as a result of increased activation in both the transient and change detection systems.

Experiment 1 of the present study employed a paired alternating pattern paradigm to compare the processing of psychological increment and decrement stimuli within the change detection system, while controlling for physical differences in the two types of deviants. The study was designed so that two alternating paired pattern conditions were presented, so that an identical 80 dB tone served as a standard and also as both decrement and increment deviants. Any differences in processing between the psychological increment and decrement could thus be attributed to physical differences between the repeated deviants.

2.1 Methods

2.1.1 Subjects. Ten young adults (4 males) between the ages of 20 and 29 years (Mean=25.4 years) volunteered to participate in this experiment. None reported a history of neurological disorder or auditory impairment. Written informed consent was obtained prior to the experiment and subjects received an honorarium for participation. The study was conducted according to the guidelines of the Canadian Tri-Council (Health, Natural and Social Sciences) on ethical conduct involving human subjects. Procedures were approved by the University of Ottawa Research Ethics Board.

2.1.2 Procedure & Stimuli. An InstEP system was used for the presentation of stimuli, and the collection and analyses of the ERP data. Subjects were seated in a sound-attenuated room during the EEG recording sessions. They were instructed to attend to a silent, subtitled film while auditory stimuli were presented via headphones. Two different types of auditory patterns

were presented to subjects. The first, the increment condition, consisted of an alternating high-low intensity "standard" pattern with stimuli presented in pairs (H-L...H-L...H-L). The second consisted of an alternating paired low-high intensity (L-H...L-H...L-H) pattern. Deviants were created by the repetition of the second stimulus in the standard pair (e.g., H-L…H-L…H-**H**…H-L in the case of the increment or L-H...L-H...L-**L**...L-H in the case of the decrement). The deviants thus represented a psychological change rather than a physical change in intensity relative to the immediately preceding stimulus. In the psychological increment condition, a standard 80-60 dB SPL pair was presented. On 12.5% of trials, this was changed to an 80-**80** dB deviant pair. In this case, because the pattern rule establishes that the second member of the pair should be low intensity (i.e., 60 dB), the presentation of the 80 dB deviant thus acts as a psychological increment (its intensity was higher than what would be expected by the rule). In the psychological decrement condition, a standard 80-90 dB SPL pair was presented. The violation of the pattern was again created by presenting the same 80-**80** dB pair, on 12.5% of trials. Because the pattern rule establishes that the second member of the pair should be high intensity (i.e., 90 dB), the presentation of the 80 dB deviant acts as a psychological decrement. Importantly, the deviants in the psychological increment and psychological decrement conditions were physically identical (i.e., 80-80 dB pairs). Still, in this paradigm the standard stimulus pair (e.g., 80-60 or 80-90 dB) was physically different from the deviant pair (80-80 dB). Two oddball conditions were therefore run in which the standard was always an 80-80 dB pair. The deviant pair was either 80-90 dB in the oddball increment condition (L-L…L-L…L-l…L-H…L-L) or 80-60 dB in the oddball decrement condition (H-H…H-H…H-H…H-L…H-H). The deviant occurred with the same probability of occurrence as in the paired alternating paradigm. Presentation of the oddball conditions served to provide a standard (80-80 dB) that resolved the

problem of having physically different standard pairs in the increment and decrement pattern conditions. The standard pairs in the oddball increment and decrement conditions were physically identical (80-80 dB) and they were also physically identical to the psychological increment and decrement deviants in the paired pattern paradigm. The ERPs to the standard 80-80 dB pairs in the oddball conditions were then subtracted from the physically identical 80-80 deviant pairs in the psychological increment and psychological decrement conditions.

Separate increment and decrement conditions were presented corresponding to each of the two sequences (alternating pattern and oddball). Thus, each participant was presented with auditory patterns corresponding to four separate conditions: psychological decrement (L-H…L-H…L-**L**…L-H), psychological increment (H-L…H-L…H-**H**…H-L), oddball decrement (H-H…H-H…H-**L**…H-H) and oddball increment (L-L…L-L…L-**H**…L-L). Stimuli in all conditions were presented in pairs with a within-pair SOA (offset-to-onset) of 100 ms and a between-pair SOA of 1800 ms. All stimuli had a frequency of 1000 Hz and a total duration of 55 ms (5 ms rise/fall). Within each condition, the standard and deviant stimuli were presented in pseudo-randomized order, with the constraint that a deviant was followed by a minimum of 3 standard pairs. Similarly, a minimum of 3 standard pairs were presented at the beginning of each condition prior to the occurrence of a deviant to allow for the standard pattern to be established in memory. Three blocks of each of condition were presented (i.e., a total of twelve blocks), with each block containing a total of 160 stimulus pairs. The conditions within each block were presented in random order.

2.1.3 Performance Task. The amplitude of the MMN is affected by perceptibility of the deviant. Deviants that are easy to perceive elicit a larger amplitude and shorter latency MMN. The perceptibility of the increment and decrement deviants was therefore determined in a

separate behavioural discrimination task following the physiological recording sessions. The same stimulus pairs were used. A single block of stimuli was presented for the psychological increment and the decrement conditions. Subjects were instructed to press a keyboard button as quickly and accurately as possible upon detection of a violation of the standard L-H or H-L pattern (i.e., a repetition of the same stimulus). Both accuracy of detection ("hits") and reaction time (RT) were recorded. A response had to be made within 1000 ms after stimulus onset in order to be considered a hit.

2.1.4 Physiological Recording. The EEG was recorded from 10 scalp sites representing frontal (F3, Fz, F4), central (Cz, C3, C4) , parietal (Pz), temporal (T7, T8), and occipital (Oz) areas of the scalp using silver/silver chloride electrodes attached to an electrode cap (Electro-Cap International Inc., Eaton, OH). Two additional channels were recorded from individual electrodes placed on the left and right mastoids (M1, M2). The nose served as a reference. A true N1 and MMN will invert in polarity (i.e., be recorded as a positive potential) at the mastoids when a nose reference is used. Vertical eye movements and blinks were recorded from electrodes placed at the infra- and supra-orbital ridges of the left eye. A horizontal EOG was recorded from electrodes placed at the outer canthus of each eye. The ground electrode was located between the Fz and FPz sites. Inter-electrode impedances were kept below 5 kΩ.

The physiological signals were digitized continuously at a 256 Hz sampling rate and stored on hard disk. The high frequency filter was set at 35 Hz and the time constant at 2 s. Offline, an inverse FFT high digital filter set at 15 Hz was applied to the data. Eye movements and blinks were corrected using an algorithm operating in the time and frequency domains [23]. The participants' continuous data were partitioned into 600 ms epochs beginning 100 ms before onset of the second stimulus in the pair and continuing for another 500 ms following it and

baseline corrected. Epochs containing EEG that exceeded ±100 μV were considered to be artefact and excluded from further analyses. Individual participant's data were then averaged according to electrode site and stimulus type (oddball standards (i.e., 80-**80** dB) and pattern increment and decrement deviant (i.e., 80-**80** dB)). The second stimulus within a pair of repetitive stimuli was considered to be the deviant within a condition. The three pairs of stimuli presented immediately following the deviants were omitted from averaging to allow reformation of the memory for the standard sequence pattern required for change from this pattern to be detected. Similarly, the first three pairs of stimuli in each condition were also omitted from averaging (a memory for the standard pattern would not yet have been formed).

2.1.5 Quantification of the MMN. The standard stimuli in the oddball conditions (80-80 dB) were subtracted from the physically identical deviant occurrences of these pairs in the psychological increment and decrement conditions in order to isolate processing that is unique to the detection of the deviants. Difference waves were computed by subtracting point-by-point the ERPs elicited by the auditory standard from the deviant pairs at each electrode site.

There are problems with the use of common statistical procedures. Previous studies have indicated that the MMN and P3a may be much reduced or absent following presentation of some physical decrement deviants. It is unknown whether this will be the case following the psychological increments and decrements used in this study. The observation of a significant difference in, for example, the amplitude of the MMN elicited by the increment and decrement deviants cannot be used as evidence that the MMN was elicited in both conditions. To avoid these ambiguities, it is necessary to first demonstrate that a significant MMN and P3a was indeed elicited in the different conditions. A scoring method described by Alho, Sams, Paavilainen, Reinikainen, and Näätänen [24] was used for this purpose. The average of all data points in the

100 ms pre-stimulus period served as a zero amplitude voltage baseline from which all amplitudes were measured. The post-stimulus sweep period was subdivided into seven 50 ms latency intervals, beginning at 50 ms and continuing until 400 ms. Within each of these intervals, the average of all data points was computed, yielding an average amplitude measure. Confidence intervals were computed for each 50 ms window. This procedure determined the probability that the mean MMN amplitude value fell within an upper or lower range of the pre-stimulus baseline zero voltage level. Thus, when the lower limit of a confidence interval was significantly less than 0 μV, (i.e., was negative-going), the interval was considered to contain a significant negativity. This procedure is equivalent to computing a *t*-test between the standard and deviant waveforms [25]. Because a negative directionality was predicted in the case of the MMN and a positive directionality was predicted in the case of the P3a, one-tailed tests of significance ($p<0.05$) were applied to the confidence intervals. To restrict the likelihood of chance findings, the negativity had to conform to the usual latency (100-250 ms) and scalp distribution (fronto-central maximum, inversion in polarity at the mastoids) of the MMN, while the positivity had to conform to the usual latency (200-350 ms) and scalp distribution (centro-frontal maximum) of the P3a.

A problem with the averaging of all data points within time windows is that the amplitude of a peak spanning across intervals tends to be "smeared" (underestimated). Thus, the peak amplitude and latency of the MMN and P3a were also measured manually. These data were then subjected to one-tailed t-tests comparing the amplitude of responses elicited by the increment to those elicited by the decrement. One tailed t-tests were applied because previous findings have indicated that the increment would elicit a larger MMN than the decrement [21]. Performance data (i.e., hit rates, reaction times) were also analyzed via one-tailed t-tests. In the case of the

performance data, the use of one-tailed tests of significance would increase the likelihood of findings differences in perceptibility of the increment and decrement deviants.

2.2 Results

2.2.1 Performance Data. Subjects' ability to identify the psychological increment and psychological decrement deviants in the alternating pattern paradigms did not significantly differ, $t<1$. Reaction times were, however, found to be significantly faster when the 80-80 deviant pair represented a psychological increment (i.e., from the 80-60 dB standard), as compared to a psychological decrement (i.e., from the 80-90 dB standard), $t(9) = 6.14$, $p<0.01$.

2.2.2 Physiological Data. This study examined differences in the MMN that were elicited by the psychological decrement and increment deviants in different conditions. Because the MMN is measured in a difference wave (i.e., deviant minus standard ERPs), an assumption is made that the processing of the standards is constant across the two conditions. Any differences observed in the difference wave could therefore only be attributed to the processing of the psychological detection of change (i.e., the processing of the deviant). The assumption that processing of the standards was constant in the two conditions was tested. Figure 1 depicts the ERPs elicited by the same standard auditory stimulus pairs (80-80 dB) in the increment and decrement oddball conditions. Two distinct negative deflections are apparent at about 100 and 310 ms. The first negative peak is the N1 to the initial stimulus (80 dB), while the second negative deflection is the N1 to the second 80 dB stimulus in the standard pair. As may be observed, the standard ERPs are very similar in both the increment and decrement oddball conditions, $F<1$ in all intervals.

The difference waves corresponding to the psychological increment condition are presented in Figure 2. The onset of the second stimulus in the pair (the deviant) occurs at 0 ms in

this figure. As may be observed, the deviant in the psychological increment condition (80-60...80-60... 80-**80**...80-60) elicited a large (M = -3.69 SD = 2.18 μV) fronto-central MMN, peaking at approximately 193 ms. Confidence interval testing revealed that the amplitude of this component differed significantly from the zero-voltage baseline ($p<0.05$) during the 150-200 ms window. The MMN inverted in polarity at the mastoids. However, this inversion failed to reach significance at either the M1 or M2 electrode sites. A centrally maximum P3a-like wave, peaking at approximately 280 ms, was evident in the difference wave. However, this positivity failed to reach significance as determined by confidence interval testing.

The difference waves corresponding to the deviant in the psychological decrement condition (80-90...80-90...80-**80**...80-90) are illustrated in Figure 3. In this condition, the psychological decrement elicited a smaller MMN (M= -2.11 μV, SD = 1.62 μV), peaking at approximately 221 ms. Confidence interval testing indicated that this negativity differed significantly from zero-voltage baseline during the 200-250 ms window ($p<0.05$), while the small inversion at the mastoids was not significant. A P3a was not elicited.

One-tailed t-tests on the Fz data (where the MMN was largest) were run to compare the MMN in the psychological increment (80-60…80-60…80-**80**…80-60) and decrement (80-90…80-90…80-**80**…80-90) conditions. The amplitude of the MMN was significantly larger following presentation of the psychological increments, $t(9) = 1.83$, $p<0.05$. Similarly, its latency was significantly shorter for the psychological increments, $t(9) = 2.90$, $p<0.01$. The MMN responses were larger in amplitude at F4 than F3 in both conditions; neither of these differences were however statistically significant.

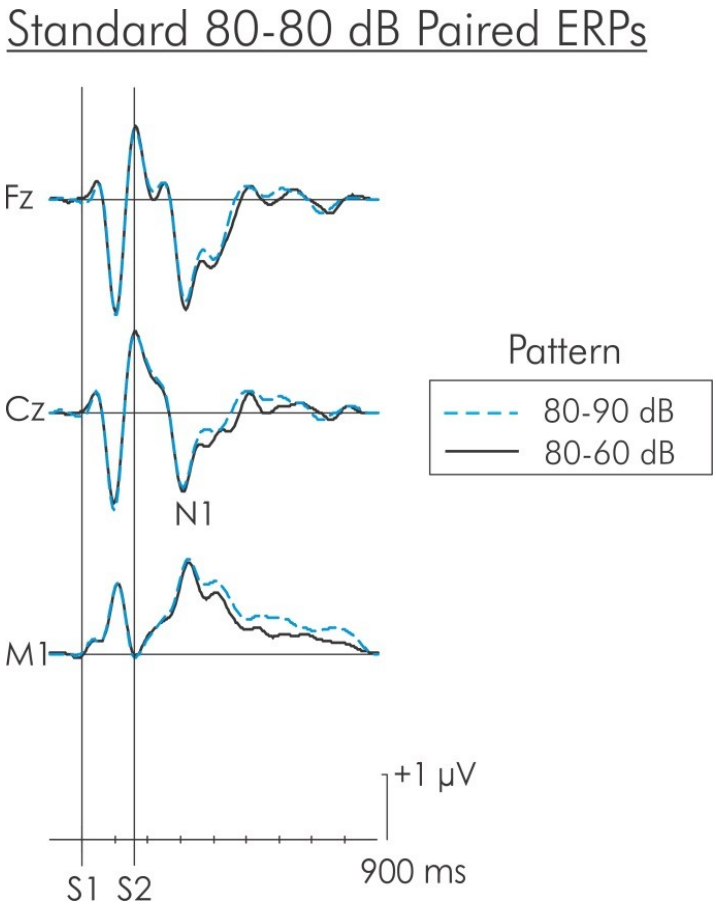

Figure 1. Grand average "raw" ERPs elicited by the standard pairs in the oddball conditions. In this and all other figures, positivity at the scalp relative to the reference is indicated by an upward deflection. The first 80 dB stimulus of the pair occurs at 0 ms and the second 80 dB stimulus occurs 100 ms after the offset of the first. The ERPs elicited by the 80-80 dB standards in the increment and decrement conditions are superimposed. The morphology of these ERPs are essentially equivalent. Both include an N1s occurring approximately 100 ms followed by a positive deflection and another N1 approximately 140 ms following the onset of the second. These standard ERPs were subsequently subtracted from the ERPs elicited by the deviant 80-80 dB pairs in the psychological increment and decrement conditions in order to isolate processing associated with the change detection process.

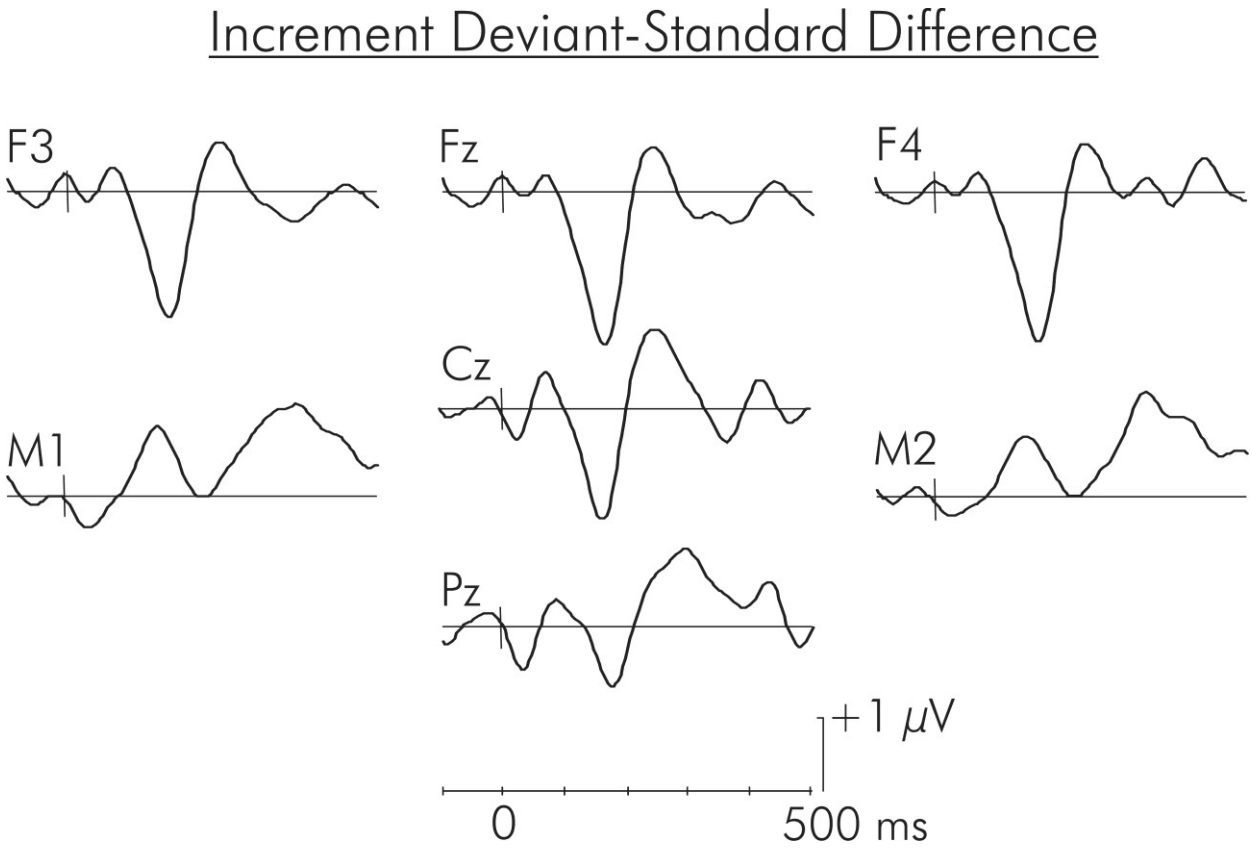

Figure 2. Grand average difference waves in the psychological increment condition. Difference waves were created by subtracting frequently occurring 80-80 dB standard pairs in the oddball decrement condition (80-80...80-80...80-60...80-80) from deviant occurrences of these pairs in the psychological increment condition (80-60...80-60...80-**80**...80-60). The onset of the second stimulus (when deviance from the standard pattern occurs) is set at 0 ms in this figure. A large amplitude MMN was evident over fronto-central areas of the scalp between 150 and 200 ms following presentation of the psychological increment. The MMN inverted in polarity at the mastoids. However, this inversion failed to reach significance at either the M1 or M2 electrode sites. A centrally maximum non-significant P3a-like wave is evident at approximately 280 ms.

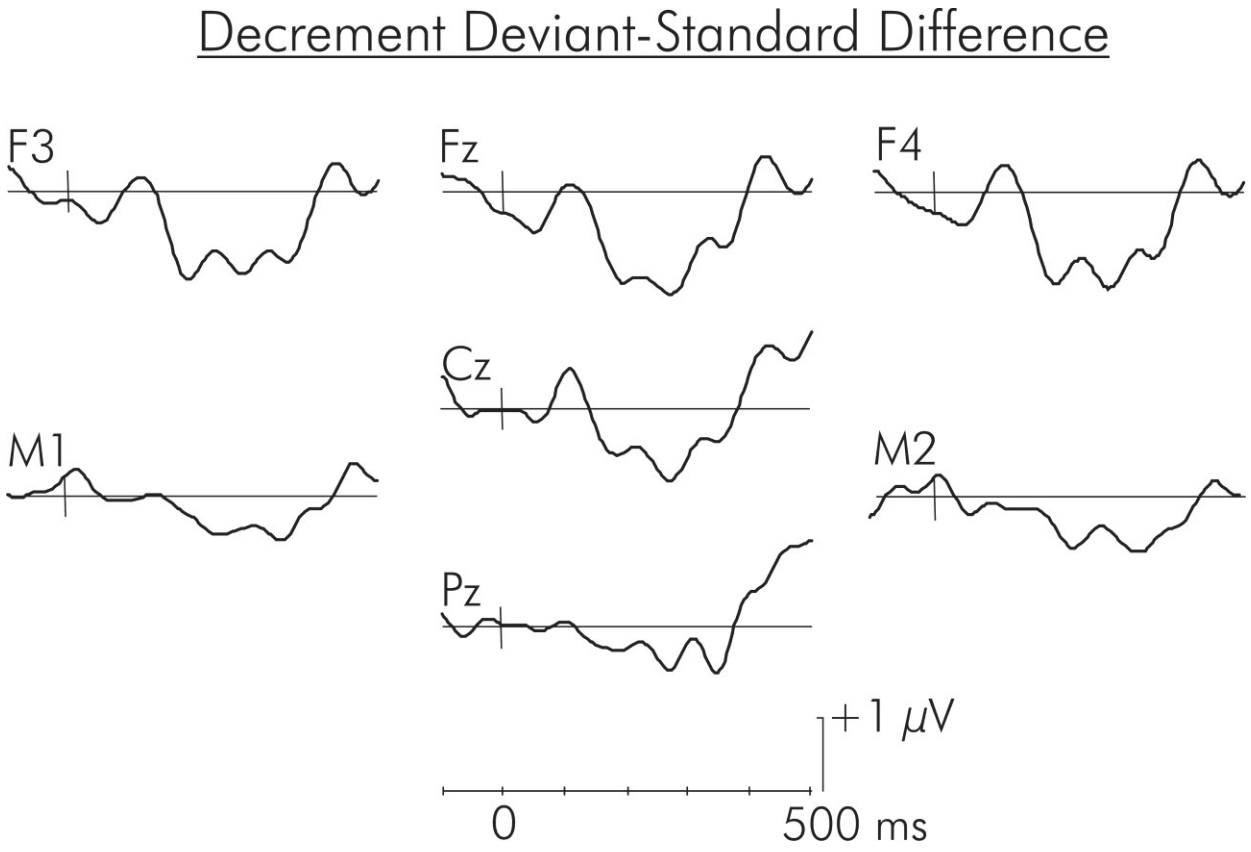

Figure 3. Grand average difference waves in the psychological decrement condition. Difference waves were created by subtracting frequently occurring 80-80 dB standard pairs in the oddball increment condition (80-80...80-80...80-90...80-80) from deviant occurrences of these pairs in the psychological decrement condition (80-90...80-90...80-**80**...80-90). Again, the onset of the second (deviant) member of the pair is set at 0 ms in this figure. The psychological decrement elicited a smaller and relatively delayed (peaking between 200-250 ms) but significant MMN. The small inversion of the mastoids was not significant. No P3a-like positivity was present.

2.3 Discussion

Deviants in both the psychological increment and psychological decrement conditions were successful in eliciting MMNs that differed significantly from the zero-voltage baseline, as determined by confidence interval testing. Deviants in the psychological increment condition elicited larger amplitude and shorter latency MMNs than those in the psychological decrement condition. Thus, a more prominent MMN was elicited when the regular 80-60 dB pattern was interrupted by an 80-80 dB deviant pair (i.e., a psychological increment). On the other hand, a smaller (but significant) MMN was elicited when the regular 80-90 dB pattern was interrupted by the presentation of the same 80-80 dB deviant pair (i.e., a psychological decrement). The deviant in the psychological increment condition also elicited a positivity, corresponding to the typical scalp-distribution and latency parameters of a P3a, but this positivity was not significantly different from the zero voltage baseline. The deviant in the psychological decrement condition did not elicit any P3a-like potential. Importantly, in contrast to the deviants employed in the Macdonald and Campbell study [21], the psychological increment and decrement were physically identical. The larger MMN observed in the psychological increment relative to the decrement condition cannot therefore easily be attributed to physical differences between the stimuli. When subjects were asked to detect the deviants, accuracy of detection (hit rate) did not differ for the psychological increments and decrements. RTs were however faster following presentation of the psychological increments. There is thus some evidence that the psychological increment was more easily perceived than the decrement.

Differences in perceptibility of the deviants might be related to the integration of the standard pairs. Integration occurs when the features of the present stimulus are added to (or "integrated" with) those of the preceding stimulus existing in sensory memory and is most likely

to occur when stimuli are presented very rapidly (e.g., less than 200 ms) [26]. The time between presentation of the two paired stimuli was 100 ms. The perception of the standard could thus be an integration of the 80 and 60 dB pairs in the increment condition, and the 80 and 90 dB pairs in the decrement condition. Because the same 80-80 dB pair served as the deviant in both conditions, the integration of the pairs would not have varied across conditions. Thus in the psychological increment condition, in which the MMN was large, the occurrence of the 80-80 dB deviant pair might be perceived as a *physical* increment in intensity relative to the integrated (80-60 dB) standard pair. In the psychological decrement condition, in which the MMN was smaller, the occurrence of the same 80-80 dB deviant pair might be perceived as a *physical* decrement in intensity relative to the integrated (80-90 dB) standard pair. It is thus possible that MMN differences between the psychological increment and decrement could still be explained by physical differences in the perceived intensity and perhaps a resulting activation of the transient detection system.

3. Experiment 2. Continuous Alternating Pattern

In order to remove the problem of possible integration, a second experiment was run in which the occurrence of low and high intensity tones again alternated. They were not however presented in pairs. The stimuli in the psychological increment condition again consisted of 80 and 60 dB tones, while those in the psychological decrement condition again consisted of 80 and 90 dB tones. The time between the alternating stimuli was however 500 ms, well exceeding the minimal 200 ms time window usually associated with stimulus integration [26]. The longer SOA should thus overcome the problem of feature integration and the possible increased activation of the transient detector system following presentation of the psychological increment. MMN

differences between the increment and decrement deviants could thus be attributed to differential activation of only the change detection system.

3.1 Methods

3.1.1 Subjects. Eleven young adults (6 males) between the ages of 19 and 33 years (Mean= 26.4 years) volunteered to participate in this study. None reported a history of neurological disorder or auditory impairment. Written informed consent was obtained prior to the experiment and subjects received an honorarium as compensation for participation. The study was again conducted according to the guidelines of the Canadian Tri-Council (Health, Natural and Social Sciences) on ethical conduct involving human subjects.

3.1.2 Procedure & Stimuli. Again, subjects were instructed to attend to a silent, subtitled film while auditory stimuli were presented via headphones. The auditory paradigm consisted of an alternating low-high intensity pattern (L-H-L-H-L-H) but in this experiment, the offset-to-onset SOA between the auditory stimuli was long, with a stimulus being presented every 500 ms. The alternating pattern was again violated by repeating the 80 dB SPL stimulus. Two different pattern violations were presented (L-H-L-H-L-**L-**L-H or L-H-L-H-**H-**H-L-H) in separate psychological increment and psychological decrement conditions. In the psychological increment condition, 80 dB and 60dB SPL tones were presented in an alternating pattern with the deviant created by the repetition of the higher intensity (80 dB) tone (60-80-60-80-**80**-80-60). In the psychological decrement condition, 80 dB and 90 dB SPL tones were presented in an alternating pattern with the deviant created by the repetition of the 80 dB tone (90-80-90-80-**80**-80-90). The decrement and increment deviants each occurred 75 times within separate blocks of 600 stimulus pairings, making the total probability of a deviant repetitive pair .125 in each condition. The frequency of the tones was again 100 Hz and the total duration was 110 ms, (10 ms rise/fall

time). The deviant pattern (H-H or L-L) was presented pseudo-randomly with the constraint that it followed a minimum of three and a maximum of 20 standard (L-H) stimulus pairings. Similarly, a minimum of 3 H-L or L-H standard alternations were presented at the beginning of each condition prior to the occurrence of a deviant repetitive stimulus to allow for the initial establishment of the standard pattern within memory. Two blocks of the psychological increment and psychological decrement conditions were presented to each participant (i.e., a total of four blocks) in random order. The auditory sequences were presented using E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA) on a PC using Windows XP as an operating system.

3.1.3 Physiological Recording. The number of scalp sites was increased to allow for the scalp distribution mapping of the MMN and possible P3a elicited by the psychological increments and decrements. EEG activity was recorded from 63 sites over frontal, central, parietal, temporal, and occipital sites using an active silver-silver chloride electrode system attached to an electrode cap (Brain Products, GmbH, Munich, Germany). Activity from the left and right mastoids was also recorded. An electrode was placed on the infra-orbital ridge of the left eye to record vertical eye movements. The tip of the nose was used as a reference for all channels. Inter-electrode impedances varied from 20 to 50 kΩ. A high filter was set at 500 Hz. The time constant was 2 s. The EEG was continuously digitized at a 250 Hz sampling rate and stored on hard disk for later analyses.

Offline, the data were reconstructed using Brain Products' Analyzer2 software. The continuous data were digitally filtered using a high filter set at 15 Hz. EEG channels displaying high levels of noise were replaced by interpolating the data of the surrounding electrode sites [27]. Following offline inspection, the data of two participants were rejected. The first of these

subjects' data were discarded due to excessive levels of artefact across multiple channels, while the other subject failed to elicit either a sensory-related ERP (N1-P2) to the standard stimulus or an MMN in response to either deviant.

A vertical EOG was computed by subtracting activity recorded at FP1 from that at the lower EOG. A horizontal EOG was computed by subtracting the FT9 from the FT10 activity. Because of the large number of electrode placements, it was possible to use Independent Component Analysis (ICA) to identify eye movements and blinks that were statistically independent of the EEG activity [28]. These vertical and horizontal eye movements were then partialled out from the EEG.

The continuous EEG was segmented into discrete, 700 ms epochs including a 100 ms pre-stimulus baseline. The single trials epochs were subsequently baseline corrected. Any trials containing EEG activity exceeding ±100 μV on any channel were rejected from further analysis. The single epochs were sorted and averaged on the basis of electrode site and stimulus type (standard, decrement or increment).

3.1.4 Quantification of the MMN. As in the previous experiment, the MMN response was isolated in a difference wave representing the difference in processing between the standard and the deviant. The standards from the increment and decrement patterned paradigms (an 80 dB tone that followed a 60 dB or 90 dB tone, respectively) were subtracted from the deviant occurrences of the 80 dB stimuli (the repetition of an 80 dB tone, 80-**80**). Thus, as in Experiment 1, in all conditions the standards and deviants were physically identical (i.e., an 80 dB tone). The MMN and P3a data were again quantified using the data point averaging method over consecutive 50 ms intervals and subjected initially to one-tailed confidence interval testing. Again, when confidence interval testing revealed a significant negativity (or positivity), the peak

amplitude and latency of the MMN and P3a were measured manually. The MMN was measured as the maximum negative peak occurring between 100 and 250 ms. The P3a was as the maximum positive peak occurring between 200 and 350 ms.

3.2 Results

In the present experiment, it was expected that the MMN observed in the difference wave would be larger in the increment condition. Again, however it is possible that the larger negativity in the difference wave would not be a result of an MMN to the deviant but rather of a smaller N1 to the standard. The raw waveforms corresponding to the grand averages of the 80 dB standards in the psychological increment and psychological decrement conditions are represented in Figure 4. The N1 to the same 80 dB standard stimulus was in fact larger in the increment (80-60 dB pattern) condition than in the decrement (80-90 dB pattern) condition.

The difference waves in the psychological increment condition are illustrated in Figure 5. As may be observed, the deviant in the increment condition (60-80-60-80-**80**-80) elicited a large MMN at Fz (M = -2.60 μV, SD =1.99 μV), peaking at approximately 161 ms. The negativity in the 150-200 s interval differed significantly from zero voltage baseline, as determined by confidence interval testing, $p<.05$. The MMN inverted in polarity at the mastoids, although only the left mastoid positivity reached significance, $p < .05$.

The difference waves corresponding to the deviant in the psychological decrement condition are illustrated in Figure 6. This deviant elicited a smaller negativity (M= -0.71 μV, SD = 1.19 μV), peaking at approximately 181 ms. The amplitudes of the negativity in the 150-200 and 200-250 ms intervals failed to significantly differ from the pre-stimulus zero voltage baseline. The negativity was accompanied by inversion of polarity at the mastoids, although neither inversion reached statistical significance

The scalp distribution of the small negativity in the decrement condition did however correspond to that of a true MMN, even though it did not differ significantly from the zero voltage pre-stimulus baseline level. The spline scalp distribution maps in the decrement and increment conditions are illustrated in Figure 7. As may be observed, the maps of the MMN elicited by the 80 dB psychological decrement and the 80 dB psychological increment are very similar.

The MMN was followed by a positivity, a P2/early P3a, at about 230 ms in both the psychological increment and decrement conditions. Its amplitude at Cz did not significantly differ between the two conditions, $t<1$. A second centro-frontal maximum (late P3a) positivity peaking at approximately 320 ms was also apparent but only following presentation of the psychological increment.. This positivity (Mean = 0.67 μV, SD= 1.32 μV at Cz) did not however significantly differ in amplitude from the zero voltage pre-stimulus baseline level, $p> .05$.

The averaging of all data points within the 50 ms interval might have underestimated the amplitude of the peak of the decrement MMN. Furthermore, as is apparent in Figure 6, the MMN peaked later in the decrement condition. The collapsing of all data points within a 50 ms interval does not of course allow for a measurement of peak latency. The MMN in the decrement and increment conditions were therefore also analyzed using the maximum peak detection method. The maximum peak amplitude of the MMN was measured at a region of interest (ROI), the fronto-central electrode sites (Fz, F3, F4, FCz, FC3, FC4) where the MMN is largest. Peak amplitude data at these sites were then subjected to an ANOVA with repeated measures on condition (increment, decrement), electrode region (anterior, posterior), and hemisphere (left, right). A significant main effect of condition was revealed for the amplitude of the MMN, $F(1,8) = 5.26$, $p <.05$. Increment deviants elicited a significantly larger amplitude MMN than

decrement deviants. No main effects or interactions involving either anterior-posterior or inter-hemisphere electrode site were found, $F < 1$ in all cases. A two-tailed t-test was used to compare the latency of the MMN response (at Fz) in the psychological increment and psychological decrement conditions. The latency of the MMN response was shorter in response to the deviant in the psychological increment condition than the psychological decrement condition, but this difference failed to reach significance, $t(8) = 1.93$, $p < .09$.

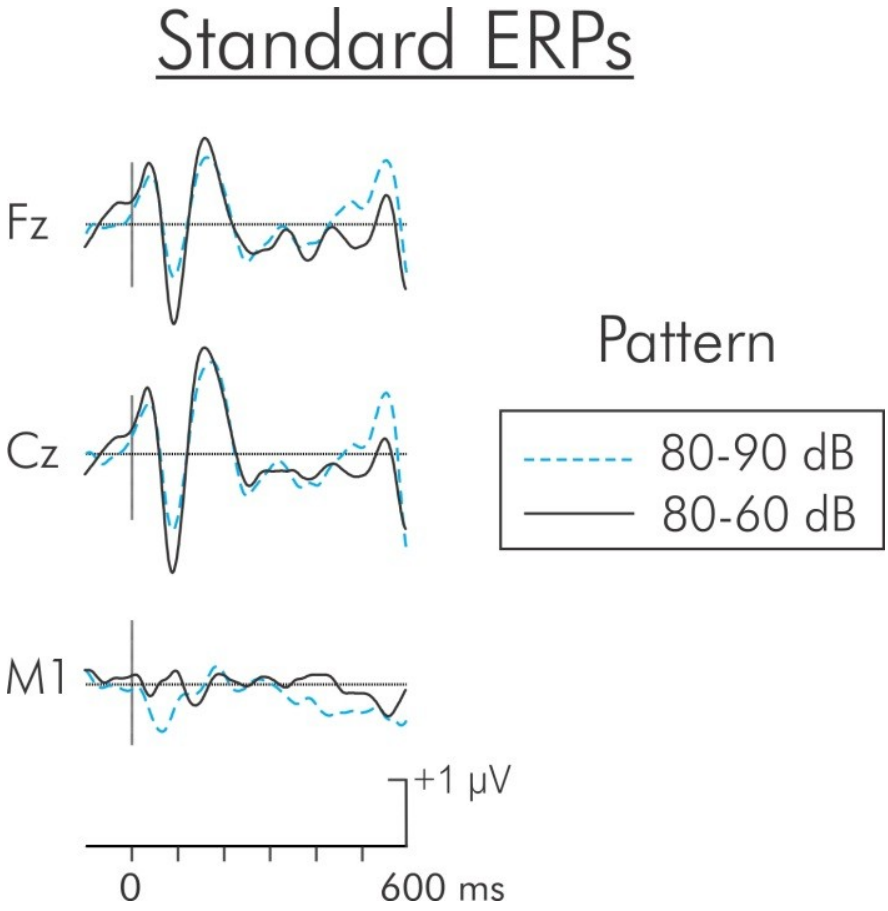

Figure 4. Grand average "raw" ERPs elicited by the same standard 80 dB tones in the psychological increment and decrement conditions. ERPs corresponding to the standards in the two conditions are superimposed in the figure. N1, peaking at about 100 ms was slightly larger when elicited by the standard 80 dB tones in the increment condition than that elicited by the physically identical standard 80 dB tones in the decrement condition. This might be because the 80 dB standard alternated with a lower intensity (60 dB) tone in the decrement condition but alternated with a higher intensity (90 dB) tone in the increment condition.

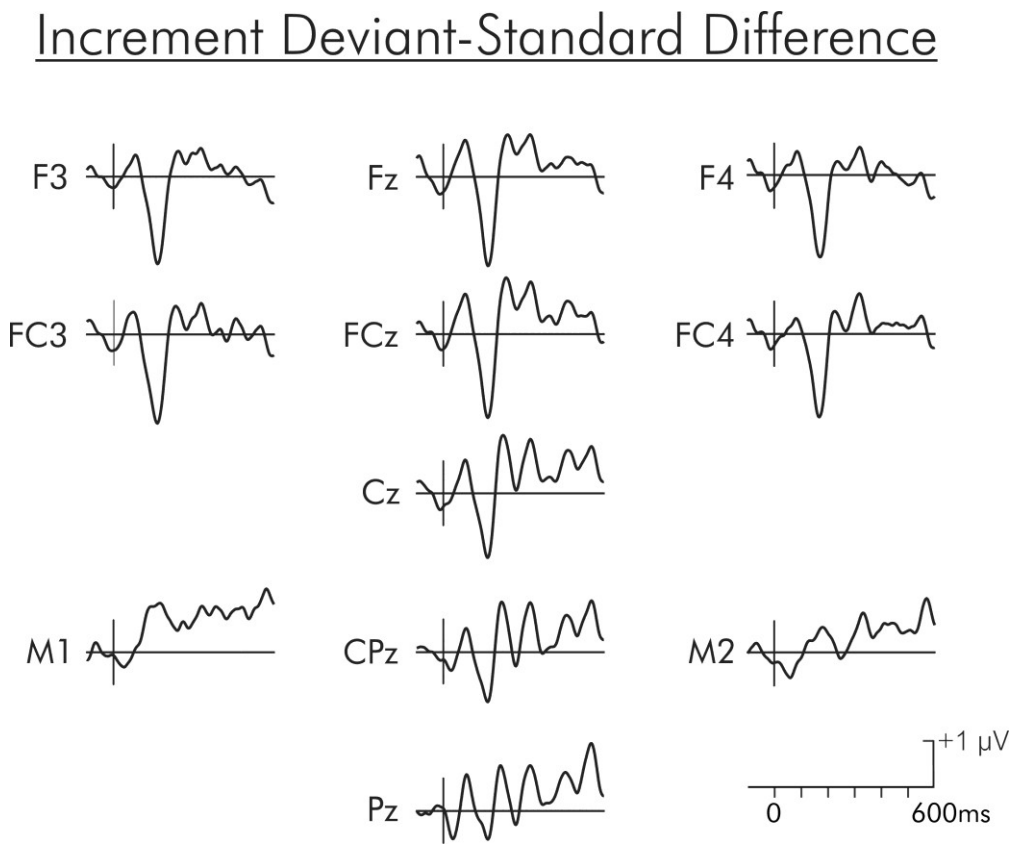

Figure 5. Grand average difference waves in the psychological increment condition. A large amplitude front-central maximum MMN occurring between 150 and 200 ms was evident following presentation of the psychological increment. A significant P3a-like centro-frontal maximum positivity peaking between 200 and 250 ms was also evident in the grand average waveform.

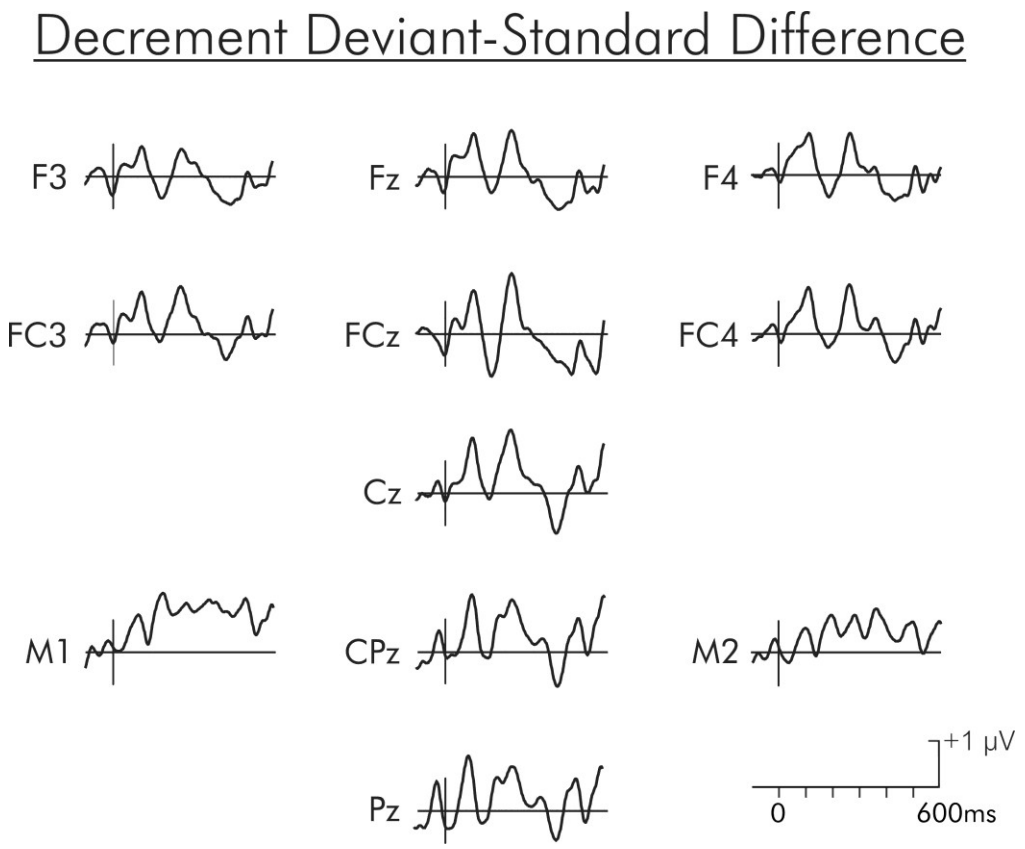

Figure 6. Grand average difference waves in the psychological decrement condition. The psychological decrement elicited a smaller non-significant negativity corresponding to the typical scalp distribution and latency of an MMN. No P3a-like positivity was apparent.

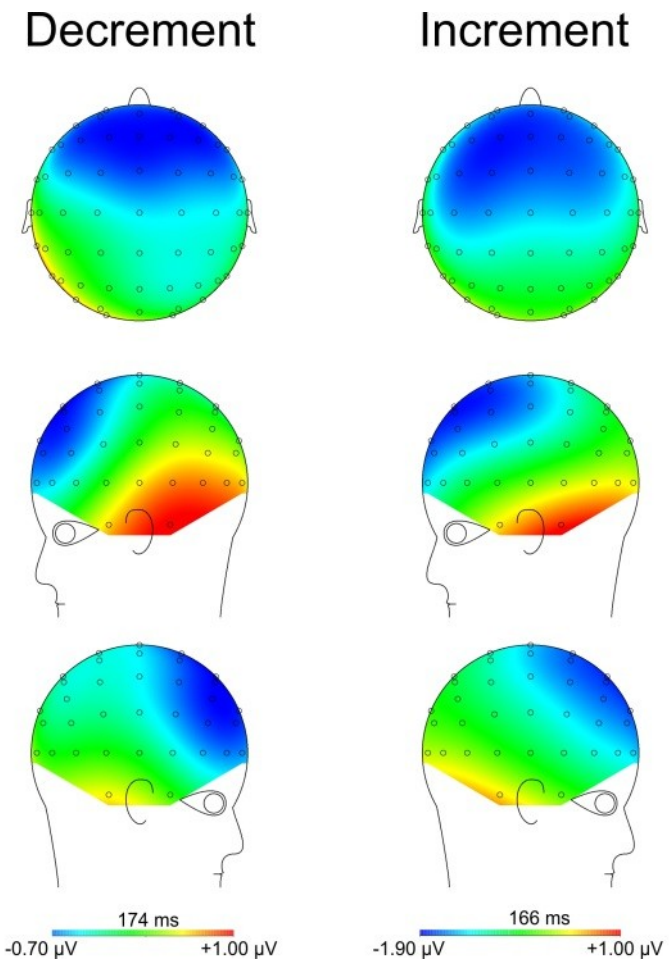

Figure 7. Spline scalp distribution maps of the MMN following presentation of the psychological decrements and increments. Although the MMN elicited by the psychological decrement did not attain significance, its scalp distribution was very similar to that elicited by the psychological increment. The MMNs were maximum over fronto-central areas and inverted in amplitude over inferior-lateral regions.

3.3 Discussion

The results of Experiment 2 largely replicate those of Experiment 1. Thus, the amplitude of the MMN was significantly larger to the psychological increment than to the psychological decrement deviant. Indeed, in contrast to the psychological increment, the negativity elicited by the psychological decrement failed to reach statistical significance from the zero voltage pre-stimulus baseline level when confidence interval testing was applied. The deviant in both conditions elicited an early positivity between 200 and 250 ms. This might correspond to a P3a. Its latency was, however, shorter than is typically associated with the P3a. Moreover, it is unlikely that a P3a would have been elicited in the psychological decrement condition when in the same condition a significant MMN was not elicited. It is possible that this positivity is not representative of a P3a component, but rather an enhancement of a P2 wave. There was no evidence of the P3a to the psychological decrement. The elicitation of a P3a-like component in response to the psychological increment but not in response to the psychological decrement is also consistent with the results of Experiment 1, though, again, the positivity elicited in Experiment 1 failed to reach statistical significance. The latency of the positivity elicited by the increment in Experiment 2, was however much shorter than that of the non-significant positivity elicited in Experiment 1.

The larger MMN in the increment condition could not be attributed to a smaller N1 to the standard in this condition. In fact, the standard N1 was larger in the psychological increment than in the psychological decrement condition. The difference in the standard N1 might be explained by the relative perceptibility of the standards in the different conditions. The 80 dB standard in the increment condition alternated with a 60 dB tone and thus was more intense. The 80 dB standard in the decrement condition alternated with the 90 dB tone and was less intense.

There was also a trend toward shorter latency MMN in response to the psychological increment as compared to the decrement deviant, although this difference failed to reach significance. Thus, again, a larger and shorter latency MMN was elicited when the alternating 80-60 dB pattern was interrupted by the presentation of an 80-80 dB deviant pair (i.e., a psychological increment).

4. General Discussion

So critical is the detection of a change of an auditory stimulus that it occurs at various levels of the auditory system beginning as early as 10-40 ms after stimulus onset [31]. Detection of a change in the intensity of the stimulus is particularly relevant. Previous studies have indicated that in oddball paradigms, a deviant that represents a physical increment in intensity elicits a much larger DRN (probably a composite N1 + MMN) and P3a than a physical decrement. In the Näätänen model, this is probably because the increment causes greater activation of two different systems, the transient detector system (thus an increase in N1) and the change detection system (thus the MMN) than the standard, whereas the decrement results in only greater activation of the change detection system. The Macdonald and Campbell study [21] employed an alternating high and low intensity pattern, creating a deviant by the repetition of the standard. The psychological increment elicited a larger and shorter latency MMN than the psychological decrement and this was explained as a result of differential activation of only the change detection system. A problem with this interpretation was that the psychological increment and decrement deviants were also physically different, which may have confounded interpretation of the results. Experiments 1 and 2 of the present study employed physically identical standards and deviants. The psychological increment in Experiment 1 elicited a larger amplitude and shorter latency MMN than that elicited by the psychological decrement, mirroring the results of the Macdonald and Campbell [21] study. The time between the stimulus pairs in

Experiment 1 was however short (100 ms) allowing for possible integration of the intensity of the standard pairs. The intensity of these pairs varied between the increment and decrement conditions. Thus, it was possible that the larger MMN in the increment condition may still have represented a physical increase in intensity of the deviant pair (80-80 dB) compared to the standard pair (80-60 dB). In Experiment 2, the time between stimuli was much longer, 500 ms, removing the possibility of stimulus integration. Again, the MMN to the psychological increment was significantly larger than that to the decrement. Similarly, the latency of the increment MMN was shorter, but the difference was not significant. Further, the psychological increment elicited P3a-like components in both experiments. The psychological decrement did not. The appearance of a P3a is thought to reflect a switching of attention from current cognitive activities to the potentially more relevant auditory channel (with more obtrusive stimuli eliciting larger P3as).

The present findings have been interpreted in the context of a violation of an alternating pattern rule (L follows H, H follows L), the violation of this rule leading to a psychological increment or decrement, respectively. As Macdonald and Campbell [21] have pointed out, the alternating sequence might also establish two additional global-rule based streaming sequences, every other stimulus is low intensity (L-H-L) and every other stimulus is high intensity (H-L-H). The automatic perception of streaming does require a relatively rapid rate of stimulus presentation and a large difference among features [29],[30]. The difference in intensity of the two high and low intensity stimuli employed in this study was sufficiently large to permit easy detection of the pattern change and thus allow for perceptual streaming. The rate of stimulus presentation was however relatively slow in both experiments. The SOA between stimulus pairs was very long (1800 ms) in the first experiment and thus it was very unlikely that perceptual streaming could have occurred. If streaming had, in fact, occurred in either of the experiments,

this should have resulted in a more perceptible H-H-H stream because of the higher intensity of these stimuli, causing this stream to "stand out" to the subject. Differences in MMN amplitude could thus be attributed to the differential perceptibility of the two streams. If this were the case, the MMN elicited in response to the deviant in the decrement condition (in which the deviant represents a disruption of the more readily perceived H-H-H stream) should have been larger than that elicited in the increment condition (in which the deviant represents a disruption of the less readily perceived L-L-L stream). This was, however, not the case. The deviant in the decrement condition resulted in a *smaller* amplitude MMN than that elicited in the increment condition.

The differential processing of the psychological increment and decrement deviants in Experiment 2 cannot be attributed to either differences in the physical parameters of deviant stimuli or the effects of stimulus integration or perceptual streaming. The consistently larger MMN and subsequent P3a-like component to both physical and psychological increments thus present convincing evidence of the greater biological relevance of these auditory stimuli. The findings of the present experiments suggest this increased salience is not solely afforded to stimuli representing a *physical* increment relative to the immediate auditory past and thus activating both the change and transient detection systems. It is also afforded to any auditory deviant that violates an expectancy for a lower intensity stimulus, even if this deviant is physically identical to the immediate auditory past and thus results in increased activation of only the change detection system.

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Chapter 5

Summary and Conclusions

The present thesis employed event-related potentials to examine the differences between the processing of increases and decreases in auditory intensity in light of their differing biological relevance to an organism. The manner in which stimulus intensity was manipulated varied across the studies of the thesis, with deviants in the first study representing a *physical change* relative to immediately preceding stimuli, and deviants in the latter two studies representing a *psychological change* created by the violation of an established pattern.

Study 1 of this thesis investigated the processing of physical intensity change during a state in which an organism is left particularly vulnerable to the surrounding environment, that of natural sleep. For this purpose an oddball paradigm (80 dB standard, 90 dB increment, 60 dB decrement) was presented to subjects both during the waking state and during sleep while EEG was recorded. Both increment and decrement stimuli were successful in eliciting a DRN (likely representing a composite MMN+N1 in the case of the increment deviant, and an isolated MMN in the case of the decrement), and a subsequent P3a in the waking state. The P3a elicited by the increment deviant in the waking state was significantly larger than that elicited by the decrement. During sleep, only the increment deviant continued to elicit ERPs related to the detection of change. More specifically, during the REM stage of sleep, the increment deviant resulted in a (non-significant) DRN followed by a significant P3a, thought to reflect the automatic detection of the intensity increase, and the subsequent probing of sensory memory, respectively. The continued processing of the increment, but not the decrement, stimuli during sleep supports the notion that these deviants are more salient to an observer. This differential salience could be attributed to the fact that increments in intensity result in increased activation of the change and

transient detector systems while decrements in intensity result in greater activation of only the change detection system. In addition, there has been some suggestion that the occurrence of attention capture (and the associated elicitation of a P3a) is strongly dependent on the activation of the transient detection system. The follow-up studies in this thesis determined whether the increased salience of stimuli representing increments in stimulus intensity could be attributed to the activation of both the transient detector and change detection systems, or if it would be maintained when deviance-related processing was isolated to the change detection system.

In order to address this question, an auditory paradigm was employed, consisting of tones alternating in intensity (HLHLHLHL) with deviants created by the repetition of a tone in the sequence (HLHLH**H**HL) that, while physically identical to the immediately preceding stimulus, violated the expectancy for a higher or lower intensity tone. Because the deviant stimuli were physically identical to the immediately preceding standard, this manipulation should not have led to increased output of the transient detection system (i.e., an enhancement of N1), allowing for isolation of the output of the change detection system (the MMN). In three separate conditions, the extent of separation was varied (63 vs 90 dB, 72 vs 81 dB, 75 vs 78 dB) to determine whether extent of deviance would have an effect on the amplitude or morphology of the MMN in such a paradigm. The violation of the expectation for both an increment and a decrement (psychological decrements and increments, respectively) were successful in eliciting an MMN, but only when the extent of separation was very large. However, the latency of this component was shorter, and the amplitude larger, in response to the psychological increment. Though a positivity corresponding to the typical latency and scalp distribution of the P3a was apparent in the difference wave corresponding to presentation of the increment deviant, this positivity failed to reach statistically significant difference from zero voltage baseline. No such positivity was

evident in the difference wave corresponding to decrement deviant presentation. The shorter latency and larger amplitude MMNs elicited in response to the increment as compared to the decrement deviants were interpreted as providing evidence that increment stimuli maintain their increased salience, even when deviance-related processing is isolated to the change detection system. A confounding factor in the interpretation of these results, however, was the physical differences between the stimuli representing the psychological increment (90 dB) and the psychological decrement (63 dB). It was suggested that differences seen between the ERPs elicited in response to these deviants could be explained by the difference in their physical features.

The third study of this thesis thus consisted of two separate experiments which compared the processing of psychological increments and psychological decrements, while controlling for the potential confound of the physical differences between the deviant stimuli. These experiments again employed paradigms consisting of stimuli alternating in intensity with deviance created by the repetition of a stimulus (HLHLH**H**HL). Separate psychological increment (80-60-80-60-80-**80**-80-60) and psychological decrement (80-90-80-90-80-**80**-80-90) conditions were presented in which 80 dB tones served as both the deviants and the standards. In the first of these studies, a paired alternating intensity pattern was employed, with a within-pair SOA of 100 ms and between-pair SOA of 1800 ms. Both psychological increment and psychological decrement stimuli were successful in eliciting significant MMNs. The latency of this component was again significantly shorter, and its amplitude significantly larger, in response to the psychological increment. Again, a positivity corresponding to the typical scalp distribution and latency of a P3a was evident in the difference wave corresponding to the increment, though it failed to reach statistically significant difference from zero voltage baseline. There was no

evidence of a P3a for the decrement deviant. These results could be interpreted as evidence that the differences in the physical features of the increment and decrement stimuli cannot account for differential processing of these stimuli. However, a different interpretation of the results is possible. The time between the stimuli within the pairs (100 ms) was very short. This may have allowed for temporal integration of the representations of the paired stimuli. This effectively would have resulted in the creation of an oddball paradigm. In the case of the psychological increment, this would have been (80+60… 80+60…80+60…**80+80**….80+60) while in the case of the psychological decrement, this would have been (80+90…80+90…80+90….**80+80** …80+90). Thus, in the case of both the increment and decrement stimuli, these might have represented either psychological or physical deviants. If such integration had taken place, this may have compromised the attempt at circumventing activation of the transient detection system by transforming the paired alternating pattern into an oddball pattern.

In order to address this issue, the second experiment of Study 3 employed a non-paired alternating intensity pattern in separate increment and decrement conditions consisting of the same stimuli (80, 60, 90 dB) used in Experiment 1, and increased the SOA to 500 ms. The increment and decrement deviants both elicited negativities corresponding to the typical latency and scalp distribution of an MMN, though this failed to reach statistically significant difference from baseline in the decrement condition. The increment, but not the decrement deviant, again elicited a P3a-like positivity, though this did not differ significantly from zero. Thus it appears that psychological increments result in stronger and faster activation of the change detection system than do psychological decrements and these differences cannot be attributed to the physical differences between deviant stimuli or to the effects of stimulus integration.

Taken together, the studies of this thesis provide convincing evidence that the increased biological relevance of stimuli representing increments in intensity have led to the development of mechanisms for faster and more robust change detection, and perhaps more readily activated attention capture to these types of change. Further, the increased salience of increment stimuli cannot be solely explained by the contribution of transient detection system activation, as it appears to persist even when deviance-related processing is isolated to the change detection system.

The findings of this thesis include the following:

- Rarely occurring physical increases in intensity will result in greater likelihood of an interruption of the central executive and subsequent attention capture during the waking state. A decrement will be much less likely to do so. These processing differences were reflected by a larger deviant-related negativity and P3a. Remarkably, these differences are also apparent during an unconscious state, stage REM during sleep.
- A physical increase in intensity will result in greater activation of the transient detector system. When deviance-related processing is isolated to the change detection system, by using an alternating intensity pattern paradigm,
    - Violation of this pattern by repeating the preceding stimulus (i.e., either a low or high intensity stimulus) will still elicit an MMN provided the separation between the two intensities is sufficiently large.
    - The amplitude of the MMN is still larger and the latency shorter in response to psychological increments (when the *expectation* of a decrement is violated).

    - The MMN remains larger to psychological increments when possible contributions of differences in the physical features of the deviant stimuli are removed (i.e., the deviants are physically identical).
    - Furthermore, the MMN remains larger to psychological increments when the possible effects temporal integration of stimuli within a paradigm are controlled.
- This thesis has thus demonstrated that increments in intensity are much more salient to the observer than decrements. This cannot be explained simply by the effects of a physical increase and activation of a separate system (the transient detector system) uniquely responsible for detection of brief, transient increases in intensity.