

ANGLIA RUSKIN UNIVERSITY

NEUROCOGNITIVE SIGNATURES OF AUDITORY AND
VISUAL SENSORY GATING

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ANGLIA RUSKIN UNIVERSITY

ABSTRACT

FACULTY OF SCIENCE AND TECHNOLOGY

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The aim of this thesis was to investigate the neurophysiological phenomenon of auditory and visual sensory gating, and primarily, explore the notion of a cross-modal mechanism. The electrophysiological characterisation and associated cognitive functions of both visual and auditory sensory gating were examined to determine similarities and differences across the two input modalities. In order to explore this, three issues were addressed: 1) The latency and surface scalp location(s) of the maximal or most reliable sensory gating was identified; 2) the associated cognitive mechanism(s) were explored using 11 diverse tasks incorporating attentional inhibition; 3) the sensitivity of the gating mechanism was examined with regards to changes in stimulus form/location or changes in attentional demand.

Despite limited consideration in the literature to date, this thesis reports evidence that sensory gating is a phenomenon that exists within the visual modality and moreover, can be reliably observed. Compared to standard auditory gating procedures, visual gating is found at a later latency and further back in the central-parietal or central-occipital electrode sites. Correlations between visual and auditory gating with latent inhibition and the continuous performance task suggests gating, independent of

modality, may reflect the encoding of target and non-target stimuli/stimulus features alike, and the subsequent categorisation and inhibition of those deemed irrelevant. Additionally, a comparable limitation was observed for both modalities, with regards to sensitivity of sensory gating, with spatial features being processed as a priority over the perceptual stimulus features.

In conclusion, the differences in latency and component of the observed gating presented in this thesis, indicates that visual and auditory sensory gating are not products of the same intra-cortical mechanism. Rather the gating observed in each modality is a functionally distinct mechanism that is qualitatively analogous across modalities.

Keywords: auditory sensory gating, visual sensory gating, cognitive inhibition, MLERPs, electroencephalogram (EEG)

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Table of contents

Chapter 1: General introduction: Sensory gating and cognitive inhibition

1.1. Working memory: Sub-systems and Capacity.....	1
1.2. Stages of Information Processing.....	5
1.3. Neurological Measure of Inhibition: Sensory Gating.....	8
1.4. The Modality of Sensory Gating.....	11
1.5. Cognitive Inhibition.....	14
1.6. Models of Inhibition.....	16
1.7. Components of Inhibition.....	18
1.8. Inhibition or Episodic Memory Retrieval.....	23
1.9. Summary and aims.....	24

Chapter 2: Methodology

2.1. Participants.....	26
2.2. Sensory gating Procedures.....	29
2.3. Behavioural tasks and procedures.....	36
2.4. Psychometric tasks.....	43

Chapter 3: Comparing the location and latency of auditory and visual sensory gating

3.1. Introduction and rationale.....	45
--------------------------------------	----

3.2. Design.....	59
3.3. Results.....	60
3.4. Discussion.....	74
3.5. Conclusions.....	80

Chapter 4: Cognitive mechanisms associated with auditory sensory gating

4.1. Introduction and rational.....	82
4.2. The Present Study.....	91
4.3 Design.....	92
4.4. Results.....	92
4.5. Discussion.....	100
4.6. Conclusions.....	105

Chapter 5: Cognitive mechanisms associated with visual sensory gating

5.1. Introduction and rational.....	106
5.2. Present study.....	113
5.3. Design.....	114
5.4. Results.....	115
5.5. Discussion.....	124
5.6. Conclusions.....	127

Chapter 6: The sensitivity of auditory and visual sensory gating

6.1. Introduction and rational.....	129
6.2. Present study.....	132
6.3. Experiment 4.....	133
6.3.1. Design.....	133
6.3.2. Results.....	135
6.3.3. Discussion.....	140
6.3.4. Conclusions.....	144
6.4. Experiment 5.....	144
6.4.1. Rational.....	144
6.4.2. Design.....	147
6.4.3. Results.....	148
6.5. Comparison between experiments 4 & 5.....	153
6.6. General discussion.....	154
6.7. Conclusions.....	158

Chapter 7: General discussion

7.1. Theoretical contribution.....	161
7.1.1. The existence of visual sensory gating.....	161
7.1.2. Cognitive relevance of sensory gating.....	163
7.1.3. Sensitivity to stimulus changes.....	167

7.1.4. The effects of attention on sensory gating.....	169
7.1.5. A qualitatively similar mechanism across modalities.....	171
7.2. Final conclusions.....	174
References.....	175
Appendix	
Glossary of abbreviations.....	204

List of figures

Figure 1:	Visual representation of sensory gating as measured using the ERP P50.....	11
Figure 2:	Time course of a single experimental trial for the visual modality in experiments four and five. Example is depicting the condition of different location and different stimulus (DLDS).....	33
Figure 3:	Average ERP waveforms from experiment one. Panel A – waveform from the auditory paradigm for electrode Cz. Panel B – waveform from the visual paradigm for electrode Pz.....	62
Figure 4.	Average response amplitude to the first and second stimulus presentation for the auditory modality.	63
Figure 5.	Average response amplitude to the first and second stimulus presentation for the visual modality	64
Figure 6.	Mean amplitude (μ V) of the response to the first stimulus presentation in the auditory modality for components P50, N1 and P2.	66
Figure 7.	Mean sensory gating ratio for the three locations in the visual modality for the component P1.....	68
Figure 8.	Average peak latency (ms) of the auditory modality ERPs, in response to the first a second stimulus presentations. Latencies for components P50, N1, and P2 at the two locations, central and parietal.	71
Figure 9.	Average peak latency (ms) of the visual modality ERPs, in response to the first a second stimulus presentations during experiment one. Latencies for components C1, P1, and N1 at the three locations, central, parietal, and occipital.....	71
Figure 10.	Average waveform from experiment two and Scatterplot displaying the relationship between the P50 amplitudes for stimulus 1 and 2.	93
Figure 11.	Scatterplots for significant correlations between cognitive performance measures plotted against the P50 ratio from experiment two.....	97
Figure 12.	Average waveforms from experiment three. Average sensory gating ratio observed at electrodes Pz and Oz.....	118

Figure 13.	Scatterplots for significant correlations following a bivariate and partial correlations from experiment three, adjusting for Cattell's Culture Fair score (fluid intelligence) and/or the OSPAN absolute score (working memory).....	121
Figure 14.	Average sensory gating ratios for each experimental condition for the visual (P1 and electrode Pz) and auditory (P50 at electrode Cz) modalities combined in experiment four.....	137
Figure 15.	Average sensory gating ratios for each experimental condition for the visual and auditory modalities (auditory component P50) from experiment five.....	152
Figure 16.	Comparison of the magnitude of the average auditory and visual sensory gating observed during experiments four and five.....	154

List of tables

Table 1:	Participant demographic information for all experiments.....	26
Table 2:	Number of participants for each behavioural task employed in experiment two that also had useable EEG data.....	28
Table 3:	Average sensory gating ratio for ERP components P50, N1, and P2 for the auditory modality, and C1, P1, and N1 for visual.....	67
Table 4:	Bivariate correlation results for both the auditory and visual paradigms from experiment one.....	73
Table 5:	Test information and descriptive statistics for all cognitive control measures used in Experiment two.....	94
Table 6:	Correlation coefficients from bivariate correlation between sensory gating and the measures of inhibition and psychometric tests in experiment two.....	98
Table 7:	Correlation coefficients after partial correlation controlling for fluid intelligence (CCF-IQ) and working memory (OSPAN) in experiment two.....	100
Table 8:	Descriptive statistics and group-level effects for all cognitive control measures used in experiment three.....	116
Table 9:	Correlation coefficients from bivariate correlation between sensory gating and the measures of inhibition and psychometric tests in experiment three.....	120
Table 10:	Correlation coefficients after partial correlation controlling for fluid intelligence (Cattell's Culture Fair) and working memory (OSPAN) in experiment three.....	123
Table 11:	Averages and standard deviations for the ERP amplitudes and latencies, and the sensory gating ratio for each condition and modality for experiment four.....	138
Table 12:	Averages and standard deviations for the ERP amplitudes and latencies, and the sensory gating ratio for each condition and modality for experiment five.....	151

Chapter 1

General introduction: Sensory gating and cognitive inhibition

This chapter addresses the neurological mechanism of sensory gating, in terms of its measurement and proposed cognitive function. Moreover, the modalities in which sensory gating has been investigated are covered and atypical findings described. In order to examine the claim that sensory gating may reflect a form of cognitive inhibition, the conceptual basis of cognitive inhibition is considered with reference to influential models and proposed sub-components of working memory and executive function.

1.1. *Working memory: Sub-systems and Capacity*

Working memory is characterized as a cognitive system that provides a functional relationship between sensory registers and long-term memory stores. Working memory temporarily maintains and stores information to facilitate the processing necessary for numerous cognitive tasks such as comprehension, reasoning, and learning (Atkinson & Shiffrin, 1968; Baddeley & Hitch, 1974). Originally, Atkinson and Shiffrin (1968) proposed that sensory information from the environment enters corresponding sensory registers that transfer the information into a short-term memory store. This short-term store provides a functional link between the temporary store of sensory information and long-term memory. However, lack of evidence for a unitary system lead to Baddeley and Hitch's (1974) notion of a three component model of working memory, which serves to aid performance on complex cognitive tasks through the maintenance of memory and attentional control (Baddeley & Hitch, 1994). The three discrete but related systems are that of a central executive, which acts to control the focus of attention towards different sensory inputs while providing a link with long-term memory and two peripheral storage systems, the phonological loop (auditory information and language) and visuospatial sketchpad (visual and spatial information)

(Baddeley, 2003; Miyake, Friedman, Rettinger, Shah, & Heggarty, 2001). Evidence for three distinct components was subsequently found through the meta-analysis of 400 studies, which identified visuospatial, verbal/arithmetic, and Spearman's general factor (or 'g') - components that closely resembled those proposed by Baddeley and Hitch (Carroll, 1993). In addition to the multi-component model of working memory, an episodic buffer was later included, which is asserted to combine the memory representations from long-term memory and the sensory inputs from the phonological loop and visuospatial sketchpad (Baddeley, 2000).

A key feature of this proposed processing system is that of limited capacity (Baddeley, 2003; Baddeley & Hitch, 1974). It is suggested that the mental resources used by this system are finite and must be allocated to individual operations serving the processing and storage of information in the completion of cognitive tasks (Daneman & Carpenter, 1980; Shiffrin & Schneider, 1977). Different tasks require a different amount of processing (Eysenck & Eysenck, 1979) and thus those tasks that are considered to have a low demand for working memory elicit a superior performance than tasks that load heavily on working memory, and thus require more of the limited working memory capacity (Navon & Gopher, 1979; Wright, 1981). Working memory capacity likely reflects a domain free capability independent of task demands (Engle, Cantor, & Carullo, 1992; Kane, Bleckley, Conway, & Engle, 2001). It is this limited capacity that necessitates an inhibitory process or gating mechanism that can control the information encoded into working memory. One of these proposed functions is sensory gating, which will be discussed in detail in section 1.3.

The capacity of the two sensory sub-components of working memory has been investigated independently. The phonological loop is proposed to only retain the memory traces of auditory and verbal information for a brief period of time before these traces decay. The only way to preserve these traces is through re-articulation and rehearsal. As the amount of information increases it becomes increasingly difficult to retain the memory traces, due to the inability to rearticulate all items before some of those items traces have decayed (Baddeley, 2003). Similarly, the visuospatial sketchpad is also limited in capacity (Luck &

Vogel, 1997), which is supposedly the cause of phenomena such as change blindness whereby people fail to notice changes in their visual environment due to the inability to perceive the entirety of their visual environment all of the time (O'Regan, Rensink, & Clark, 1999).

The primary focus of working memory capacity appears to be that of the number of 'chunks' or items of information that can be processed, and thus an individual's working memory capacity is judged according to the number of items that can be remembered (Daneman & Carpenter, 1980; Graesser, Mandler, 1978). However, it is now suggested that working memory capacity is not the product of simple memory ability, and that a higher capacity is the result of superior attentional control, especially in the face of interference (Kane & Engle, 2003). This control enables information to be actively maintained in working memory and retrieved as soon as that information is required. This information can include stimulus representations, task demands, and goals (Kane & Engle, 2002). Evidence for an attentional model of working memory comes from antisaccade tasks, which require participants to move their gaze in the opposite direction to a presented stimulus. In this task, those with a low working memory span perform significantly worse than those with a high span (Engle, 2002; Kane et al., 2001). This is purported to occur because low span individuals are less capable of suppressing the reflexive saccades towards an appearing stimulus. The antisaccade task requires minimal demands on memory aside from that of maintaining the task instructions, and task demands are qualitatively different to those required during a working memory span task. Thus, it is suggested that the antisaccade task is a simple measure of attention and performance on such measures most likely reflect attentional control rather than working memory capacity per se.

Attentional control at different stages of information processing can alter working memory performance (these stages are discussed in section 1.2.). Consistent with this claim, significant correlations between measures of attentional control and working memory have been reported (Shipstead, Lindsey, Marshall, & Engle, 2014; Unsworth & Spillers, 2010). The influence of attention on working memory is evident during both the initial

encoding of stimuli in working memory, and the subsequent maintenance of those stimuli. According to the attentional control theory of working memory, this control is required in order to encode and maintain information in WM in the presence of competing or distracting stimuli, which is achieved by preventing irrelevant stimuli from entering working memory while maintaining an active representation of the relevant stimuli (Unsworth, Fukuda, Awh, & Vogel, 2014; for reviews see Awh, Vogel, & Oh, 2006 and Chun 2011).

During the encoding of information in working memory, focused attention can modulate the cortical activity towards relevant stimuli, resulting in superior encoding and thus better working memory performance (Gazzaley, 2011). Moreover, this relationship between cortical activity modulation due to selective attention and working memory performance can occur within 100ms of stimulus onset (Rutman, Clapp, Chadick, & Gazzaley, 2010). The increase in attention leading to cortical modulation, enhances the representation of relevant stimuli within working memory and thus benefits the maintenance of that representation. As discussed by Gazzaley and Nobre (2012), this relationship may be the result of activity in the prefrontal cortex (PFC) during selective attention. The modulation of the activity within the sensory cortices following PFC activation, and the functional connectivity between these areas and the PFC, significantly correlate with working memory performance. Moreover, a functional MRI study assessing the common activations between selective attention and working memory encoding found a significant overlap (Mayer et al., 2007). This study also found that increasing the attentional demand of a task reduced working memory performance.

Following the encoding stage, attentional control can also affect the encoded stimuli in working memory. If distractions or secondary tasks are added to a working memory task, performance is typically reduced (Clapp, Rubens, & Gazzaley, 2010). The ability to divert attention away from distractors improves the ability to maintain the relevant stimuli within working memory. Indeed, an EEG study found that increased cortical activation to irrelevant stimuli, suggesting an increase in encoding, negatively correlated with working memory

performance, reflected in a decrease in recognition of previously encoded target stimuli (Berry, Zanto, Rutman, Clapp, & Gazzaley, 2009).

A comparison of working memory and short-term memory provides further evidence for a model of working memory that includes processing beyond simple memory ability. Tasks that are purported to measure working memory span and short-term memory were tested alongside a measure of intelligence (Conway, Cowan, Bunting, Theriault, & Minkoff, 2002). The results demonstrated that the working memory and short-term memory tasks significantly correlated, however only working memory correlated with intelligence. This suggests that the component of working memory capacity that correlates with intelligence (and other cognitive tasks) is not the component of simple information retention. If this were the case, then tasks measuring short-term memory would also correlate with these complex cognitive tasks. Thus, other features such as attentional control likely underlie these correlations. (Kane & Engle, 2003). Additional evidence that working memory may encompass an attentional control mechanism is provided in studies of working memory span and performance on dichotic listening tasks. For example, Conway, Cowan & Bunting (2001) showed that those with a lower (relative to higher) span were more able to detect their name even when it was being presented to the to-be-ignored channel. This indicates that low span individuals are less capable of ignoring interfering sensory information. Taken together, this evidence suggests that working memory may involve a form of executive attention whereby relevant stimulus representations, goals, and task demands are actively maintained in memory even in the presence of interference.

1.2. Stages of Information Processing

Information processing refers to the modification of information that is acquired from a stimulus, until a noticeable and appropriate response is made as a result of those modifications (Massaro, Cowan, 1993). In this definition, a response primarily refers to overt

behaviour, such as pressing a response pad or moving one's eyes in the direction of a target (either reflexively or purposefully). However, information processing can still be measured in the absence of a physical response, as a result of covert cognitions regarding the presented stimuli. These cognitions, such as the recognition of a target, or ignoring a distractor, can be measured using brain imaging techniques. For example, the cortical response within the visual cortex can be enhanced when a presented stimulus is relevant, indicating that the stimulus has been successfully encoded into working memory and that subsequent categorisations have been made regarding the relevance of that stimulus within the current context (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010). One can also measure the inhibition of a stimulus at the cortical level, prior to any overt responses being made, indicated by a decrease in cortical activity towards irrelevant stimuli (Rossi & Pourtois, 2012). Central to this definition of information processing, is that there is a progression from stimulus to response during which several operations are performed at different stages throughout. How this progression occurs can be based on either discrete or continuous models of information processing. Discrete models (Sperling, 1960) imply that through each sequential stage, the completed output from one operation is transferred to the subsequent operation until a response is made. This model demands that each stage is only activated once the preceding stage is complete (Sternberg, 1969). Alternatively, in the continuous model (Turvey, 1973) each stage does not need to be completed in order for the next stage to be active. Any information that a stage has processed is immediately and continuously transferred to the subsequent stage, as each stage is activated in a parallel fashion concurrently providing new information to the following stage. Through a series of experiments, Miller (1982) provided evidence for the continuous model of information processing. These experiments demonstrated that a prepared response can be made based on incomplete information before full categorisation of the target stimuli is complete. Osman and colleagues (Osman, Bashore, Coles, Donchin, & Meyer, 1992) found similar results in that preparation of an appropriate response was made during a go/no-go task, before processing of the task demands (whether to go or not) was complete. More current research

indicates that a continuous model of information processing is more accurate, with multiple anatomically distinct areas functioning in parallel (Singer, 2013). Animal research using patch clamp or single neuron recordings are examples of how these functional connections are determined, measuring the direct neural connection and transmission of bioelectrical signals from one area to another at a structural level (Kotter, 2004). Human and animal research using more macroscopic imaging techniques of neuronal populations, can elucidate more widespread and diffuse connections, interpreting the correlations in activations during experimental procedures, and the changes in functional connectivity (Buzsáki, & Draguhn, 2004; Van Essen et al., 2013). Combined, these methods have shed light on the interconnected cortical areas during different cognitive states, resulting in a human connectome (Sporns, Chialvo, Kaiser, & Hilgetag, 2004; Van Essen et al., 2013). Thus it is instructive to conceptualise cognition and information processing as a network phenomenon involving functional integration, with spatially distributed areas functioning in a dynamic manner, dependent on the context (for discussion see Sporns, Tononi, Kotter, 2005).

There are several theories regarding the number and type of operations required during information processing. Sternberg (1969) proposed stages that are in some parts unique to the task demands, but in general consist of a perceptual encoding stage, followed by a series of internal or cognitive processes whereby stimuli are given a representation in working memory and assessed with regards to task demands. This is then followed by the organisation of a motor response and subsequently an overt motor response is then made. A similar model was suggested by Miller (1982), during which a stimulus is perceived, a response decision is made, this response is transferred to the motor system and an overt response is executed. Sanders (1990) considered the role of motivation amongst other factors resulting in a seven-stage model of information processing. The basics of this model can be described as, a perceptual encoding stage, followed by the central stages (cognitions), and finally the output stage. Whenever a response is required based upon the presentation of a stimulus or stimuli, every model appears to consist of three common stages that can be sub-divided based upon the specific task demands. These three stages

are the input stage (perceptual encoding), internal stage/stages (cognitive processing), and the output stage (overt behavioural response).

1.3. Neurological Measure of Inhibition – Sensory Gating

In order to protect the limited processing resources within working memory, it is proposed that excessive sensory information that is deemed irrelevant is filtered out during the early stages of information processing (Boutros, Korzyukov, Jansen, Feingold & Bell, 2004; Venables, 1964). This inhibitory mechanism prevents the ‘flooding’ of extraneous sensory information while simultaneously allowing working memory or more generally, the central nervous system (CNS), to respond to unusual or threatening stimuli (Freedman et al., 2002). This differentiation between relevant and irrelevant stimuli allows the CNS to adapt to changing contextual situations (Majic et al., 2011).

One way in which this proposed inhibitory mechanism can be assessed is by measuring the modulation of the cerebral response to repeated sensory information, a phenomenon referred to as sensory gating (Freedman et al., 2000). Sensory gating is measured using an electroencephalogram (EEG) recording during a conditioning-testing paradigm (paired stimulus paradigm), which involves presenting two identical stimuli with an inter-stimulus interval of less than one second (Arnfred & Chen, 2004). Sensory gating is operationalised using the event related potential (ERP) P50; an ERP being the measure of electrical activity at a particular time and location within the brain. More specifically, an ERP is measured as a voltage change within the cortex in response to a sensory or cognitive event. Using EEG, these voltage changes are detectable when large populations of neurons fire simultaneously in response to an event, and the produced electrical signal is transmitted to the surface of the scalp (Woodman, 2010) (for more detail regarding EEG methodology see section 2.2.). Sensory gating refers to the attenuation (gating out) of the P50 response to the second stimulus (Anokhin, Vedeniapin, Heath, Korzyukov & Boutros, 2007), see

Figure 1 for a visual representation. The presentation of the first stimulus elicits an excitatory response of a set of neurons within the brain that generates the ERP P50, while simultaneously activating a second set of interneurons that inhibit any further excitatory response (Adler, Waldo & Freedman, 1985; Anokhin et al., 2007). This gives rise to a reduced response of the ERP P50 to the presentation of the second stimulus; the difference in this P50 response indicates the strength of inhibition activated during the response to the first stimulus (Freedman et al., 2002).

Sensory gating, as measured using EEG, is not dissimilar to the repetition suppression effects observed using single-unit recordings and functional magnetic resonance imaging (fMRI) studies (Desimone. 1996; Henson & Rugg, 2003). In this line of research, the suppression effect is describe as the attenuation of neural responses to repeated stimuli relative to the response to a single stimulus (Larsson & Smith, 2012). Sensory gating can also be understood in terms of sensory adaptation with the term 'gating' being used to conceptualise the notion of a mechanism that controls the entrance and exclusions of information into working memory. A further comparison with sensory gating and other phenomena is that of habituation, however these are two distinct concepts. Sensory adaptation/gating is the reduction in firing of neuronal populations to unchanging stimuli, an event which occurs from the second presentation of that unchanging stimulus, and gating in particular is concerned with this initial decrease. Habituation, however, is the phenomenon of a continuous decrease in the response to unchanging stimuli, with further attenuation following each successive presentation. Additionally, gating describes the changes in neuronal sensitivity, whereas habituation explains the reduction in the response.

In sensory gating research, the primary focus is of the component P50. P50 refers to a positive deflection, meaning an increase in amplitude relative to either the post stimulus baseline period or the preceding peak, as measured using EEG, and occurs around 50ms post stimulus onset. In the context of sensory gating P50 is often located using the EEG electrode CZ at the vertex, which is the point on the scalp that is equidistant from the nasion (bridge of the nose) and inion (back of the scalp), and either ear (Brockhaus-Dumke,

Mueller, Faigle, & Klosterkoetter, 2008; Brockhaus-Dumke et al., 2008). Calculating the ratio of the elicited P50 amplitude of the second stimulus to the P50 amplitude elicited by the first stimulus, multiplied by 100 operationalises the degree of sensory gating (Boutros et al., 2004). A lower ratio indicates greater attenuation of P50 to the second stimulus and thus stronger sensory gating (Moran et al., 2012). Sensory gating can also be operationalised by calculating the absolute difference in P50 amplitude between the first and second stimulus (Brockhaus-Dumke et al., 2008).

Using this method, studies that explore sensory gating in patients with schizophrenia indicate that these patients have a higher sensory gating ratio than controls (Bramon, Rabe-Hesketh, Sham, Murray, & Frangou, 2004; Patterson et al., 2008; Popov et al., 2011; Yee et al., 2010). Specifically, patient groups tend to have a gating ratio ranging from 56 to 158%, while controls have a ratio between 9 and 73.4% (Patterson et al., 2008). Although researchers describe the plethora of results regarding reduced sensory gating in patients to be robust (For reviews see, Patterson et al., 2008; Potter, Summerfelt, Gold, & Buchman, 2006), other studies have failed to find a significant difference in sensory gating between controls and medicated (Light, Geyer, Clementz, Cadenhead, & Braff, 2000) and unmedicated (Arnfred, Chen, Glenthøj, & Hemmingsen, 2003) patients with schizophrenia. Differences restricted to specific subgroups of patients have also been reported (Bramon et al., 2004; Jin et al., 1998).

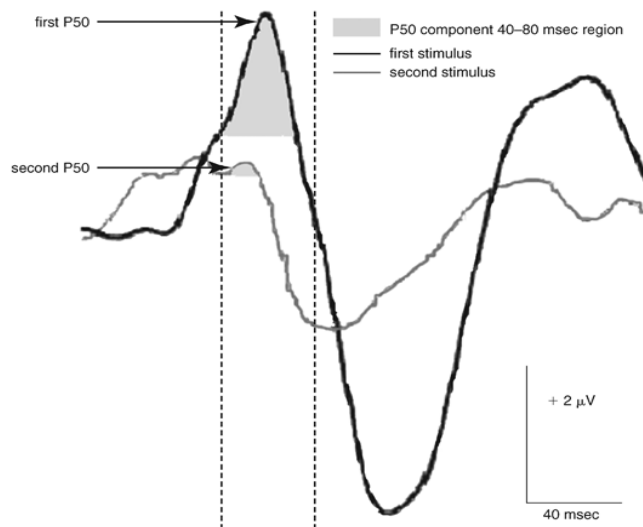


Figure 1. Visual representation of sensory gating as measured using the ERP P50.

1.4. The Modality of Sensory Gating

1.4.1. Auditory

Research in the area of schizophrenia has found impairments in the auditory, visual and somatosensory modalities (Adler et al., 1985), although the majority of sensory gating research focuses on the auditory modality. This method involves presenting a participant with two identical auditory stimuli in quick succession, usually two clicks, while their brain activity is monitored using EEG. These sounds can be presented through speakers or headphones and the participants may or may not be given a simple task during the study in order to direct attention towards the stimuli. Using the typical paired-click paradigm, with an inter-stimulus interval (ITI) of 500ms and an inter-trial interval (ITI) of 8-10 seconds, studies have shown that the P50 sensory gating ratio was significantly higher in patients with schizophrenia compared to healthy controls (Adler et al., 1982; Boutros et al., 2004; Bramon et al., 2004; Brockhaus-Dumke et al., 2008; de Wilde, Bour, Dingemans, Koelman, Linszen, 2007; Light et al., 2000; Thoma et al., 2003). One meta-analysis found that the mean gating

ratio for patients with schizophrenia was 79.9% while the mean ratio for controls was around 55.6% (Patterson et al., 2008). Despite the evidence for a sensory gating impairment in patients with schizophrenia, not all studies replicate these findings (Arnfred et al., 2003; Guterman & Josiassen, 1994; Kathmann & Engel, 1990). These inconsistencies are often attributed to the heterogeneity of the methods (de Wilde et al., 2007). Some of the differences that are said to affect the sensory gating ratio are: clinical subtype (Boutros, Zouridakis, Rustin, Peabody, & Warner, 1993), current symptomology (Ringel, Heidrich, Jacob, & Fallgatter, 2004), nicotine (Griffith et al., 1998), and medication (Light et al., 2000).

In an attempt to enhance the external validity of these auditory sensory gating findings, studies have been conducted using concurrent visual stimuli in order to mimic a more perceptually rich and thus naturalistic environment (Moran et al., 2012). A study using random flashes of light throughout a typical auditory paired-click paradigm, found that the P50 ratio increased compared to the paired-click paradigm alone (Jin & Potkin, 1996). This may suggest that gating of stimuli in one modality becomes increasingly difficult when the cognitive resources are processing more than one modality (or more complex stimuli).

1.4.2. Somatosensory

Another modality that has received less attention with regards to sensory gating is that of somatosensory processing. These studies use a paired-pulse paradigm similar to the auditory counterpart, during which the median nerve is electrically stimulated twice from electrodes placed at the wrists. EEG or magnetoencephalography (MEG) recordings are taken from areas pertaining to the primary somatosensory cortex. Such studies have found similar gating effects as the paired-click paradigm in the normal population (Arnfred, Chen, Eder, Glenthøj, & Hemmingsen, 2001). However other researchers failed to find similar sensory gating deficits in patients with schizophrenia (Arnfred & Chen, 2004), even when the same population demonstrated the usual auditory sensory gating deficit (Edgar et al., 2005).

This may imply that although sensory gating is observable across modalities, patients with schizophrenia may only exhibit a deficit in the auditory modality. Conversely, a sensory gating deficit in patients with schizophrenia has been found in the secondary somatosensory cortex as opposed to the primary cortex (Thoma et al., 2007). Correlations have been found between sensory gating in the primary and secondary somatosensory cortices and the auditory modality (Arnfred & Chen, 2004; Thoma et al., 2007), implying a shared circuit or mechanism.

1.4.3. Visual

In light of a possible shared mechanism, additional research on a potential visual sensory gating effect must be taken into account. One issue with this line of enquiry is that there is no consensus on the most appropriate methods. For example, studies have employed the same methods as with auditory stimuli but replace the click stimuli for light flashes (Adler et al., 1985) or white circles on a black background (Gjini, Sundaresan, & Boutros, 2008). Others use checkerboard stimuli and reduce the ISI to 50ms (e.g., Gawne, Osbourne, & Risner, 2011). Additionally, although the ERP P50 is often found at the electrode CZ in auditory studies, the few visual studies that have been undertaken to date use a variety of central and occipital sites and sometimes focus on later ERPs. The study conducted by Adler and colleagues (1985) showed no visual sensory gating effect. Indeed, they observed an increase in P50 to the second stimulus rather than a decrease. Conflicting research has found observable but small sensory gating effects in the visual evoked potential (VEP) (Gawne et al., 2011; Gjini, et al., 2008).

1.5. *Cognitive Inhibition*

Although research has been conducted with the aim of identifying the analogous cognitive mechanism of sensory gating, its functional relevance has yet to be identified with any measure of certainty (Potter et al., 2006). This is with regards to both optimum and deficient sensory gating functioning. Evidence that there may be a cognitive mechanism that reflects electrophysiological gating comes from previous research that has already demonstrated significant correlations between sensory gating and behavioural tasks measuring different forms of cognition (Cadenhead, Light, Geyer, McDowell, & Braff, 2002; Wan, Friedman, Boutros, & Crawford, 2008; Yadon et al., 2009). These studies do not measure gating simultaneously with the behavioural tasks, and thus do not purport that performance on these tasks reflect a cognitive component of gating. Therefore, one aim of this thesis is to further the research in this area, and contribute to the efforts in identifying a distinctive cognitive mechanism. By ascertaining which cognitive task corresponds best with the neurological measure of sensory gating, we can isolate the specific components involved.

To date, the principal cognitive dimension that has been correlated to sensory gating is that of attention (Yadon, Bugg, Kisley, & Davalos, 2009). However, the concept of attention can encompass a wide range of cognitive mechanisms and thus is too broad a term to adequately answer the question regarding the cognitive relevance of such a specific mechanism as sensory gating. A more focused approach within the sensory gating literature, which is less explored, is the inhibitory function of attention, but this too is a broad category of cognitive components (Friedman & Miyake, 2004), meaning it is not sufficient to state that sensory gating is an inhibitory process. The scope of inhibition will be discussed later in the chapter. This point is demonstrated by an absence of observed correlations between every inhibitory task and sensory gating. For example, Yadon and colleagues (2009) investigated the relationship between sensory gating and four different cognitive inhibition tasks only to find a correlation between sensory gating and two of those tasks, the Stroop and go/no-go

paradigms. In addition to this, they also found a double dissociation between those two tasks. Sensory gating was negatively correlated with Stroop interference indicating that those with worse sensory gating were better at inhibiting the irrelevant word dimension. Conversely, sensory gating was positively correlated with go/no-go, in that participants who demonstrated worse sensory gating were also worse at inhibiting the prepotent motor response to 'go' during this task. Thus, further studies using multiple tasks are urgently required to identify and distinguish between candidate cognitive mechanisms associated with sensory gating.

As suggested, cognitive inhibition is a broad concept associated with a range of mechanisms, and consequently all inhibitory tasks that assess cognitive inhibition do not significantly correlate with one another (Kramer, Humphrey, Larish, Logan, & Strayer, 1994, Yadon et al., 2009). Within the domain of inhibition for example, the Stroop and stop task, which measures the ability to suppress a prepotent motor response, are typically weakly correlated (Shuster & Toplak, 2009). This has been explained by defining both tasks as a test of conflict resolution with the critical distinction being what the focus of that conflict is. The Stroop task involves competition between verbal responses, while the stop task is a conflict between motor responses (MacLeod, 1991).

In light of these issues, this thesis aims to explore the relationship between inhibitory processes and sensory gating. Firstly, cognitive inhibition refers to one facet of executive function, thought to be coordinated and controlled by a set of higher-order processes (Pennington & Ozonoff, 1996; Miller & Cohen, 2001). The purpose of this form of cognitive control is to limit the processing of information in our environment (Frith, 1979). This is accomplished by the suppression of previously encoded information or goals once they are deemed irrelevant and previously existing cognitive processes that do not favour current goals (Aron, 2007). Additionally, inhibitory mechanisms allow for the suppression of attention or responses to irrelevant or distracting stimuli in the environment (Enticott, Ogloff, & Bradshaw, 2006). All these mechanisms enable the efficient and restrictive control of attention to stimuli or processes relevant to current goals and task demands (Bjorklund &

Harnishfeger, 1995; Nigg, 2000). It is also an adaptive system that responds accordingly to changes in the environment in the ongoing service of purposive behavior (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004).

As described above, current theory assumes that the influx of perceptual information into consciousness must be restricted, due to the limited capacity of the cognitive system (for reviews see Luck & Vogel, 2013; Baddeley, 2012). Consequently, cognitive inhibition is a feature of most tasks and purposive behaviours in our day to day lives. Specifically, tasks that require some form of attentional focus, deletion of information no longer relevant from working memory, and control over prepotent cognitive and motor responses (Lustig, Hasher, & Zacks, 2007). How these mechanisms work, is still an area of contention. For example, the ability to focus attention towards a target stimulus in the presence of distractors, may be the result of preventing the distracting stimuli from entering working memory (inhibition), enhancing the processing of the target stimulus (facilitation), or both of these processes simultaneously.

1.6. Models of Inhibition

The cognitive mechanisms involved when distractors are present during any task are a primary focus of inhibition research. Distractors can interfere with the efficient processing of stimuli that are relevant for current goals and task demands (Watson & Humphreys, 1997). There are three main theories, as mentioned above, regarding the cognitive control of distractors and how interference is regulated. These are inhibition, facilitation, and inhibition and facilitation together.

1.6.1. Inhibition

One theory is that of inhibition alone (Anderson & Bjork, 1994). This theory has several implications, one being that if separate stimuli require a different response the conflicting response is suppressed in order to allow for the execution of the primary, desired response (Cansino, Guzzon, Martinelli, Barollo, & Casco, 2011). Additionally, any erroneous distractors that may disrupt the processing of the primary response are prevented from reaching working memory (Hasher, Stoltzfus, Zacks, & Rypma, 1991). Inhibition also plays a role in suppressing any internal stimuli that may cause conflict. Internal stimuli can refer to previous goals or tasks demands within working memory, or representations of stimuli previously encountered. These internal stimuli could be previously relevant but due to a change in task demands are subsequently deemed irrelevant (Nigg, 2000). Prepotent or reflexive behaviours may also need suppressing in order to perform a target response.

1.6.2. Activation/Facilitation

Others authors have proposed that interference is not mediated by inhibition, but rather activation (MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003). Cansino and colleagues (2011) propose that it is inefficient to be actively inhibiting irrelevant information when one could just enhance the attention given to the relevant information. However, perhaps it is not a question of efficiency and rather the attentional spotlight can only be focused so much (Eriksen & Hoffman, 1973; Heitz & Engle, 2007) and thus extraneous stimuli are inevitably processed, at least perceptually, and consequently require suppressing from working memory. In fact, research suggests that even stimuli that participants are instructed to ignore, manage to be at least partially processed at the early stage of perceptual encoding (Eriksen & Eriksen, 1974). As a result, this does not support the notion that activation alone is responsible for the processing of relevant stimuli.

1.6.3. Inhibition and Facilitation

The final theory of interference control is the use of activation and inhibition, either concurrently or at different stages in cognitive processing (Kane, Conway, Hambrick, & Engle, 2007). According to this theory, in the early stages of information processing there is an unconscious and automatic analysis of stimuli within the attentional spotlight. As a result, related pathways within the brain are activated. For example, corresponding internal representations are activated with regards to spatial or categorical information provided by the stimuli. Ultimately, deeper processing encounters limited efficiency within working memory with an increased load. Consequently, during a more conscious and effortful control of attention, inhibition is required to filter out the irrelevant information (Neill & Westberry, 1987). However, some authors claim that in some cases, passive decay of irrelevant information - and not inhibition - enables the efficient processing of the relevant information (Beech, McManus, Baylis, Tipper, & Agar, 1991; Tipper, 1985).

Experimental and imaging techniques have provided support for a biphasic model of interference control, demonstrating early activation followed by later inhibition due to task irrelevant stimuli (Klein, 2000; Lepsien & Pollmann, 2002). It has also been suggested that when the irrelevant stimuli elicit low interference, perhaps due to minimal salience, inhibitory processes are not required. However once the irrelevant stimuli elicit interference beyond that of a certain threshold, inhibition is required alongside activation (Cansino et al., 2011).

1.7. Components of Inhibition

It is proposed within attentional inhibition research that there are different forms of inhibition. Such dichotomous dimensions of inhibition include behavioural/cognitive, automatic/intentional, and inhibition/resistance.

1.7.1. Behavioural Versus Cognitive

This is the distinction between intentional inhibition of competing motor responses, and intentional inhibition of competing representations within working memory (Nigg, 2000). The difference in these forms of inhibition can be reflected in the different stages of information processing at which they occur. As stated earlier (section 1.2), the general stage model includes an input (perceptual), central (cognitive), and output (behavioural) stage. Behavioural inhibition may refer to a prepotent automated response such as a reflex, which is apparent in tasks that require participants to perform the opposite behaviour to typical unconscious and automatic responses. For example, the antisaccade task where participants are instructed to move their gaze in the opposite direction to where a stimulus appears (Roberts, Hager, & Heron, 1994). This task is referred to as having a reflexive quality in both primate and human studies, when saccades are made to stimulus presentations even when the opposite is required (Munoz & Wurtz, 1992). A distinction has been made between two governing systems for saccades: a fixation system that is automatic and unconscious, and a voluntary system that controls saccade initiation or suppression (Fischer, Biscaldi, & Gezeck, 1997). Alternatively, behavioural inhibition is evident when there are two competing physical responses and the instigation of each response is dependent upon two corresponding stimuli. In line with the activation and inhibition theory, while the act to make one response is activated, the opposing action must be inhibited. This is made harder in tasks where the response to be inhibited was once the activated response, for example the stop task (Logan, Schachar, & Tannock, 1997). Harnishfeger (1995) describes behavioural inhibition as the control of overt behaviour and thus is relevant when an overt behavioural response is required at the output stage (response) during the completion of a cognitive task. Alternatively, cognitive inhibition refers to the inhibition of dimensional representations within working memory. Cognitive inhibition can include the control of any cognitive construct such as task demands, goals, and stimulus dimensions

(Nigg, 2000). When one is presented with a target and distractor stimuli, in order to allow for efficient processing of the corresponding representation to the target stimulus, the perceptual representation of the distractor stimuli must be inhibited in order to prevent interference with the target stimulus representation (MacLeod, 2007; Melara & Algom, 2003). Tasks involving selective attention require cognitive inhibition (Kopp, Mattler, & Rist, 1994).

1.7.2. Automatic Versus Intentional

Automatic, or unintentional inhibition is a form of attentional control that occurs without conscious awareness (Kok, 1999). Due to the limited processing capacity, cognitive contents are filtered out of consciousness. Either previously activated cognitive representations or stimuli that no longer provide relevant or consequential information regarding the environment, are automatically suppressed. This can be seen in tasks such as retrieval-induced forgetting and sensory gating respectively (Anderson, Bjork, & Bjork, 1994; McDowd, Filion, Harris, & Braff, 1993). Intentional inhibition however, as demonstrated in tasks such as directed forgetting (Harnishfeger & Pope, 1996), is a conscious process that is deliberately elicited to moderate the effects of irrelevant stimuli. Stimuli that are, or eventually become, irrelevant are suppressed from working memory via voluntary control (Collette, Germain, Hogge, & Van der Linden, 2009).

1.7.3. Inhibition versus Resistance to Interference

While inhibition can be characterized as the active process of modulating relevant and irrelevant information through suppression or removal of information from working memory due to task demands, resistance to interference is the ability to maintain a standard of performance in the presence of competition (Nigg, 2000). This competition can occur at any stage during information processing: either the interference of distractor stimuli at the perceptual encoding stage, whereby information is filtered out before it enters working

memory (Badcock & Hugdahl, 2012), the competition between task sets and stimulus representations during cognitive processing, and finally the conflict between two competing behavioural responses at the output stage. Interference is deemed to be the decrement in performance as a result of any of these forms of conflict and the response cost elicited due to the requirement of conflict resolution (Harnishfeger, 1995). In contrast to resistance to interference, inhibition is the active removal of irrelevant information that has previously been encoded into working memory (Harnishfeger & Bjorklund, 1994), for example the suppression of a repeated, once relevant response, to allow for a new response during a task-switching paradigm. While interference is a result of conflict at any stage of information processing, inhibition is only relevant to the cognitive and behavioural stages where information is removed from working memory. This is because information at the perceptual input stage is still in the process of encoding and is consequently not fully represented within working memory. Although all tasks containing task-irrelevant distractors will involve both these mechanisms, it is important to make the distinction between the two related but fundamentally different concepts that occur at different stages (Harnishfeger, 1995).

During selective attention tasks, evidence does suggest that irrelevant stimuli can be both actively suppressed from working memory and passively ignored so as to not enter working memory (Kok, 1999). In one such task involving visual spatial processing, a distinction was made between the likely processes involved when a cue was presented either before or after a probe trial. When the cue was presented prior to the probe trial, participants are able to ignore the irrelevant stimuli and only attend and process the relevant, thereby reducing interference. However, a cue that is presented after the probe trials creates the need for the irrelevant stimuli already encoded to be actively removed (inhibited) from working memory (Cansino et al, 2011). A similar theory to that of inhibition and resistance to interference was proposed by Hasher and colleagues (1991), which made comparable distinction between controlling information entering working memory, and filtering out irrelevant information already there. The terms access, deletion respectively, were used to make these distinctions (Lustig et al., 2007).

More minor dichotomous components evident within the literature include task specific/everyday relevance, and spatially separate/integrated interference. The former conceived by Yadon and colleagues (2009) denotes the difference between a stimulus containing information that is relevant to the current task, and information that has everyday relevance. Although the information provided by this form of stimulus is irrelevant to the task, it retains everyday relevance, in so much as to be unavoidably processed due to a preconceived notion of salience. Yadon suggested this distinction could explain why sensory gating is correlated to the Stroop effect but not the flanker, implying that they have some distinguishing component even though both tasks are used to measure inhibition. The irrelevant information within the Stroop task is the colour word, and although participants are to respond to the ink colour, a known word is proposed to have everyday relevance. On the other hand, the irrelevant information in flanker task is the to-be-ignored stimuli which are presented either side of the target stimulus. These flanker stimuli can be the same or require the opposite response to the target stimulus and are consequently assigned task related relevance.

The notion of spatial integration can be explained using the same two tasks. Distractor stimuli or dimensions in cognitive tasks can be integrated with the target stimuli. Within the Stroop effect, the relevant (ink colour) and irrelevant (colour word) dimensions are spatially combined. In tasks such as this, the irrelevant dimension will inevitably be processed, as demonstrated by increased response latency during incongruent trials, resulting from participants failing to suppress the automatic process of reading (Nigg, 2000). Conversely, in tasks such as the flanker task, the irrelevant distractors are spatially separate from the target stimulus. If enough space is given between the two types of stimuli, participants are able to ignore the distractors and prevent perceptual processing (Eriksen & Hoffman, 1973).

1.8. Inhibition or Episodic Memory Retrieval

The tasks mentioned so far in this chapter, are currently used to measure several different facets of inhibition. However, there is some debate with tasks such as negative priming, as to whether or not inhibition is in fact being measured. Some researchers assert that the basis for negative priming is actually episodic memory retrieval (Neill, 1997). The idea behind this argument is that memory is automatically accessed during any task in order to ascertain if there is any relevant information which may facilitate in the efficient processing of the current task (Logan, 2002). When this happens, if there is any disparity between the memory that is retrieved and the current task, there is a behavioural cost due the time needed to resolve the conflict (Macleod, 2007). Within the domain of negative priming, the probe display activates the relevant memory from the previous prime display. Conflict occurs when the probe display requires the response to a target that was a distractor and to be ignored in the prime display. This is because the response accessed from memory of the prime display is contradictory to the current appropriate response. The response cost seen during these incongruent trials is a result of the required conflict resolution before a response can be made.

Evidence that negative priming is dependent upon the perceptual similarity between the prime and probe displays as a whole supports the episodic memory retrieval theory (Fox & De Fockert, 1998). Conversely, evidence from Mayr (2002) demonstrated that backward inhibition is still evident even when the action rules for the trials n and $n-2$ were the same. According to the memory retrieval view, there should have been facilitation due to the memory of the action rule from the $n-2$ trial being accessed and not conflicting with the response required in the n trial. This argument highlights the importance of looking at possible alternate underlying mechanisms active during a test designed to measure inhibition, in order to ensure that proposed components are accurate.

1.9. Summary and aims

This chapter has discussed the limited capacity of working memory, specifically, how this requires the ability to filter out certain sensory information throughout the stages of information processing. One purported mechanism for this is sensory gating, which is typically measured at an early stage in information processing, and in the auditory modality. Although some research has been conducted in other modalities, the visual modality has received limited attention. The few studies which are available have not been replicated, and/or have not provided detailed comparison with results from the auditory modality. The first aim of this thesis was to replicate previous auditory methods, and compare these with analogous visual methods. This will help elucidate whether or not there is a shared multi-modal gating mechanism, a series of qualitatively similar but functionally separate mechanisms, or if a similar sensory gating mechanism is not observable in the visual modality.

The second focus of this thesis pertains to the cognitive mechanism that may underlie this cerebral measure of inhibition. This chapter has detailed the breadth of theories regarding cognitive inhibition, and where available, how the measures of cognitive inhibition relate to sensory gating. However, little research is currently available that addresses the potential cognitive mechanism related to sensory gating. One issue with this is that too few tasks are used, and consequently it is difficult to pinpoint the precise mechanism within that task, that may relate to gating. Moreover, many of the tasks used in previous research do not measure the same facet of inhibition, and yet the specific mechanisms underlying each task are not explored. A more comprehensive approach must be taken in order to ascertain the cognitive components associated with sensory gating. With a more detailed exploration of the cognitive components within cognitive tasks, and the use of multiple qualitatively different tasks, this thesis aims to identify the potential underlying cognitive mechanism

related to sensory gating. This issue will be addressed for both the auditory and visual modalities.

Chapter 2

Method

2.1. Participants

Opportunity samples were used in each experiment of this thesis (see Table 1 for sample size, age and gender information). Volunteers were predominantly Anglia Ruskin University Psychology students, and were recruited through online advertisements. Participants received credits for the completion of the study. All participants self-reported that they had normal or corrected vision and hearing and were excluded if they had a history of brain damage, epilepsy, and alcoholism or were taking medication affecting the central nervous system at the time of participation. For the EEG investigation participants were asked to avoid alcohol 24 hours prior to testing and were encouraged not to smoke immediately before.

Table 1

Participant demographic information for all experiments.

Experiment	Sample size	Sex (male)	Mean age (years)	Age range (years)
1	24	10	23	19 - 40
2	60	22	21	19 - 30
3	31	10	20	18 - 36
4	29	12	27	19 - 40
5 (auditory)	10	2	21	19 - 26
5 (visual)	10	1	21	19 - 23

Note: Experiment 5 was a between subjects design and thus different participants completed the visual and auditory experiments.

2.1.1. Excluded participants

After filtering the EEG data and removing data that had no observable component(s) (no ERP of interest could be visibly detected within the EEG waveform in response to the presentation of the first stimulus; see section 2.2.4. for a more detailed description of EEG data pre-processing and analysis), experiment two had a sample size of 51. In addition to this, experiment two had a varying number of participants that completed each of the behavioural tasks. See Table 2 for the number of participants for each behavioural task that also has useable EEG data. Experiment four is a within subjects design that consists of a visual and analogous auditory experiment. Again due to no observable ERP component, two cases were removed from the visual experiment, although these participants did have usable EEG data for the auditory experiment. Finally, experiment five also consists of an auditory and visual experiment (between-subjects design), and two participants from the auditory experiment were removed from further analysis. Note that no participants or data was removed from experiments one or three.

Table 2

Number of participants for each behavioural task employed in experiment two that also had useable EEG data.¹

Behavioural task	Final sample size for analysis
Stroop	43
Simon	39
Flanker/executive control (ANT)	41
Latent inhibition	19
Novel pop-out	19
Negative priming	43
Go/No-go	43
Switch	43
Antisaccade	43
Orienting (ANT)	41
Alerting (ANT)	41
Continuous performance	43
Cattell's Culture Fair (CCF-IQ)	43
OSPAN	43

¹ Variability in the completion of the behavioural tasks was primarily due to participants not returning for a second or third day of testing. There were several technical issues with the computer running the latent inhibition and novel pop-out effect experiments.

2.2. Sensory gating Procedures: The source of ERPs

EEG measures the voltage changes over time as a result of the summed electrical activity of large populations of neurons that is conducted through the brain, skull and scalp. During an EEG experiment, when experimental trials are time-locked to an event of interest (e.g. stimulus presentation) and averaged, the resulting changes in the voltage amplitude of the signal are referred to as Event-Related potentials (ERPs). Time-locking trials to an event allows for the investigation of the neural activity preceding, during and after stimuli are presented. However, in order for these ERPs to be interpreted correctly, it is important to appreciate the underpinnings of the electrical activity that produces them (Luck, 2014; Picton et al., 2000).

The signal recorded at the scalp reflects changes that occur in the membrane potentials of neurons as they are activated. At rest, the inside of a neuron is negatively charged relative to the outside. When the neuron becomes active, ion channels in the membrane open, allowing the ions outside the cell to enter. Consequently, the inside of cell becomes positively charged with respect to the outside (depolarised), resulting in an action potential. This signal then travels down the neuronal axon to the synapse. Communication between neurons occurs when neurotransmitter molecules are expelled from one cell into a synapse and, by diffusion, reach the next cell. These neurotransmitter molecules trigger an influx of positively charged ions in the post synaptic neuron, resulting in a post synaptic potential. It is this chemical change that is measured by the EEG, however in order for these voltage changes to be detected, large populations of neurons must fire synchronously. Moreover, these cells need to be spatially aligned in order for neurons with positive and negative dipoles to not cancel each other out. As a result, each electrode on the scalp measures the sum of the current flow that is directed at it. Which may originate from several sources within the cortex. Additionally, the activity recorded at the scalp will only be a small

proportion of the total activity within the cortex due to other neurons that may cancel each other out, or are not arranged in the optimal orientation (Makeig, 2016).

This being said, it is possible to ascertain the likely source(s) of an EEG signal measured at an electrode. Using a dense electrode array (commonly 128 electrodes) and certain statistical methods (e.g. independent component analysis), one can compare the signal detected at each electrode, and using the knowledge of volume conduction and the patterns of how sources propagate the signal to the scalp, can estimate the likely cortical source(s) of each electrode (source localisation) (Acar & Makeig, 2010). The use of these methods has highlighted that several cortical sources contribute to the ERP seen at any one electrode, indeed no more than 30% of the variance recorded at one electrode is produced by a single source (Makeig & Miyakoshi, 2015). Moreover, due to the nature of volume conduction, one source will likely be detected by several neighbouring electrodes.

2.2.1. Auditory sensory gating procedure

This procedure was employed for experiments one and two. Participants sat in a dimly lit, sound attenuated Faraday cage. The electrode cap was fitted using a chinstrap and/or chest strap depending on the fit. Participants were instructed to minimise any body, face, and eye movements. They were provided with an example of the auditory stimuli to be used in the experiment and the volume was adjusted to ensure a comfortable volume for all participants. Stimulus volume was first set at 75dB using an SPL meter for all participants but was reduced marginally if participants found this volume uncomfortable. During recording, they were monitored for signs of drowsiness by visual and EEG monitoring. Each trial consisted of a conditioning stimulus and a test stimulus that were both beeps: bursts of 4100 Hz of at an intensity of 70 –75 dB, delivered using headphones. Each stimulus had a 10ms duration with an inter-stimulus interval (ISI) of 500ms. There was an inter-trial interval

(ITI) of 10s in order to allow brain activity to return to baseline (Sánchez-Morla et al., 2013).

The experiment consisted of 100 paired-beep trials with an additional 15 click trials (click trials consisted of only 1 stimulus presentation -4ms stimulus duration; 4100 Hz with an intensity of 70 –75 dB) and was approximately 30 minutes long with two breaks. Participants were instructed to focus on a central black fixation cross on a white background throughout the experiment and to press the response pad whenever they heard a click. The primary reason for this task was to engage the participants. Subsequent analysis revealed all participants had an accuracy of at least 90%.

2.2.2. Visual sensory gating procedure

This procedure was employed for experiments one and three. The visual paradigm consisted of 100 pairs of stimuli: flashes of white circles presented in the centre of a screen on a black background in 72 dpi resolution. The size of the stimuli were 1.6 degrees square and centred 2.26 degrees from the centre of the screen (subtending visual angle of 16 degrees by 10.35 degrees), presented using E-prime software, on a 20" CRT monitor with a refresh rate of 60Hz. An additional 15 stimuli were blue squares also presented in the centre on a black background. No fixation cross was used for this procedure to reduce, as much as possible, any visual stimulation outside of the conditioning and testing stimuli. Each stimulus presentation was 50ms, with an ISI of 500ms and an ITI of 10s. Stimulus presentations were longer for the visual study compared to auditory due to the different speeds at which information is perceived between the modalities. Visual stimuli are processed slower in part because of signal transduction, with photons being converted into bioelectrical signals slower than sound waves. Thus the visual stimuli require additional time to be successfully perceived. Participants were seated in a sound attenuated faraday cage for the EEG portion of the study. The electrode cap was then fitted to participants' head using a chinstrap and/or

chest strap depending on the fit of the cap. Participants were instructed to minimise any body, face, and eye movements. During recording, they were monitored for signs of drowsiness by visual and EEG monitoring (alpha wavelengths). During the study, there was no fixation cross in order to avoid complication associated with visual stimulation prior to the stimulus presentation. Thus participants were instructed to maintain their gaze on the centre of the screen as much as possible. Participants responded whenever they saw the blue square. These responses were not recorded and were simply used to engage the participant. To ensure participants were making correct responses, response triggers set up in the EEG recoding software were monitored throughout the study.

2.2.3. Altered sensory gating procedure

This procedure was employed for experiments four and five. The visual stimuli consisted of a black and white checkerboard stimulus (2x2) and a solid red circle stimulus. The size of the stimuli were 1.6 degrees square and centred 2.26 degrees from the fixation point (subtending visual angle of 16 degrees by 10.35 degrees) in 72 dpi resolution and on a white background using E-prime software, on a 20" CRT monitor with a refresh rate of 60Hz. For the auditory experiment, two WAV sounds were used, a click and a beep. Both sounds were 44100 Hz lasting approximately 10ms with an intensity of 70 –75 dB, delivered using headphones. In order to ensure the same volume was presented to each participant, an SPL meter was used to measure the volume of the first few stimuli while the participant was familiarised with the sounds being presented. Some participants did find this intensity uncomfortable, and in such cases the volume was marginally reduced to a more comfortable setting.

In the visual experiment, the participants were first presented with a fixation cross alone in the centre of the screen for 500ms. Then the first stimulus (conditioning stimulus)

appeared to the left side of the fixation cross for 50ms before being presented with the second stimulus (test stimulus) also to the left of the fixation cross for a further 50ms with an inter-stimulus interval (ISI) of 500ms. An example of one trial can be seen in Figure 2. The screen was divided into quadrants with the stimuli appearing in either in the bottom left or top left quadrant. Both the conditioning and test stimuli could appear in the top or bottom quadrants, or the conditioning stimulus could appear in the top, followed by the test stimulus in the bottom (or vice versa), leading to a possible four location conditions which were randomized. This was based on the study by Gawne and colleagues (2011).

For the auditory experiment, again each trial consisted of a conditioning phase and a test phase. The first stimulus (conditioning stimulus) was presented from either the left or right headphone speaker for 10ms followed by the second stimulus (test stimulus) from the left or right speaker for another 10ms with an inter-stimulus interval (ISI) of 500ms. For both experiments, there was a random inter-trial interval between 6 -8s (Popov *et al.*, 2011). The experiment lasted for a maximum of one hour and breaks were given every 10 minutes.

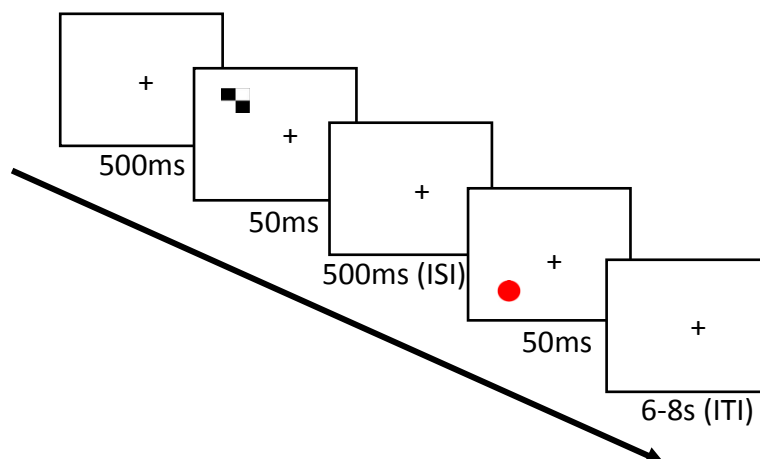


Figure 2. Time course of a single experimental trial for the visual modality. Example is depicting the condition of different location and different stimulus (DLDS)

For experiment five the same procedure was used for each modality, with the addition of a task to engage the participants. Participants were instructed to respond using a button on a response pad, whenever they saw the blue square (heard the bell ring). These were the same stimuli as described above. Accuracy was monitored during the experiment to ensure that participants were in fact attending to the stimuli. No issues were encountered with participants failing to accurately respond whenever the blue square/bell ring was presented. The experiment lasted approximately 30 minutes with a total of two breaks.

2.2.4. EEG recording and analysis

ERPs were recorded via two 32-channel DC amplifiers, using Brainvision Recorder and ActiCap software. Twenty-four electrodes were mounted on a cap while four additional ocular electrodes were placed on the outer canthi and above and below one eye, which monitored horizontal (+HEOG, -HEOG) and vertical (+VEOG, -VEOG) eye movements. According to the international 10/20 system, the electrodes recorded ranged from the vertex Cz, towards Oz across the midline, and extended out left and right towards C3 and C4. These electrodes were chosen to include the standard electrode sites from previous research (Cz, Pz, Oz) while including neighbouring electrodes to further assess the optimal location of each component. Electrode impedances were kept under 5 k Ω and the sampling acquisition rate was 2000 Hz. Fz was the reference electrode during acquisition; the data was re-referenced to the average mastoids (TP9 and TP10) offline.

Using Brainvision Analyser, trials contaminated with eye movements and other artifacts were rejected. Raw data was filtered using a 50Hz notch filter and a 0.1-50Hz band pass filter (24-dB/octave roll-off). An addition 10Hz high band pass filter was employed for data which contained excessive alpha frequency band waves. Ocular corrections were made using Gratton and Coles algorithm. For each participant, segmentations were made based

on marker position for stimulus 1 (S1) and stimulus 2 (S2), which included 100ms prior to stimulus onset and up to 250ms post stimulus onset. Baseline corrections were carried out 100ms before stimulus onset before the average for each stimulus was obtained. A combination of the following event-related potentials was used for each of the analyses. Based on the previous literature pertaining to the early and mid-latency ERPs for each modality, three components were chosen for the auditory and visual paradigms (P50, N1, P2 and C1, P1, N1 respectively). For the auditory components, the P50 ERP was identified as the most positive peak within a 40ms period between 40ms and 80ms post stimulus onset, N1 was identified as the most negative peak between 60ms and 150ms post stimulus onset, and P2 as the most positive peak between 150ms and 250ms (Boutros et al., 2004; Rentzsch, Jockers-Scherübl, Boutros, & Gallinat, 2008). For the visual components, C1 was the most negative component between 40-100ms post-stimulus onset (representing the earliest of the two-part component), P1 was the most positive peak between 80-150ms, and N1 was the most negative peak between 140-220ms (Barnhardt, Ritter, & Gomes, 2008; Clark & Hillyard, 1996; Foxe & Simpson, 2002). Experiment one used a number of electrodes to measure these components. In this experiment, nine electrode sites were chosen in order to identify the presence of sensory gating in both the auditory and visual modality: C1, Cz, C2, P1, Pz, P2, O1, Oz, and O2. In order to provide more detail regarding the comparative locations of any gating, these electrodes include the typical sensory gating area at the vertex and then extend this region to both hemispheres and towards the occipital lobe. These electrodes were chosen as this was deemed sufficient to investigate the optimal gating compared to the previous studies investigating midline electrodes only (Adler, Waldo, & Freedman, 1985; Gawne et al., 2011; Oranje et al., 2006). The inclusion of electrodes either side of the midline was to ascertain if any lateralisation was present. During analysis of the auditory paradigm, the raw data for the occipital electrode sites was deemed too noisy and lacking in any visible components. Due to this, these sites were removed from the analysis. The findings of experiment one indicated that there was no lateralisation of sensory gating, and there were specific optimal locations for this gating. Consequently, for all

subsequent auditory analysis, the electrode Cz was chosen to measure sensory gating, and for the visual modality, electrodes Pz and Oz were used. This is also in keeping with electrodes used in previous research.

For each component, the amplitude was obtained by calculating the difference between the peak/trough of interest and the preceding trough/peak. This method was used over the baseline to peak method due to its prevalence in the auditory sensory gating literature. This is because the early components can ride on the following peak and thus be undetectable if comparing to the baseline (e.g. Anokin *et al.*, 2007; Arnfred & Chen, 2004). Based on Gjini, Arfken, and Boutros, (2010), if no obvious component was observed for S1, the participant was removed, however if no component for S2 was observed then this was deemed to be full suppression and a value of 0.01 μ V was given. For each participant, the component amplitude was obtained for S1 and S2. A sensory gating measure was established by calculating the component ratio. The sensory gating ratio was calculated by dividing the average amplitude for S2 by the average amplitude for S1 (S2/S1 ratio). A smaller ratio (<100) is indicative of intact sensory gating. Any ratio above 200 was truncated to 200 to avoid outliers having a disproportionate effect on the analysis (Gjini *et al.*, 2011).

2.3. Behavioural tasks and procedures

2.3.1 General procedure

Participants completed a series of cognitive tasks alongside the EEG recordings during experiments two and three. These tasks were all conducted in dedicated, air-conditioned laboratories. Participants were tested one at a time and completed the tasks over 2-4 days in order to avoid fatigue in experiment two, however this resulted in many tasks having a reduced final sample size. Consequently, testing for experiment three was completed over 1 or 2 days with several breaks throughout. This was to reduce to number of participants

failing to complete the entire study; in fact, all 31 participants completed each component of this experiment. For each computer task, with the exception of the paper based IQ test (Cattell's Culture Fair (CCF-IQ)), participants were sat approximately 60 cm in front of a high-resolution 17" LCD colour monitor. Most tasks were conducted on a Dell PC running E-Prime Professional 2, except for the Simon Task and the ANT which were run on a 15" Toshiba LCD laptop running Psychology Experiment Building Language (PEBL) software (Mueller, 2013). The EEG task employed a dedicated response pad. All other task responses made by participants were recorded via a standard computer keyboard. All letter (block capitals), fixation stimuli, and arrow stimuli were black, bold, and in font courier new size 18, and were presented on a white background, unless otherwise specified. Practice trials for all tests were administered according to published guidelines (where available). For tests in which an appropriate number of practice trials is unspecified in the literature, 10 practice trials were administered.

2.3.2. Stroop task

Participants were informed that they were going to be presented with a series of words and asked to identify the ink colour of the word as quickly and accurately as possible. Response keys were coloured with all featuring colours (blue, green, purple, red, and yellow), and all words were written in block capitals, Courier New font size 18. For each trial the presentation of the colour word was terminated when a response was made. There were 30 trials that lasted approximately 1 minute. During each trial the colour word could be the same colour as the ink (congruent) or a different colour to the ink (incongruent). The Stroop effect was operationalized by the difference in response times between congruent and incongruent trials (incongruent – congruent).

2.3.4 Simon task

During each trial a fixation cross first appeared in the centre of the screen for 800ms. Following a blank screen for 250ms, a red or blue circle appeared either to the left or to the right side of the cross (visual angle 17.06°) for a maximum of 1s if there was no response, or until the participant made a response. Participants were instructed to press the left shift key when they saw a blue circle and the right shift key when they saw a red circle, with the location of the stimulus treated as irrelevant. Half the trials were congruent (stimulus location corresponds to the response key) and the other half incongruent (stimulus location is opposite to response key). One hundred and fifty trials were presented in a random order and the task lasted approximately 2 minutes. For each participant, the Simon effect was operationalised as the difference in average reaction time between congruent and incongruent trials (incongruent – congruent)

2.3.5 Latent inhibition

Stimuli consisted of five randomly connected straight black 1 cm lines on a white background subtending 10° of visual angle. Four designs were created. These were presented in an array containing 20 identical stimuli (target-absent condition), or 19 identical and 1 unique (target-present condition). Participants were instructed to identify whether there was a unique element within each array. The position of each stimulus was randomly generated in an imaginary 8 x 12 matrix. Participants were presented with 100 pre-exposure trials (50 target-present and 50 target-absent) in a random order. Only two of the stimuli were used in the pre-exposure phase (this was counterbalanced across participants). Stimuli remained on screen until the participant made a response. The test phase began immediately following the pre-exposure phase and participants were informed that they would be completing the

same task but the stimuli would change from trial to trial. The experimental session lasted approximately 8 minutes.

There were seven possible relationships between the distractors and targets from the pre-exposure phase to the test phase, as described in Lubow and Kaplan (1997). However, only three are relevant to this study: 1) Target and distractor stimuli in the pre-exposure phase swap roles in the test phase (PE); 2) target in the pre-exposure phase became the distractor in the test phase, and the test phase target was novel, assessing the novel pop-out effect (NPE); 3) both the target and the distractor in the test phase were novel (NOV). The average reaction time was recorded for each participant in each of the three main conditions. The effect of latent inhibition is measured by the reaction time difference in the PE condition minus the NPE condition. A novel pop-out effect is indexed by the NPE condition minus the NOV condition. Stimuli were counterbalanced across conditions.

2.3.6. Negative priming

Participants were required to respond to a target symbol, 'O' and ignore a distractor symbol ('X') that appeared in one of four corners of a virtual square, subtended 0.6 x 0.6 degrees of visual angle. The location of the target symbol was identified by pressing 'D' indicating top left, 'C' indicating bottom left, 'K' for top right and 'M' for bottom right on a keyboard (corresponding to the location on the screen). Each trial consisted of a prime and probe display. In each trial, the prime and probe displays remained on screen until a response was made. Each screen was followed by a grey mask lasting 1350ms. There was an inter-trial interval of 8-10s. A fixation cross appeared in the centre of the screen 800ms before each display to prepare participants. There were a total of 75 trials, which lasted approximately 18 minutes. There were three conditions: 1. both the target and distractor were in different places from the prime to the probe display (control); 2. the target in the probe display was in

the same location as the distractor in the previous prime display (ignored-repetition); 3. no distractor was used (neutral). A negative priming effect is indicated when participants take longer to respond during the probe display of the ignored-repetition trials compared to the control trials (ignored repetition – control).

2.3.7. Go/No-go and Switch Procedures

Participants were required to respond to a series of arrows based on the subsequent appearance of a target letter. All stimuli were white and presented centrally (visual angle 0.8°) on a black background. Participants were asked to produce speeded responses with the left or right index finger, according to the direction of the arrow presented prior to the target letter, '<' corresponding to the left hand and '>' corresponding to the right hand. They were instructed only to make a response when the letter 'Z' appeared (go trials, 80%), and withhold the response when the letter 'T' appeared (no-go trials, 20%). Visual feedback was presented immediately after participants' response. For each trial, the arrow was presented for 750ms, followed by the letter (either target or non-target) for 1.5s, with an inter-stimulus interval of 500ms. There was an inter-trial interval of 1000ms between each trial. The experimental session had 60 trials and lasted for approximately four minutes. The ability to withhold a response was represented as the number of errors made during no-go trials.

This procedure was immediately followed by the switch task. This was identical to the go/no-go task except that when 'T' was presented participants had to respond with the opposite hand, that is, when the 'T' was presented they had to respond with the opposite hand to the direction of the arrow, and when 'Z' appeared they had to respond with the same hand as indicated by the direction of the arrow. The experiment session lasted for approximately 6 minutes and consisted of 100 trials. A response deficit for switch tasks is

operationalised by the difference in response times between switch trials and repetition trials (switch – repetition).

2.3.8. Antisaccade Task

Participants were required to fixate on a central fixation cross for 200 ms before the trial commenced. The central fixation cross then illuminated green to indicate a pro-saccade trial (to look at the target) or red to indicate an anti-saccade trial (to look at the mirror location to the target). At the same time, a laterally displaced target (either 8° to the left or right of the centre) appeared. This remained on screen until the participant made a correct saccade, as recorded by the Tobii 1750 eye-tracker. The central fixation cross disappeared after 200 ms of fixation at the target. There was a random inter-trial-interval of between 2000 and 2500 ms. The targets were presented in white on a black background. The time to make the correct saccade was measured. Participants completed a total of 180 trials (divided equally among pro- and anti-saccade trials of which half involved a target presented to the left and half involved a target presented to the right). The task measures the ability to inhibit a pre-potent response, and is indexed by the difference in reaction time to make anti-saccades compared to pro-saccades.

2.3.9. Attentional Network Task (ANT)

During this task all stimuli were presented in white on a black background. Each trial consisted of a fixation cross in the centre of the screen for 400-1600ms, followed by a second fixation period that could contain a cue stimulus in the form of an asterisk for 100ms. In no-cue conditions, the fixation cross appeared alone for 100ms. After the cue, there was a

further 400ms fixation period before the presentation of target stimuli. During the target stimulus display, there were a total of seven stimuli, three flankers either side of one target stimulus. The six flanker stimuli appeared for 50ms. While the flankers remained on the screen, the target appeared in the centre for 100ms, thus the flankers were on screen for a total of 150ms. This target and flanker array would appear either above or below the fixation cross but with the target stimulus centrally aligned with the cross. The inter-trial interval was dependent upon the participant's response time to the target stimulus and the variable time of the first fixation period. Participants were instructed to report the direction of the central arrow (visual angle 0.8°) amongst three flanker arrows on each side (visual angle: outside edge 4.9° , inside edge 2.2°) pointing either left (<) or right (>). Participants made their responses by pressing 'z' for left and 'm' for right' on the keyboard. There were a total of 290 trials lasting approximately 30 minutes. Trials were presented in a random order.

The six flankers were identical and could either be the same as the target stimulus (congruent), the opposite stimulus (incongruent), or unrelated. Additionally, during the second fixation period when a cue could be presented, there were a further four conditions. Either no cue would be presented (no cue), a cue indicating the appearance of the target stimulus in the centre where the fixation cross was (centre cue), a cue appearing both above and below the fixation cross also providing temporal information (double cue), and a cue which would appear either above or below the fixation cross providing temporal information as well as spatial information by indicating where the target stimulus will appear.

Only correct responses were used to calculate the various attentional measures. The executive functioning component of this task (the flanker task) is indexed by a slower responding during incongruent trials compared to congruent (incongruent-congruent). The alerting component is operationalised by the difference in response time between the centre cue condition and the no cue conditions (no cue-central cue). Finally, the difference in response time between the trials with a spatial cue compared to no cue, provide a measure for orienting proficiency (no cue – spatial cue).

2.3.10. Continuous performance task

This task began with a fixation cross in the centre of the screen. This remained on screen until the participant pressed the 'space' key to begin the trial. Following this, letter strings were presented centrally for 250ms each, with an ISI of 750ms. Participants were required to press the spacebar whenever they saw the target letter 'X'. There were a total of 273 trials in which 30% were a target 'X'. The experimental session lasted approximately 5 minutes. Average accuracy and response times were recorded for target trials. Due to results obtained in experiment 2 an additional condition was added for experiment 3 in order to explore this task in more detail. The CPT task in experiment 3 was altered to include salient and neutral stimuli. The procedure was the same as before except for the addition of a salient red 'X' as well as the standard black 'X' as target stimuli. In this procedure, the target stimulus still occurred 30% of the time, with 10% being red instead of black.

2.4. Psychometric tasks

2.4.1. Cattell's Culture Fair measure of fluid intelligence (CCF-IQ)

Participants completed the Cattell Culture Fair Intelligence Test Scale 2, form A (Institute for Personality and Ability Testing, 1973), which was used to assess individual differences in fluid intelligence. This IQ test has been widely used and has good construct and concrete validity scores, (.81 and .70 respectively); test-retest, internal and external reliability scores of .73, .76, and .67 respectively.

2.4.2. OSPAN

Working memory proficiency was measured using the automated-OSPAN task (Unsworth, Heitz, Schrock, & Engle, 2005). Participants were required to memorise letters while solving mathematical problems. This task consisted of mathematical stimuli such as “ $(3 \times 2) + 4 = 11?$ ” When an equation was presented, participants were instructed to click the mouse when they had solved the equation, which then brought up a single digit in the centre of the next screen. They then had to indicate whether the digit was correct by clicking a “true” or “false” box with a computer mouse. After each equation, a letter appeared and participants were informed that they would be asked to recall these letters at a later point in the same order in which they were presented. The number of compound stimuli (one mathematical followed by one letter) presented, before recall of the letters was required, varied from 2 to 7. When participants were required to recall the letters, 23 letters (correct and incorrect) were presented as a 4 x 3 matrix and participants had to click a box next to the appropriate letters in the correct order using the computer mouse. It was emphasised during the task that the mathematical problems must be answered correctly; feedback was displayed in red at the top right of the computer screen indicating the percentage of correct answers, which was kept above 85%. This task lasted approximately 10 minutes. The absolute OSPAN score is the number of correct letters remembered in the correct order but only from sets in which all letters were recalled correctly.

Chapter 3

Experiment 1: Comparing the location and latency of auditory and visual sensory gating

3.1. Introduction and rationale

This chapter investigates both the auditory and visual sensory gating mechanism in order to establish if a) sensory gating can be observed within the visual modality and b) if this mechanism is likely to be measured from the same surface scalp area and within the same latency period as auditory sensory gating. The principal aim was to clarify whether or not these two forms of cortical gating are part of a cross-modal, shared mechanism, if they are qualitatively similar but functionally distinct mechanisms, or if they are entirely unrelated.

The typical sensory gating paradigm involves presenting a series of identical paired-clicks to participants and comparing the amplitude of the P50 event-related potential (ERP) when the second stimulus is presented to when the first is presented (Anokhin et al., 2007; Arnfred & Chen, 2004). P50 is a positive deflection in the wavelength, peaking between 20-80ms post stimulus onset, and is the earliest component of the mid-latency auditory-evoked responses (MLAERs) (Grunwald et al., 2003). Gating measures can be in the form of a ratio ($S2/S1 \times 100$) or a difference ($S1-S2$) (Boutros et al., 2004; Brockhaus-Dumke et al., 2008; Moran et al., 2012). In healthy participants, successful gating is observed when the P50 amplitude after the second stimulus is smaller than the P50 amplitude after the first stimulus (Clementz, Geyer, & Braff, 1998). Thus, a smaller ratio is indicative of better inhibition. However, there is significant variation in the ratios observed in studies, ranging from 17.2% to 44% (Adler et al., 1985; Boutros, Belger, Campbell, D'Souza, & Krystal, 1999; for review see Potter et al., 2006). Moreover, there is a positive correlation between the number of

stimulus repetitions and the sensory gating ratio, indicating an increase in inhibition with more stimulus repetitions (Cacace, Satya-Murti, & Wolpaw, 1990). This particular finding agrees with fMRI and single-unit recording studies which demonstrate sensory adaptation, and research into habituation which shows a further decrease in the response to each successively presented stimulus (for further discussion on the adaptation/gating and habituation see section 1.3.). It is important to note here that not all studies have reported the typical P50 suppression in the normal population (i.e., they have failed to demonstrate sensory gating or have only found it in a minimal number of electrode sites (Grunwald et al., 2003; Kathmann & Engel, 1990)).

While the primary focus of sensory gating research is the 'gating out' of irrelevant or inconsequential stimuli using this conditioning-testing paradigm, another aspect of this mechanism is that of 'gating in'. Boutros and colleagues have extended the definition of sensory gating to include the augmentation of the cerebral response to a salient or relevant stimulus (Boutros et al., 1995). The P50 sensory gating ratio with non-identical pairs of stimuli is larger (less inhibition) compared to the ratio resulting from identical stimuli (Boutros et al., 1995). MRI studies have also demonstrated an increase in activity to the non-identical stimulus (Mayer et al., 2009). Furthermore, the increase in the P50 amplitude to the non-identical stimulus is not related to the type of change in the stimulus (e.g. frequency), but rather the fact that it is deviant (Boutros & Belger, 1999). In order to further explore this facet of sensory gating, researchers monitor the mismatch negativity (MMN) during an oddball paradigm (Gjini *et al.*, 2010; Kisley, Noecker, & Guinther, 2004). During this paradigm, a series of repetitive stimuli are presented to a participant with infrequent deviant stimuli presented throughout. Mismatch negativity is the increase in amplitude of an event-related potential when the deviant stimulus is presented (Sams, Paavilainen, Alho, & Näätänen, 1985). This increase in activity, as with the increase in P50, is purported to represent the 'gating in' of the novel stimulus into working memory. Research into the gating in and out of sensory information has elicited conflicting results, with some suggesting they reflect the

reverse components of the same function (Gjini et al., 2010), while others have found no correlation between the two, implying that they are independent mechanisms (Kisley et al., 2004).

3.1.1. Later MLAERs

Although most research uses the P50 sensory gating ratio or difference, this is just the earliest of the MLAER components. With regards to the broader definition of sensory gating, the concept of gating is likely to be a multistage/multicomponent mechanism (Lebib, Papo, de Bode, & Baudonnière, 2003). Indeed, a study on rats has found that sensory gating is not limited to a single cortical area or ERP (De Bruin et al., 2001). Whereas P50 is purported to be an early preattentive stage of sensory gating, N1, and P2 are later stages reflecting higher order cognitive processes, early attentive and attentive respectively (Kisley & Cornwell, 2006; Gallinat et al., 2002). Typically, N1 is the largest negative deflection occurring between 60-150ms post stimulus onset and P2 is the largest positive deflection between 150-250ms, however different studies report different mean latencies (Boutros et al., 2004; Rentzsch, Jockers-Scherübl, Boutros, & Gallinat, 2008). Boutros and colleagues reported the average latencies as 115ms (N1) and 178ms (P2) (Boutros et al., 2004). A common characteristic of all three MLAERs is that they are exogenous in nature, in that participants are not required to perform any mental task in order for a cerebral response to be observed. Conversely, later ERPs such as P300 or N400 are only brought about during some cognitive task (Anokhin et al., 2007).

In terms of the similarities between the three MLAERs, as with P50, N1 and P2 gating has also been observed in healthy participants (Boutros et al., 1999; Hetrick et al., 1996) albeit to a lesser degree in both N1 and P2 (Rentzsch et al., 2008). They also share the same deficiency in patients with schizophrenia (Clementz & Blumenfeld, 2001), and the

same increase in suppression ratio (less gating) with longer inter-stimulus intervals (De Bruin et al., 2001). Moreover, when comparing the three MLAERs, Fuerst and colleagues found that any amplitude to the first stimulus (S1) in the paired-click paradigm could predict any other S1 amplitude, as well as any of the difference scores (Fuerst, Gallinat, & Boutros, 2007). This relationship amongst the components suggests that they may reflect the same mechanism. However, this may just reflect their joint but functionally different involvement in the same overall sensory gating system.

Conversely, several studies that demonstrate different source localisations (Oranje, Geyer, Bocker, Leon Kenemans, & Verbaten, 2006), a lack of correlation between the different component amplitudes and ratios (Boutros et al., 2004; Davies et al., 2009), and different behavioural indices (Kisley et al., 2004), imply that the components are unrelated and play qualitatively different roles in the gating process. Finally, researchers suggest that N1 and P2 are affected by attentional manipulations compared to P50, which is largely immune to such changes (Jerger, Biggins, & Fein, 1992; Lijffijt et al., 2009; White & Yee, 1997). A more detailed discussion of this argument can be found in chapter six.

3.1.2. Cortical generators of sensory gating

Although these EEG components are primarily recorded at the vertex (electrode Cz) during a conditioning-testing paradigm, researchers have pinpointed more than one cortical location as the possible origin or mediator of the gating process. Using techniques such as EEG source localisation, fMRI, MEG, and intracranial electrodes, researchers have most reliably associated sensory gating with three main areas. One area that has elicited the most conflicting data is that of the hippocampus, or more specifically, the pyramidal cells of CA3 area. It is proposed that cholinergic receptor neurons (afferents) in the area excite inhibitory neurons when sensory input has been received. These inhibitory neurons inhibit for a certain

period of time, the response of the pyramidal cells to any further sensory information coming from the afferents (Miller & Freedman, 1995). Moreover, an fMRI study found gating related hippocampal activation amongst other areas (Tregellas et al., 2007), leading to the conclusion that this area may be the cause of the P50 suppression in normal subjects (Bak et al., 2011). Conversely, several other studies using fMRI and intracranial electrode recordings have failed to find activation in the hippocampus that can be interpreted as the source of P50 suppression (Boutros et al., 2005; Grunwald et al., 2003; Mayer et al., 2009).

The most obvious regions associated with sensory gating are the temporal lobes, or more specifically, the auditory cortex located in the superior temporal gyrus. Several studies have indicated bilateral activation of the auditory cortex as the source of sensory gating (Bak et al., 2011; Boutros et al., 2005; Grunwald et al., 2003; Korzyukov et al., 2007). Others have suggested an asymmetry in temporal lobe activation, with a left hemisphere bias (Mayer et al., 2009; Thoma et al., 2003). However, more complex models of sensory gating propose that the auditory cortex processes basic stimulus properties and may gate basic sensory information when required, but additional and more goal-directed gating processes are generated from the prefrontal cortex (Grunwald et al., 2003; Jensen, Oranje, Wienberg, & Glenthøj, 2008; Mears, Klein, & Cromwell, 2006; Oranje et al., 2006; Tregellas et al., 2007). A fronto-temporal interaction is the most likely generator of sensory gating (Korzyukov et al., 2007). Further support for frontal involvement is that aspects of frontal executive dysfunction appear to correlate with sensory gating (e.g., Boutros et al., 2009) and deficits in sensory gating have been observed in patients and animals with prefrontal lesions (Knight, Staines, Swick, & Chao, 1999; Rosenkranz & Grace, 2001).

3.1.3. Visual evoked potentials

As with the ERP P50 being the more widely researched component in the sensory gating literature, preferential focus is also given to the auditory modality. It has been suggested that this modality bias may be due to the relationship between sensory gating and schizophrenia (Gjini *et al.*, 2008). As a result of schizophrenia being the most common disorder for studying a deficit in sensory gating, and auditory hallucinations being more common in the disorder compared to visual (Mueser, Bellack, & Brady, 1990), this may explain why researchers choose to explore this modality above all others. However, there is evidence both within and outside sensory gating research, which suggests that a similar mechanism might operate in other modalities. Sensory gating in the visual modality has received very limited attention to date, and is the primary focus of this thesis.

The principal visual event –related potentials (VEPs) are C1, P1 and N1, ranging from 50-110msec, 80-150msec, and 140-220msec post-stimulus onset respectively (Barnhardt, Ritter, & Gomes, 2008; Clark & Hillyard, 1996; Foxe & Simpson, 2002). The earliest component C1 has been localised to the primary visual cortex (striate) and is measured primarily at the midline occipital area of the cortex (Clark & Hillyard, 1996; Rossi & Pourtois, 2012). A proposed feature of C1, much like the auditory component P50, is that it is immune to attentional manipulations unlike later VEPs, which is confirmation that C1 solely reflects initial processing in the striate (Di Russo *et al.*, 2003). However, others have found evidence to suggest extrastriate activity contributing to C1 (Clark *et al.*, 1994; Vanni *et al.*, 2004), as well as effects of spatial selective attention (Poghosyan *et al.*, 2005; Proverbio *et al.*, 2010), top-down manipulations (Rauss, Schwartz, & Pourtois, 2011), and perceptual load (Rossi & Pourtois, 2012). Consequently, a more complex model of C1 was proposed, consisting of two separate phases (Foxe & Simpson, 2002). The first is a negative phase occurring around 50-62msec at central parieto-occipital sites, thought to reflect striate activity. The second is a positive phase from 62-80msec at more eccentric parieto-occipital

sites and because extrastriate areas, including frontal regions, have become active by this point, it is suggested that these activations contribute to this later phase of C1.

The component C1 does not have an agreed upon polarity which is most likely a result of its sensitivity to the location of the stimulus. As a result of the retinotopic organisation of the primary visual cortex being that of a cruciform model, stimuli presented to the upper or lower regions of the retina will elicit opposite polarities (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Rauss et al., 2011). Stimuli presented to either part of the visual field will activate the geometrically opposite neurons and thus the observed VEP is of the opposite polarity. Thus, a stimulus presented to the upper visual field will elicit a negative polarity, and a stimulus presented to the lower visual field will elicit a positive polarity.

The later components P1 and N1 are positive and negative deflections respectively, which originate from extrastriate locations (Foxe & Simpson, 2002), and are subsequently measured most reliably at parietal and occipital sites (Barnhardt *et al.*, 2008). Neither component is affected by the location of the stimulus like C1, however research frequently demonstrates effects of attention. Amplitudes for both components are enhanced for attended stimuli compared to unattended stimuli (Anllo-Vento & Hillyard, 1996; Clark & Hillyard, 1996). The P1 attention effects are attributed to ventral-lateral extrastriate occipital cortex (Clark & Hillyard, 1996; Heinze et al., 1994), more specifically, an early P1 (80-110msec) is generated from the lateral occipital cortex, and a late P1 (110-140msec) at ventral occipital locations (Di Russo et al., 2002). The N1 attention effect is considered to have multiple generators and is associated with contralateral occipito-temporal (180msec), occipito-parietal (150msec), and frontal sites (140msec) (Clark & Hillyard, 1996).

With regards to attentional inhibition, fMRI research has suggested that inhibitory effects can be observed in both the striate and extrastriate cortex (Slotnick, Schwarzbach, & Yantis, 2003). In this study, possible attended locations were divided into quadrants with participants focusing upon one quadrant. The inhibitory mechanism functioned to reduce the perception of stimuli that were outside the attended location even within the same quadrant.

However, this degree of inhibition was primarily observed in the striate and not the extrastriate cortex. Inhibition in the extrastriate cortex was only seen for stimuli outside the attended quadrant. The authors proposed that this was due to the receptive fields in the striate being smaller than the in the extrastriate. Thus, receptive fields in the extrastriate are large enough to encompass competing stimuli within close proximity. Under such conditions, the receptive field responds as if only the attended to stimulus is present (Zani & Proverbio, 2009).

These gating responses in the striate and extrastriate are potentially reflected in the C1 and P1 components, respectively (Luck et al., 1994). This study further indicated that a more efficient suppression and activation mechanism is evident in the extrastriate cortex, with P1 reflecting the inhibitory function and N1 the facilitation function (similar to the 'gating in' and 'gating out' mechanisms present in auditory sensory gating). Both mechanisms functioning concurrently will improve the detectability of any target stimulus. This research and that of Slotnick and colleagues, implies a two-stage attention process that requires inhibition as well as facilitation at each stage. The need or capacity for inhibition at each stage may be reliant upon the perceptual load of the environment. Even when a stimulus is meant to be ignored, some activation in response to that stimulus still occurs, indicating that irrelevant stimuli are not always fully prevented from further processing. If this is the case, inhibition of responses to that stimulus must then occur at a later stage (Desimone & Duncan, 1995).

This is consistent with research by Lavie and colleagues, who have observed a robust effect of perceptual load on the perception of irrelevant stimuli (Lavie, 2005; Lavie & Tsai, 1994). When a task is considered to have high perceptual load, either due to the nature of the task (i.e. visual search) or the number of items in that task, participants are more likely (relative to low load tasks) to not notice any task irrelevant stimuli, this is referred to as inattention blindness (Lavie, Beck, & Konstantinou, 2014). Indeed perceptual load effects have been observed in the visual cortex, in both the striate and the extrastriate regions

(Schwartz et al., 2005), and ERP studies demonstrate that these effects can be observed as early as 70–80 ms after stimulus onset (Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009). Research regarding cross-modal interactions and perceptual load has found that, during a high load visual search task, the perception of irrelevant auditory stimuli is suppressed. Conversely, during low load conditions the irrelevant auditory stimulus is more readily perceived (Molley, Griffiths, Chait, & Lavie, 2015). This is evidenced by both behavioural and MEG findings, with perceptual load determining the magnitude of a neural response to stimuli which are irrelevant. It is the limited capacity of perception (discussed in chapter one) that underlies these behavioural and cortical effects, and cross-modal effects of perceptual load indicate a potential central attentional source. With this in mind, research has demonstrated that if perceptual load is high, irrelevant information is more proficiently inhibited at the stage of C1 in the striate cortex. However, when perceptual load is low, some irrelevant information is processed at the earlier perceptual stage and subsequently must be suppressed at later stages in the extrastriate cortex (P1) (Barnhardt et al., 2008; Rossi & Pourtois, 2012).

Similar to auditory ERPs, visual ERP research has also explored a possible frontal generator of the attentional mechanisms observed. There is evidence that there are frontal, top-down influences on the later VEPs (Fu et al., 2009; Proverbio *et al.*, 2010). In order to successfully attend to a stimulus, a mixture of stimulus driven (bottom-up), and goal-directed (top-down) processing is required (Asplund, Todd, Snyder, & Marois, 2010; Corbetta & Shulman, 2002; Desimone & Duncan, 1995). Moreover, some researchers suggest that the earlier C1 component also receives some top-down influence, due to observed contextual effects (Lamme, 1995) and perceptual learning effects (Pourtois et al., 2008) indicated by early activation of the prefrontal regions (Foxe & Simpson, 2002).

As there is evidence to support top-down input from the prefrontal cortex in both auditory and visual inhibition and attentional regulation, it is worth noting research from Oranje and colleagues, which compared the source generators of both auditory and visual

sensory gating (Oranje et al., 2006). While the temporal lobe source associated with auditory gating was not observed during the visual paradigm, both modalities did share a frontal source. This may indicate that sensory gating has a common frontal source that mediates the modality specific sources. A later study provided further support for this by demonstrating that only sensory gating and the frontal source resulted in a substantial correlation (Jensen et al., 2008).

3.1.4. Cross-modal interactions

As the focus of this chapter is the auditory modality as well as the lesser explored visual modality, it is necessary to explore the evidence suggesting that there is the possibility of an amodal sensory gating system. This comes in the form of cross-modality plasticity, cognitive interactions between the modalities, and paradigms that illustrate the effects of visual stimuli on auditory sensory gating (for review see Shimojo & Shams, 2001).

A notable study by Sur and colleagues explored cross-modality plasticity in animals by removing or depriving cortical areas in ferrets at birth, and thereby depriving them of integral areas for processing visual sensory information (Sur, Pallas, & Roe, 1990; Von Melchner, Pallas, & Sur, 2000). When these animals were presented flashes of light, areas normally devoted to auditory information were not only activated during these visual stimulations, but also enabled the animals to perceive the stimuli as visual information. Evidence of cross-modal plasticity had also been found to occur naturally in humans that have been deprived of a particular sensory input early in life. For example, participants who are blind have shown activation in the visual cortices during Braille reading (Sadato et al., 1996).

Interactions between the modalities are not limited to cortical plasticity in early development. A common example of this form of interaction is that of synaesthesia, during

which stimulation of one sensory modality can elicit sensory experiences in another seemingly unrelated modality (Hubbard & Ramachandran, 2005). Additionally, the McGurk effect and ventriloquist effect are examples of when visual information alters auditory perception, and concurrent visual and auditory stimuli can be perceived as occurring together even when there is a significant spatial separation (Bertelson, Vroomen, De Gelder, & Driver, 2000). These effects illustrate the impact visual information can have on the perception of auditory information. However, auditory stimulation can also impact upon visual perception. For example, when participants are presented with a light flash alongside either one or multiple auditory beeps, this single flash is interpreted as multiple flashes when accompanied by the multiple beeps (Shams, Kamitani, & Shimojo, 2000).

As highlighted by Donohue and colleagues, these cross-modal interactions arise due to the mechanisms required to integrate information from multiple sensory organs into one multisensory event when appropriate (Donohue, Appelbaum, Park, Roberts, & Woldorff, 2013). When the sources of each sensory input are spatially and temporally distinct, these mechanisms should separate these sources into discrete representations. However, these mechanistic interactions can be altered by the compatibility and temporal arrival of each sensory input, as well as the attention allocated to a particular event.

The examples of cross-modal interactions describe above are likely to arise after considerable encoding of each of the sensory inputs, after some higher level processing related to the integration of stimulus features. This is beyond the lower level processing investigated in this thesis, with sensory gating likely occurring at an early stage of stimulus encoding. This being said, the incorporation of visual stimuli into a standard auditory sensory gating paradigm has been shown to alter the auditory gating observed. A decrease in the gating effect has been found when concurrent visual stimuli are presented during the sensory gating procedure, either using random flashes of light (Jin & Potkin, 1996), a continuous visual scene (Moran et al., 2012), or audiovisual speech (Lebib et al. 2003).

Taken together, if the processing of one sensory modality can be influenced by another, and that the early processing reflected in sensory gating may also share this cross-modal effect, it is possible that sensory gating indicates a shared mechanism or converging mechanism, rather than distinct and separate systems within each of the primary sensory cortices. One aim of this chapter is to elucidate the similarities and/or differences between auditory and visual sensory gating, in order to help answer the question of a possible shared mechanism. However this thesis can only address this question from a functional point of view rather than a cortical source perspective.

3.1.5. Visual sensory gating

As discussed above, with regards to sensory gating, some findings have illustrated a cross-modal effect on the P50 ratio. When visual stimuli are integrated into a standard auditory sensory gating paradigm, not only is successful gating still observed when the auditory and visual stimuli are congruent, but an incongruent audiovisual stimulus can augment the auditory gating ratio (Lebib *et al.*, 2003). This was interpreted as the increase in cerebral response to concurrent visual stimuli that are not redundant, i.e. provides information that is different to the auditory stimulus. Although activation in the temporal lobes during auditory sensory gating is not found during visual sensory gating, both forms of gating do share common activation in the frontal lobes (Oranje *et al.*, 2006), an area suggested to mediate the sensory gating process (Bak *et al.*, 2011; Edgar *et al.*, 2005).

Despite this, very few studies have explored the visual equivalent of auditory sensory gating. An early study by Domino and colleagues used a photostimulator lamp to present light flashes to patients with schizophrenia and controls (Domino, Demetriou, Tuttle, & Klinge, 1979). They examined all noticeable components at several central and occipital electrode sites. Although they were not investigating the potential attenuation of responses

to repeated stimuli, this research illustrated that at central locations similar to auditory sensory gating research, responses around 50ms post-stimulus onset (referred to as primary waves) were weak, whereas secondary waves with latencies greater than 80ms were more prominent. Additionally, these secondary waves were more associated with the occipital sites. Later research on a possible visual gating mechanism, investigated the difference in cerebral response to attended and unattended stimuli (Oakley & Eason, 1990). Again, they found the response occurring around 50ms to have a small amplitude compared to latencies beyond 100ms. They also found this early component to be more negative in amplitude towards attended stimuli in contrast to the positive amplitude observed in auditory sensory gating. However, because they found attention effects in both components, the authors suggest this is evidence of an early visual gating mechanism. It is important to note that these attention effects were not observed at the central or posterior electrode sites, which is in keeping with research suggesting that early components are not affected by attentional manipulations when measured from the typical sensory gating electrode locations.

Only four studies have explored the possibility of visual sensory gating using a standard conditioning-testing paradigm. One of these used this paradigm for both the visual and auditory modality, and found the typical auditory sensory gating but failed to observe any visual sensory gating (Adler, Waldo, & Freedman, 1985). This study again used a light flash as the visual stimulus with the same inter-stimulus and inter-trial interval for both modalities. The methodological difference between each modality occurred at the analysis stage, for which the ERP P50 at electrode Cz was analysed for the auditory paradigm, but later components (N90 – P30) at electrode Oz (occipital) were used for the visual paradigm. Although this was based on the known auditory and visual evoked potentials (AEPs and VEPs), it reduces the potential to make direct comparisons between the modalities, and is based on the notion of separate but functionally similar mechanisms rather than a joint mechanism.

The only other study that used an auditory and visual variant of the same task did find successful P50 gating in both modalities (Oranje et al., 2006). This study incorporated a sensory gating paradigm into a pre-pulse inhibition paradigm, using a dot of white light as the visual stimulus. Components P50 and N1 were analysed at the same electrode site for each modality (Cz). Although they found P50 gating in both modalities, the P50 amplitude was smaller for the visual stimuli. Moreover, N1 gating was only observed during the auditory modality.

More recent research into a visual sensory gating mechanism has not made the comparison with a comparable auditory paradigm. Gjini and colleagues used pairs of centrally located white circles on a black background and investigated possible gating of components N75, P1, and N1 at occipital electrodes (Gjini, Sundaresan, & Boutros, 2008). They observed a significant gating effect for components P1 and N1. The authors suggested that the difference in results compared to the earlier research conducted by Adler, may be due to participants in Adler's study having closed eyes throughout and the difference in location of the electrodes analysed.

The most recent research exploring visual sensory gating used black and white checkerboard and red circle stimuli rather than the flashes of light/white circles used before (Gawne *et al.*, 2011). This research also presented spatially separate stimuli that were not centrally located, and used much shorter inter-stimulus and inter-trial intervals. When analysing the first most prominent positive component (P1) at occipital electrode sites, the authors found evidence for gating even when the type or location of the stimulus changed. They interpreted this as demonstrating that the visual evoked potential simply indicates that a stimulus was presented, and any additional stimuli presented within a certain timeframe will fail to elicit an additional cerebral response.

These studies highlight a lack of consistency with both methodology and analytic techniques when investigating visual sensory gating. Thus, it is essential to conduct research with a comparable method for both visual and auditory modalities, in order to

ensure a like for like comparison. Furthermore, a more comprehensive form of analysis is required, by examining additional electrode positions and components, which again may allow for a more like for like comparison between the modalities. Therefore, the aim of this chapter is to determine: 1) if sensory gating can be observed within the visual modality. Previous research indicates that visual gating can be found, but this gating is not as robust compared to the auditory modality; 2) if the gating between modalities is maximal at the same latency window and electrode location. It is hypothesised that auditory gating will be maximal at electrode Cz, but will likely be observed to the same degree at both early and mid-latency components. Visual gating however, may show maximal gating at occipital electrodes and due to discrepancies within the literature, and the nature of the primary visual cortex, it is possible that this gating will not be found for the earliest latency window. Furthermore, cross-modal interactions both within and outside the field of sensory gating, suggest that significant similarities and/or correlations will be found between the two modalities.

3.2. *Design*

This experiment employed the procedures of an auditory (section 2.2.1.) and a visual (section 2.2.2.) sensory gating paradigm. For full methods, see chapter two. The amplitudes of each stimulus presentation for each electrode and component was used to explore the presence of sensory gating. In line with published research (Clementz *et al.*, 1998; Karns & Knight, 2009), location clusters were used instead of individual electrodes. Amplitudes in response to stimulus 1 and 2 for electrodes C1, Cz, and C2 were averaged to signify a central electrode site, electrodes P1, Pz, and P2 for parietal, and finally, O1, Oz, and O2 for occipital.

To explore where sensory gating can be observed, a 2x2x3x2 within-subjects ANOVA was conducted with the factors modality (auditory/visual), location (central/parietal), component (P50/C1, N1/P1, P2/N1) and stimulus (S1/S2). Note that the component variable includes each component for each of the modalities despite being different. This is to compare the degree of sensory gating observed in the early and two mid-latency ERPs within and between each modality. Interactions were explored with further ANOVAs and Bonferroni corrected comparisons. Following this, the sensory gating ratio (S2 amplitude/S1 amplitude) was calculated for the components and locations which demonstrated significant gating in order to investigate the magnitude of the sensory gating and find out where the maximal gating may be observed. This analysis was repeated using the latency of the response rather than the amplitude in order to explore any differences between the first and second stimulus response within and between the auditory and visual modality. Finally, a bivariate correlation was conducted on the components and locations which demonstrated significant sensory gating. Cross modality correlations were used to explore the possibility of a shared mechanism for the visual and auditory gating mechanism. If gating is observed for a component at multiple location, within modality correlations will help to verify that this is likely the same component being measured at different electrodes. Furthermore, this may reveal a relationship between the components. These were not corrected for multiple correlations due to the focus on the effect size, which are more informative with correlational data.

3.3. Results

3.3.1. Spatial and temporal features of sensory gating

The average ERP waveforms for both modalities can be seen in Figure 3. The results of the 2x2x3x2 ANOVA reveal a main effect of stimulus ($F(1, 19)=73.26, p<.001, \eta^2=.79$), with the

amplitude of the stimulus 1 response (Mean=4.95 μ V, SE=0.37) being significantly larger than stimulus 2 (Mean=2.56 μ V, SE=0.18). This illustrates that overall, significant sensory gating was observed. There was a significant interaction between the stimulus factor and modality ($F(1, 19)=49.43$, $p<.001$, $\eta^2=.72$), location ($F(1, 19)=10.61$, $p=.004$, $\eta^2=.36$), and component ($F(2, 38)=59.87$, $p<.001$, $\eta^2=.76$), indicating that successful gating was not observed for all locations and components. However, there was also a significant four-way interaction between each of the factors ($F(2, 38)=4.43$, $p=.018$, $\eta^2=.19$). In order to explore this interaction, two separate ANOVAs were conducted for the auditory and visual modality. Moreover, separate ANOVAs allows the inclusion of the occipital location within the visual analysis.

For the auditory modality, a 2x3x2 within-subjects ANOVA was used with the factors location (central/parietal), component (P50/N1/P2), and stimulus (S1/S2), the results of which reveal a significant main effect of stimulus ($F(1, 21)=78.65$, $p<.001$, $\eta^2=.79$), with the amplitude of the stimulus 1 response (Mean=7.11 μ V, SE=0.58) being larger than the stimulus 2 response (Mean=2.93 μ V, SE=0.26). This indicated that successful gating was observed for the auditory modality. There were significant interactions with the stimulus factor and location ($F(1, 21)=11.96$, $p=.002$, $\eta^2=.36$) and component ($F(2, 42)=61.8$, $p<.001$, $\eta^2=.75$), however there was also a significant three-way interaction between all factors ($F(2, 42)=8.02$, $p<.001$, $\eta^2=.28$). To further investigate this interaction, an ANOVA was conducted for each location within the auditory modality, resulting in two ANOVAs with the factors component (P50/N1/P2), and stimulus (S1/S2) for the central and parietal locations, results can be seen in Figure 4. The results for the central location, again demonstrate a significant effect of stimulus revealing that successful gating was observed overall within the central location ($F(1, 23)=54.77$, $p<.001$, $\eta^2=.70$). A significant interaction between stimulus and component was observed ($F(2, 46)=43.63$, $p<.001$, $\eta^2=.66$), for which Bonferroni corrected t -tests ($p=.016$) show that the amplitude of the response to stimulus 1 was significantly larger than the response to stimulus 2, for all three components

P50 ($t(23)=5.17$, $p<.001$), N1 ($t(23)=6.76$, $p<.001$), P2 ($t(23)=7.28$, $p<.001$). The results for the parietal location are much the same, with a significant effect of stimulus ($F(1, 22)=60.04$, $p<.001$, $\eta^2=.74$), and a significant interaction between stimulus and location ($F(2, 46)=37.96$, $p<.001$, $\eta^2=.64$). Again, Bonferroni corrected t -tests ($p=.016$) indicate that the amplitude of the S1 response was significantly larger than the S2 response for all three components (P50 – $t(22)=2.60$, $p=.016$; N1 – $t(22)=6.51$, $p<.001$; P2 – $t(22)=7.49$, $p<.001$).

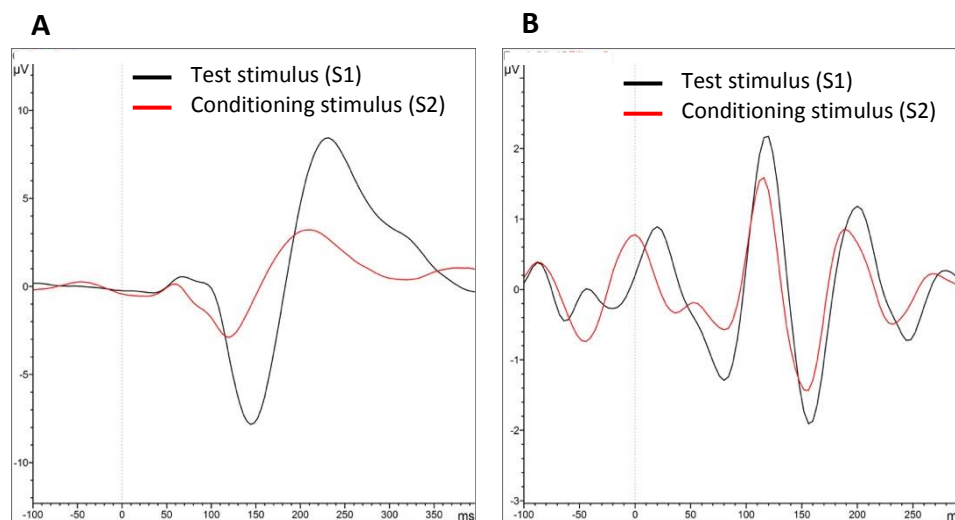


Figure 3. Average ERP waveforms. Panel A – waveform from the auditory paradigm for electrode Cz. Panel B – waveform from the visual paradigm for electrode Pz.

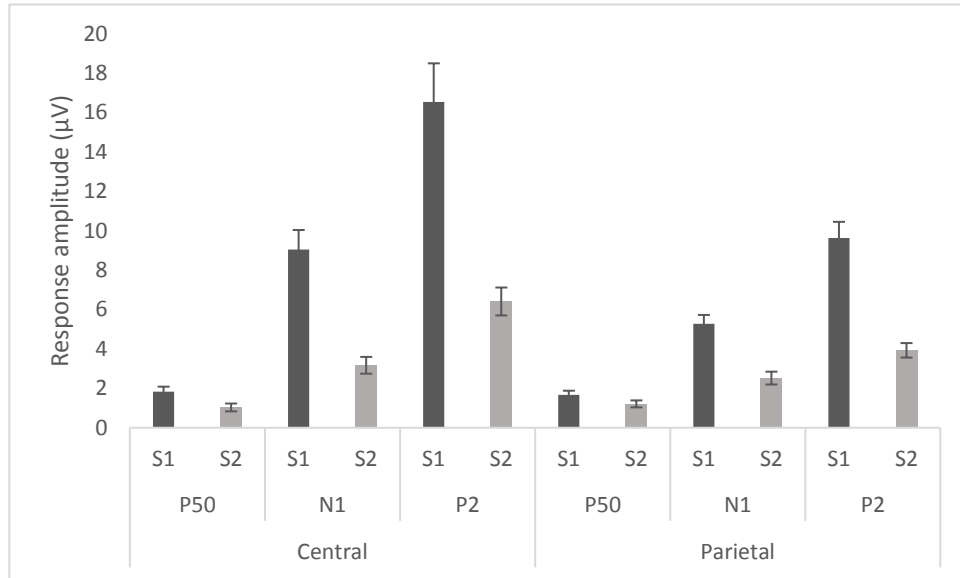


Figure 4. Average response amplitude to the first and second stimulus presentation for the auditory modality. Error bars represent the standard error. Differences between the S1 and S2 amplitudes were statistically significant for all component in both locations.

The same analysis was conducted for the visual modality. A 3x3x2 within-subjects ANOVA was employed with the factors location (central/parietal/occipital), component (C1/P1/N1), and stimulus (S1/S2). The results revealed a significant effect of stimulus ($F(1, 18)=10.66$, $p=.004$, $\eta^2=.37$), with the amplitude of the stimulus 1 (Mean= $4.59\mu V$, $SE=0.34$) responses being significantly larger than stimulus 2 (Mean= $3.81\mu V$, $SE=0.31$) and thus indicating successful sensory gating overall for the visual modality. The interactions between the stimulus factor and all other were nonsignificant ($p>.05$), however further analysis was conducted to ascertain if any locations and/or components within the visual modality did not show a significantly larger stimulus 1 response. Three 3x2 ANOVAs were conducted for each of the locations, central, parietal, and occipital, with the factors component (C1/P1/N1), and stimulus (S1/S2), these results can be seen in Figure 5. The results for the central location revealed a significant effect of stimulus ($F(1, 21)=7.85$, $p=.011$, $\eta^2=.27$) and a significant interaction between stimulus and component ($F(2, 42)=7.15$, $p=.002$, $\eta^2=.25$). Three Bonferroni corrected t -tests ($p=.016$) showed that the stimulus 1 response was

significantly larger than stimulus 2 for the N1 component only ($t(22)=2.65$, $p=.015$), however the P1 component was approaching significance ($t(22)=2.45$, $p=.023$). The results for the parietal location demonstrate that gating was observed overall for this location, with a significant effect of stimulus ($F(1, 22)=8.07$, $p=.010$, $\eta^2=.27$; S1 – Mean=3.7 μ V, SE=0.33; S2 – Mean=3.11 μ V, SE=0.3). A significant interaction between stimulus and component was again observed ($F(2, 42)=6.02$, $p=.005$, $\eta^2=.22$), for which Bonferroni corrected t -tests show that significant gating was observed for the P1 component only ($t(22)=4.12$, $p<.001$). For the occipital location, there was a significant effect of stimulus ($F(1, 20)=8.51$, $p=.009$, $\eta^2=.30$; S1 – Mean=7.87 μ V, SE=0.69; S2 – Mean=6.69 μ V, SE=0.56), however the interaction with component was not significant. The three Bonferroni corrected t -tests revealed that again, the significant effect of gating, as reflected in a larger stimulus 1 amplitude compared to stimulus 2, was only observed for the P1 component ($t(21)=3.98$, $p=.001$).

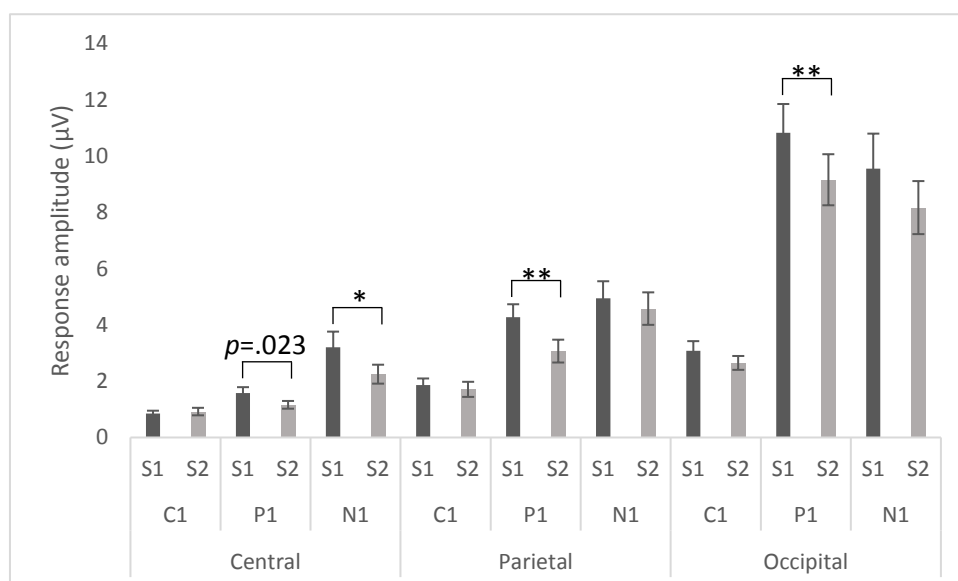


Figure 5. Average response amplitude to the first and second stimulus presentation for the visual modality. Error bars represent the standard error. * sig. to .016 ** sig. to .001.

3.3.2. Maximal gating observed

The above findings indicate that successful sensory gating was observed for all components and at all locations for the auditory modality, but in the visual modality, gating was only seen for the P1 component at the parietal and occipital locations, and the N1 component at the central location. In order to explore the differences in the magnitude of gating observed further tests were conducted using the gating ratio, with a smaller ratio indicating more gating. Descriptives for individual components and locations can be seen in Table 3.

As all components and locations revealed significant gating in the auditory modality, a 2x3 within-subjects ANOVA was conducted with the factors location (central/parietal) and component (P50/N1/P2). Two significant effects for location and component were found. The significant effect of location ($F(1,22)=10.54$, $p=.004$, $\eta^2=.32$), after corrected pairwise comparisons, indicates that more gating was observed at the central location (Mean=46.17, SE=4.38) compared to the parietal location (Mean=61.59, SE=5.24; $p=.004$). Moreover, there was a significant effect of component ($F(2,44)=4.07$, $p=.024$, $\eta^2=.16$) although corrected pairwise comparisons indicated that there was no significant difference between any of the three components. To explore this further, two t -tests were carried out between P50 and N1 at both the central and parietal locations. Tests were not performed between P50 and P2 as the means were almost identical between N1 (40.99) and P2 (40.39). These tests revealed that there was significantly more gating of the mid-latency component (Mean=40.99, SE=4.88) than the early component P50 (Mean=59.49, SE=8.6), but only at the central location ($t(23) = 2.24$, $p=.035$, $r=0.26$). There was no significant difference between the components at the parietal location. Although more gating was observed for the mid-latency components, this may be due to the larger amplitudes exhibited by N1 and P2 compared to P50. A 2x3 ANOVA conducted on the amplitude of the response to the first stimulus presentation conveys a significant effect of component ($F(2,36)=63.42$, $p<.001$, $\eta^2=.78$). The results shown in Figure 6 demonstrate that there was a significant

difference in amplitude size between all of the components, with P50 having average amplitude of less than 2 μ V. Note that the inverse of the N1 amplitude was used in order for a comparison of the magnitude.

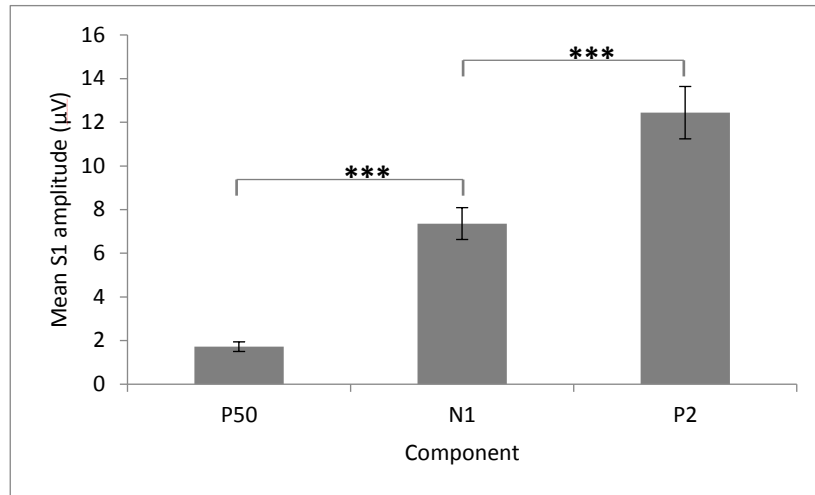


Figure 6. Mean amplitude (μ V) of the response to the first stimulus presentation in the auditory modality for components P50, N1 and P2. Absolute values were used for the negative component N1. *** is sig. to .001.

As successful gating was only found in the visual modality at certain components and locations, to explore the maximal visual gating, an ANOVA was conducted with the factor location (central/parietal/occipital) for just the P1 component. There was a significant effect of location ($F(2,44)=3.84$, $p=.029$, $\eta^2=.15$), and Bonferroni corrected pairwise comparisons indicate that there was a significant difference between the parietal and occipital locations ($p=.010$), with the parietal location exhibiting more gating. These results are summarised in Figure 7. As the N1 component at the central location also exhibited significant gating, two t -tests were conducted comparing the gating observed at the central N1 component with both the parietal and occipital P1 components. The results revealed no significant difference in the magnitude of gating.

Table 3

Average sensory gating ratio for ERP components P50, N1, and P2 for the auditory modality, and C1, P1, and N1 for visual.

Modality	Location	Component	Gating ratio (SD)
Auditory	Central	P50	57.33 (41.71)
		N1	39.29 (22.89)
		P2	38.63 (11.2)
	Parietal	P50	74.52 (48.84)
		N1	50.3 (35.48)
		P2	50.37 (39.85)
Visual	Central	C1	111.21 (52.44)
		P1	90.45 (48.67)
		N1	81.26 (37.6)
	Parietal	C1	92.37 (46.59)
		P1	73.78 (32.1)
		N1	98.88 (44.26)
	Occipital	C1	99.97 (46.83)
		P1	84.14 (22.6)
		N1	100.82 (44.14)

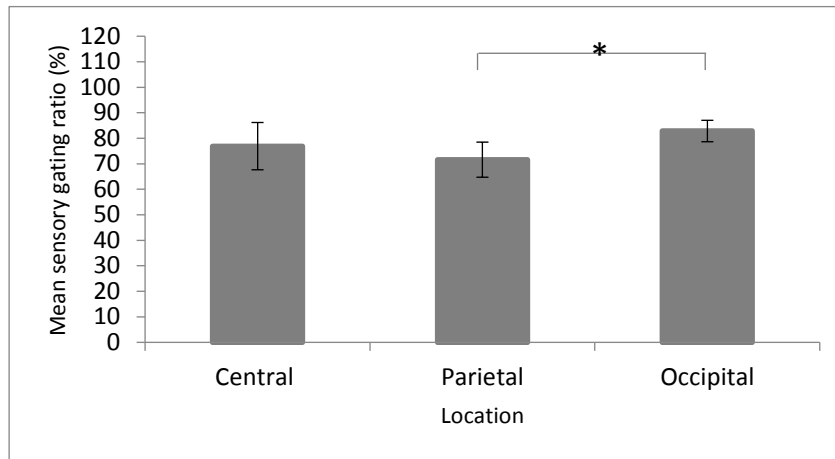


Figure 7. Mean sensory gating ratio for the three locations in the visual modality for the component P1. * is sig. to 0.05.

3.3.3. Lateralisation

In order to explore any possible lateralisation of sensory gating, another combination of electrode clusters was used, separating the data into left, centre, and right electrode sites. A 2x3x3 within subjects ANOVA was employed using the gating ratio with the factors modality (auditory, visual), location (left, centre, right), and component (P50/C1, N1/P1, P2/N1). Results revealed a main effect of component a before ($F(2,40)=4.67$, $p=.015$, $\eta^2=.20$), however there was no longer a significant effect of location or interaction with the location factor ($p>.1$). In order to confirm that no effect of location was found and that the results were not disproportionately affected by less gating in the visual modality, two separate ANOVAs were conducted for each modality with the factors location (left, centre, right), and component (P50/C1, N1/P1, P2/N1). For both modalities there was again a significant effect of component (Auditory – $F(2,42)=3.44$, $p=.041$, $\eta^2=.14$; Visual – $F(2,42)=2.56$, $p=.048$, $\eta^2=.10$) but no effect of location, nor interactions with location ($p>.1$).

3.3.4. Latency

The latency in ms was recorded for each component and averaged across participants. The mean latency for the three ERPs in each modality can be seen in Figures 8 and 9. The average mean latency for each component is within the time range discussed in the literature. In order to explore the difference between the first and second stimulus latencies, two repeated measures ANOVAs were conducted for each modality, with the variables of location (central/parietal/occipital for the visual test), component (P50/C1, N1/P1, P2/N1), and stimulus (stimulus 1, stimulus 2). Both results reveal a significant effect of stimulus (Auditory - $F(1,22)=78.26$, $p<.001$, $\eta^2=.78$; Visual - $F(1,21)=22.88$, $p<.001$, $\eta^2=.52$), indicating that the second presentation of the stimulus elicited a cerebral response quicker than the first presentation. The average difference between the first and second stimulus presentation was 14.14ms for the auditory paradigm, and 10.62ms for the visual.

For the auditory paradigm, no significant interaction between stimulus and component was found, suggesting that the shorter latency for the second stimulus was present across all components. However, a significant interaction between stimulus and location was observed ($F(1,22)=5.46$, $p=.029$, $\eta^2=.20$), implying that the effect of stimulus type on the latency is dependent upon the location. To compare the stimulus one latency with the stimulus two latency; six paired-samples t -tests were carried out for each component at each location. After correcting for multiple comparisons ($p=.008$), the results show that the shorter latency for the second stimulus was only apparent at the parietal location for component P2 ($t(22)=5.92$, $p<.001$), conversely, all components showed this pattern at the central location (P50 – $t(23)=5.20$, $p<.001$; N1 – $t(23)=4.90$, $p<.001$; P2 – $t(23)=6.57$, $p<.001$).

The visual paradigm elicited different results from the auditory. There was no significant interaction between stimulus and location, but there was a significant interaction

between stimulus and component ($F(1.44,30.16)=3.69$, $p=.050$, $\eta^2=.15$). There was also a significant three-way interaction ($F(4,84)=3.34$, $p=.014$, $\eta^2=.14$). In order to explore this interaction further, three 3x2 repeated measures ANOVAs were conducted with the variables component and stimulus, to compare the component and stimulus interaction at each of the three locations. At the central location, there was no significant effect of stimulus type, however it was approaching significance ($p=.055$). Thus the pattern of a shorter latency for the second stimulus presentation was not produced at the central sites. At the parietal and occipital locations, there was a significant effect of stimulus (parietal - $F(1,23)=26.35$, $p<.001$, $\eta^2=.46$; occipital - $F(1,22)=5.46$, $p=.029$, $\eta^2=.53$), with the expected trend of stimulus 1 eliciting a longer latency than stimulus 2. However, there was also a significant interaction between component and stimulus for each location (parietal - $F(2,44)=4.72$, $p=.014$, $\eta^2=.18$; occipital - $F(1.67,38.4)=6.61$, $p=.005$, $\eta^2=.22$). To ascertain which components were exhibiting the effect of stimulus type, t -tests were used for both the parietal and occipital locations, comparing stimulus one and two for each component. After adjusting for multiple comparisons, C1 did not show a significant difference between stimulus one and two, however components P1 (parietal - $t(22)=3.57$, $p=.002$, $r=0.29$; occipital - $t(23)=5.47$, $p<.001$, $r=0.17$) and N1 did (parietal - $t(22)=3.79$, $p=.001$, $r=0.37$; occipital - $t(23)=4.27$, $p<.001$, $r=0.35$). Thus, the reduction in latency for stimulus two was only observed in the mid-latency components at the parietal and occipital locations. This is in contrast to the auditory results, which indicated that this pattern was apparent mostly in the central location, and was also observed for the early component P50.

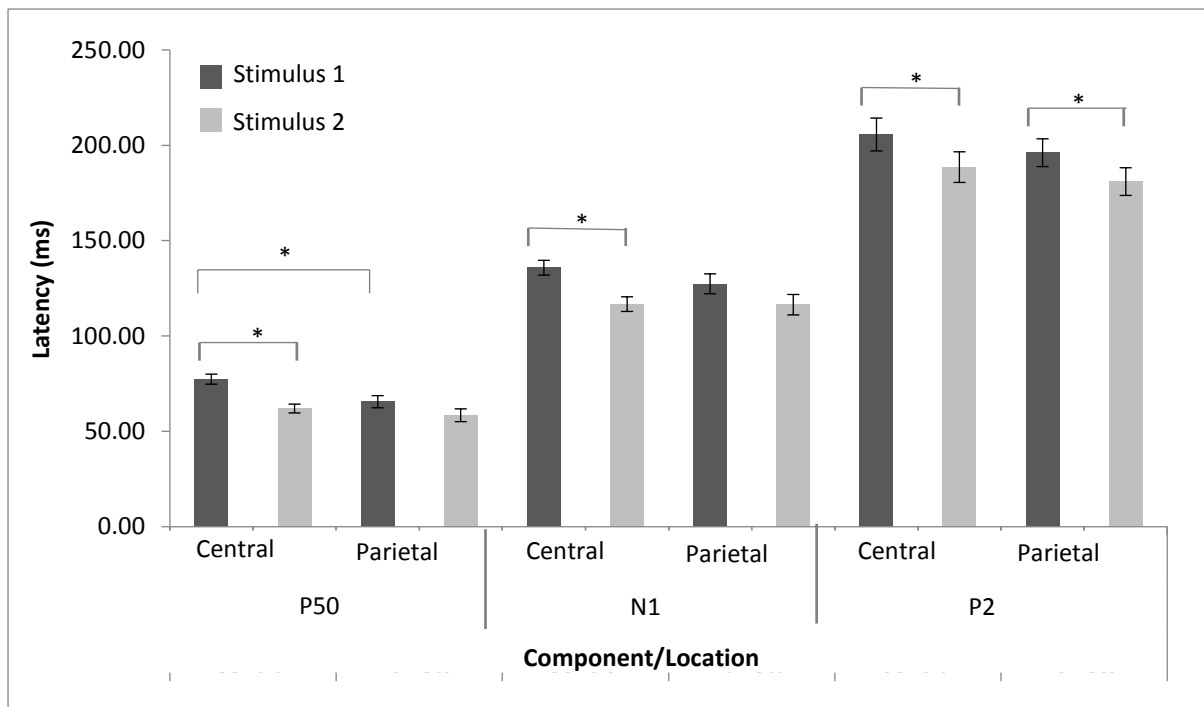


Figure 8. Average peak latency (ms) of the auditory modality ERPs, in response to the first a second stimulus presentations. Latencies for components P50, N1, and P2 at the two locations, central and parietal. * is sig. to 0.05.

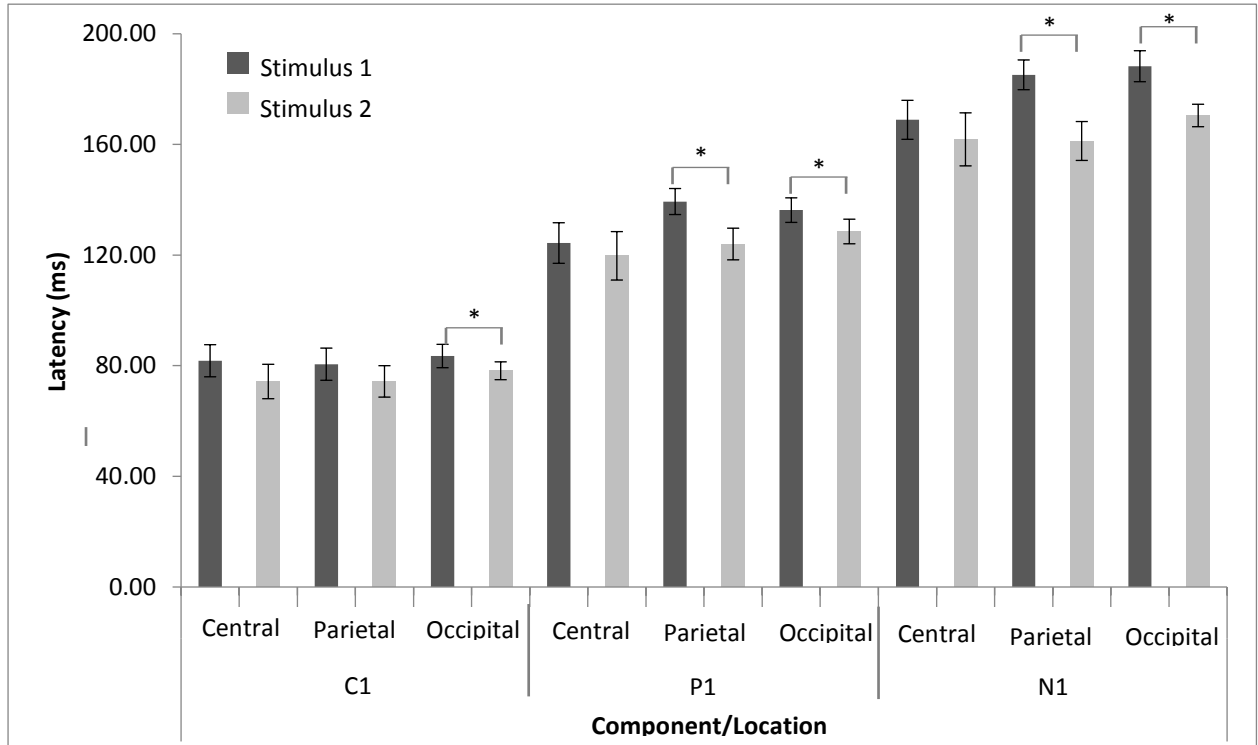


Figure 9. Average peak latency (ms) of the visual modality ERPs, in response to the first a second stimulus presentations. Latencies for components C1, P1, and N1 at the three locations, central, parietal, and occipital. * is sig. to 0.05.

3.3.5. Within and between modality correlations

A bivariate correlations was used to explore the relationships between the components within each modality (for results see Table 4). The analysis was only conducted on using the components and location that demonstrated significant gating. In the auditory modality, the significant correlations were between the same components from different locations. P50, N1, and P2 all showed significant correlations between the central and parietal locations. Additionally, there were two significant correlations between the two mid-latency components. The visual modality elicited comparable results, in that the P1 component correlated with the same component from another location, there was a significant correlation between the parietal and occipital locations. The correlations between the modalities were generally low and nonsignificant.

Table 4

Bivariate correlation results for both the auditory and visual paradigms. r value for each comparison of electrode location and component. Correlation were conducted using the sensory gating ratio.

			Auditory						Visual		
			Central			Parietal			Central	Parietal	Occipital
			P50	N1	P2	P50	N1	P2	N1	P1	P1
Auditory		P50	xxxx	0.35	0.21	0.68***	0.07	-0.25	0.42	-0.32	-0.4
	Central	N1		xxxx	0.61**	0.17	0.73***	-0.12	0.29	-0.35	-0.46
		P2			xxxx	0.11	0.46*	0.43*	0.14	-0.18	-0.16
		P50				xxxx	0.04	-0.11	0.03	-0.15	-0.19
	Parietal	N1					xxxx	0.17	0.04	-0.32	-0.23
		P2							xxxx	-0.27	-0.19
Visual	Central	N1							xxxx	0.37	-0.01
	Parietal	P1								xxxx	0.70***
	Occipital	P1									xxxx

Note. * sig. to .05, ** sig. to .01, and *** sig. to .001.

3.3.6. Summary of main findings

Significant sensory gating was found for all components and locations within the auditory modality, this is in contrast to the visual modality which only showed significant gating at component P1 (parietal and occipital) and N1 (central), thus indicating more robust gating for the auditory modality. Within the auditory modality, more gating was found in the central location and for the 2 mid-latency ERPs, although the increase gating for the later ERPs may

be the result of larger amplitudes compared to the early P50 component. Within the visual modality, only the component P1 showed significant gating at multiple locations, with the parietal location eliciting the most. Within both modalities, there was a significant effect of stimulus, in that the second stimulus elicited a longer latency compared to the first. The auditory paradigm showed this pattern of results for all components at the central location, whereas the visual paradigm demonstrated this at the parietal and occipital locations, and only for the later components (P1 and N1). There were no significant correlations between the two modalities, however a similar pattern of within modality correlations was observed. For components that demonstrated significant gating, there was a significant correlation for this component between the different locations, in addition to correlations between the 2 mid-latency ERPs for the auditory modality.

3.4. Discussion

The aim of this chapter was to ascertain if sensory gating exists within the visual modality and to investigate which visual ERPs demonstrate gating most reliably and at which electrode locations. Moreover, by comparing these findings with that of the auditory modality it was hoped that insight into commonalities/differences across the modalities of input might be revealed, thereby clarifying the extent to which these mechanisms are qualitatively similar or if they are indeed the same mechanism.

3.4.1. Auditory sensory gating

The results from the auditory paradigm show that, as expected, sensory gating can be observed at electrode Cz for component P50. However, gating was also found for other

components and at other central, parietal, and occipital sites, although the amount of gating observed overall was around 50% and not as low as other papers have reported (Potter *et al.*, 2006). With regards to the component P50, the average latency was 73ms, which falls within the typical time frame observed in previous research (Grunwald *et al.*, 2003). The components N1 and P2 also had typical latencies in this research, 127ms and 183ms respectively (Boutros *et al.*, 2004; Rentzsch *et al.*, 2008). As well as gating being observed as expected, the most effective gating was found at the central location compared to parietal, which again is in keeping with the literature. However, this research found more gating for the later components N1 and P1, contradicting other studies stating that less gating is observed for these components (Hetrick *et al.*, 1996; Kisley *et al.*, 2004). Regardless of component, this first experiment confirms previous studies that auditory sensory gating can be reliably observed and is more pronounced at central electrode sites such as Cz. Finally, there was no lateralization of auditory sensory gating, which together with the stronger gating at the central location (electrodes C1, Cz, and C2), is in keeping with the weight of published literature favouring bilateral activation of the auditory cortex as the source of sensory gating (Bak *et al.*, 2011; Boutros *et al.*, 2005). The purpose of this chapter was to ascertain the electrode location at which the maximal sensory gating could be observed and that this does not indicate the location of the underlying cortical sources.

It is important to note at this point that there is a limitation to what one can infer based on components observed at certain electrode locations. As discussed in section 2.2., due to the diffuse nature of volume conduction, each cortical source will propagate its signal to multiple neighbouring electrodes. Moreover, components measured at each electrode are likely to be the product of several cortical sources converging. Without source localisation, inferences regarding the difference in gating at different locations is limited. It is not surprising that electrodes C1, Cz, and C2 for example, produce similar components. This being said, this thesis does not investigate the cortical generators of the components, but rather discusses the electrode location of the optimal sensory gating response. Therefore,

although the gating response in itself is likely to have multiple cortical generators and be present at multiple electrodes, it is still prudent to know where the maximal gating response can be observed and how this compares across modalities, but there is a limit to how much one can infer from this, the shared or distinct sources of the gating across modalities.

3.4.2. Visual sensory gating

Sensory gating in the visual modality was not as pronounced as in the auditory modality, with an average ratio of 75% and far fewer significant findings. A potential reason for reduced sensory gating in the visual modality may be that participants are exposed to additional environmental visual stimulation beyond that incorporated within the experimental design. In the standard auditory gating procedure used in this study, participants sat in a sound attenuated room and thus the only sounds they were exposed to were the stimuli coming from the headphones. In contrast to this, although the study was conducted in a darkened Faraday cage, the visual procedure allowed participants to see more than the screen in front of them in their periphery. Even though they were instructed to maintain their gaze on the centre of the screen, they were still able to see the surrounding area and thus process it. This additional stimulation which did not occur in the auditory modality may account for the reduction in sensory gating. In support of this, studies that have used more complex stimuli or additional stimuli to closer mimic the perceptual experiences in the real world, have found that gating is reduced in these conditions compared to standard auditory gating paradigms (Jin & Potkin, 1996; Moran et al., 2012). A way to avoid this would be to have participants close their eyes and present flashes of light as stimuli. However, when earlier visual sensory gating studies have had participants close their eyes, gating effects were not observed (Adler et al., 1985). Moreover, this would increase the amount of alpha band frequency and potentially mask the later components which are best observed at a

similarly low frequency (Cardenas, Gill, & Fein, 1997). It would be interesting to see if restricting the participants' view to only the black screen would enhance the gating effects within the visual modality, in order to establish if the additional visual stimulation described above attenuates visual sensory gating. This experimental manipulation may result in a visual sensory gating ratio comparable in magnitude to that observed during the auditory paradigm.

With regards to the visual evoked potentials examined in this study, all the latencies were as expected based on the literature, with an average latency for the ERPs C1, P1, and N1 of 80ms, 130ms, and 174ms (Barnhardt, *et al.*, 2008; Foxe & Simpson, 2002). If there are indeed two parts to the C1 component, the latency and negative amplitude of C1 in this study would not coincide with the proposed characteristics of C1, as this negative component should have occurred before 62ms (Foxe & Simpson, 2002). However, the early study by Domino and colleagues (1979) found that there were stronger responses to a visual stimulus after 80ms, which is consistent with the latency of the C1 component in this research. Additionally, no gating was found for the C1 ERP, although this may be due to the perceptual load of the task used. The conditioning-testing paradigm used in sensory gating research has an arguably low perceptual load, and thus irrelevant information is not inhibited at the earliest stages of processing in the visual cortex (Rossi & Poutois, 2012). As a result, the second identical stimulus may have still been processed before being inhibited at a later stage. In fact, the results indicate that there was significant gating of the later components P1 and N1.

The component P1 demonstrated gating at the parietal and occipital locations while approaching significance at the central location, conversely, N1 showed gating at central site only. The P1 ERP purportedly represents visual processing in the extrastriate cortex and is therefore typically measured at the parietal and occipital electrode sites (Barnhardt *et al.*, 2008). However, when comparing the difference in sensory gating at the three locations,

there was significantly more P1 gating at the parietal location compared to the occipital. The fact that the N1 ERP demonstrated gating only at the central location is surprising for this visual task. We would expect to observe all of these mid-latency visual ERPs, and any subsequent gating, primarily at the parietal and occipital locations. Furthermore, the magnitude of the N1 gating was comparable to that of P1. Taken together, these results indicate that the most reliable component to demonstrate visual sensory gating is the P1 ERP, and the most pronounced gating response (irrespective of amplitude) for this component is at the parietal locations. Again there was no lateralization of the sensory gating for the visual modality.

With regards to published research on visual sensory gating, these data suggest that sensory gating does occur within the visual modality, which is in contradiction with earlier research by Adler and colleagues (1985), who only observed auditory sensory gating. Although their research used electrode Oz for analysis, they did use different VEPs which may explain why they failed to find any gating. The authors also requested participants to close their eyes throughout the procedure, which is most likely the reason for no observable gating as visual processing would have been limited. Similar to the present study, subsequent research has found successful visual sensory gating. The present study replicates several previous findings such as reduced visual gating compared to auditory (Oranje *et al.*, 2006), gating for the VEPs P1 and N1 but not earlier (Gjini *et al.*, 2008), and gating of the P1 VEP specifically at occipital electrode sites (Gawne *et al.*, 2011; Gjini *et al.*, 2008). However, none of these studies looked at more than one location. Either the typical location for auditory sensory gating (Cz) was used in analysis for both modalities, or the standard location for visual ERPs (occipital) was used and no comparison was made with the auditory modality.

3.4.3 Within and between correlations

Bivariate correlations were used to help identify any relationships between the two modalities. Using the electrode clusters it is not surprising that no significant relationships were found. Earlier research found no correlations between sensory gating for two modalities (Oranje *et al.*, 2006), in fact studies have shown that there is only a frontal source in common with a temporal source for auditory processing (measured at Cz) and an parieto-occipital source for visual processing (measured at Pz and Oz) (Jensen *et al.*, 2008). This is consistent with the results that more visual gating is observed at the parietal electrodes, whereas auditory gating is mostly exhibited at the central electrodes.

The results of the within modality correlations reveal comparable results for both auditory and visual gating. This may suggest that although the mechanisms are not the same, and thus not directly correlated, there may be a qualitative similarity in the gating for each modality. Within each modality where significant gating was found, the components were significantly correlated with the same component of another location. One explanation of these results may come from the nature of what each electrode is actually measuring, in terms of the underlying cortical sources. As discussed in section 2.2., due to the diffuse nature of volume conduction, each cortical source will propagate its signal to multiple neighbouring electrodes. Moreover, components measured at each electrode are likely to be the product of several cortical sources converging. With this in mind, it is not surprising that electrodes such as Pz and Oz would measure the same component. Consequently these findings cannot elucidate the location of components in terms of cortical sources. Another finding was that, although there were no correlations between the earliest of the components and with the later ERPs, for the auditory modality, N1 and P2 were significantly correlated, irrespective of location. This is consistent with previous research indicating that the two later ERPs are similar due to being early attentive and late attentive processes. It has been

suggested that these components reflect a gating in and out (inhibition and facilitation) activity, which together reflect the sensory gating mechanism (Luck et al., 1994).

3.4.4. Latencies

As discussed previously, the average latencies of all the components were as expected from the literature, however there was a change in the response latency between the first and second stimulus presentations. For both auditory and visual ERPs, the response to the second stimulus occurred sooner than the response to the first stimulus. This is perhaps an expectancy effect due to the repetitive nature of the experiment. For the auditory modality, this effect was seen primarily at the central location, the only exception being the P1 ERP at the parietal location. For the visual modality, this pattern was observed at both the parietal and occipital locations, but only for components P1 and N1. The components and locations for which this reduced latency pattern has been found is potentially a reflection of the very components/locations for where sensory gating is most pronounced. Additionally, the visual P1 and N1 ERPs were the only components to exhibit any gating, with the most pronounced gating occurring at the parietal region.

3.5. Conclusions

Taken together these results indicate that auditory sensory gating is best observed at the central electrode sites in keeping with previous research. However, the findings argue against a preferential focus on the early P50 ERP over the later N1 and P2 components. Visual sensory gating was only observed in the later P1 and N1 ERPs, which may indicate the lack of a gating mechanism in the component C1, or a reflection of the low perceptual

load of the standard sensory gating methodology. Within each modality, correlations were consistently observed between the same component at different locations. Another pattern that was again observed in both modalities, was an expectancy effect exhibited for the latencies of the response to the second stimulus, primarily for components and locations that displayed the most marked sensory gating. A lack of correlation between the two modalities suggests that the two gating mechanisms are separate, a concept which is supported by the fact that different locations and components exhibited sensory gating for visual and auditory stimuli. However, the similarities regarding the within modality correlations and the reduced latency effect for the second stimulus implies a qualitatively similar process.

Chapter 4

Experiment 2: Cognitive mechanisms associated with auditory sensory gating

This chapter is based on a published article (Jones, L. A., Hills, P. J., Dick, K. M., Jones, S. P., & Bright, P., (2016). Cognitive mechanisms associated with auditory sensory gating, *Brain and Cognition*, 102, 33-45).

4.1. Introduction and rationale

This chapter further explores cognitive inhibitory mechanisms described in chapter one, relating these mechanisms to performance on a range of behavioural tasks. By focusing on the underlying components of these tasks and exploring their relationship with auditory sensory gating, the aim was to better understand the cognitive mechanisms that may underpin the gating phenomenon.

The principal cognitive dimension that has been correlated with sensory gating is attention (Yadon *et al.*, 2009). As discussed in chapter one (section 1.5.), this is a broad topic and thus it is more constructive to focus on the several specific tasks and processes associated with sensory gating, rather than one task representing the broader trait of attentional inhibition. The inclusion of additional cognitive tasks may help identify or rule out the involvement of non-inhibitory mechanisms. The ability to isolate specific task effects is often complicated by a failure of published studies to adequately describe or identify the possible underlying mechanisms employed during task preparation and/or execution (Friedman & Miyake, 2004). With this in mind, this chapter addresses the tasks used during this study, with respect to the different components of inhibition (see chapter one for more details on the components of inhibition, section 1.8.). In brief, Nigg (2000) identified three

distinct forms of inhibition: executive, motivational and automatic. The current study employs Nigg's distinction between executive and automatic inhibition, but does not include assessment of motivational inhibition, which is associated with emotional processing and is thought to reflect distinct neurological systems.

4.1.1. Executive Inhibition: Interference Control

Interference control is defined as the ability to suppress unwanted information from affecting performance (Nigg, 2000). The Stroop task (Stroop, 1935) is the classic measure of interference control, involving focused attention and response competition (Kok, 1999). A typical Stroop paradigm uses compound stimuli of colour words in which the colour of the ink and the word itself can be congruent (e.g., a blue word in blue ink) or incongruent (e.g., a blue word in red ink) (Lu & Proctor, 1995). Participants must identify the colour of the ink and therefore necessarily inhibit the more automatic response tendency of reading the word during presentation of incongruent trials. Longer reaction times are typically observed in these trials relative to the congruent trials (MacLeod, 1991).

A key feature of the Stroop effect is that of spatial integration: the task-irrelevant and task-relevant components of the Stroop are spatially integrated. This may enhance any possible conflict (Kaplan & Lubow, 2011), a claim supported by the observation that when the relevant colour and irrelevant word are perceptually separated using a time delay, the usual Stroop interference effect is significantly smaller (e.g. Dyer & Severance, 1973). Furthermore, when the word and colour are spatially separated but still presented simultaneously, there is typically no longer an interference effect (e.g. Flowers & Stoup, 1977).

A task that also measures interference control is the flanker task (e.g. Kaplan & Lubow, 2011). The flanker task measures the effects of irrelevant spatially separate distractor stimuli on the identification of a target stimulus. In general, the target stimulus appears in the centre of

the visual field with distractor stimuli flanking it. As a result of the spatial arrangement, this task requires no visual search (Kaplan & Lubow, 2011). Flankers tend to slow response times to identify the target centre stimulus compared to when it appears alone (Eriksen & Hoffman, 1972). If these flankers are congruent with the target, response competition (Yücel *et al.*, 2002) is minimal and response times are faster than if these flankers are incongruent with the target (Eriksen & Eriksen, 1974). Incongruent distractors interfere with the desired response, and/or activate the opposing response in working memory (Ridderinkhof *et al.*, 2004). In such tasks where the irrelevant and relevant information is presented simultaneously, the ability to focus attention on the target is required in order to allocate processing resources to the designated or relevant information (Kok, 1999).

A similar task that affects response-selection and comes under executive inhibition is that of the Simon task. Like the Stroop task, the Simon task is assumed to measure the ability to inhibit a response to and actively ignore a task-irrelevant stimulus dimension (Simon & Rudell, 1967). When a response to a particular dimension of a stimulus is made, the ability to make this response is affected by the relative spatial location of that stimulus to the response (Craft & Simon, 1970; Hommel, 1993). Faster responses are made to trials in which the task-irrelevant location of the stimulus is congruent with the location of the response (right visual field responded to by the right hand). Slower response times reflect a failure to inhibit a response to the task irrelevant dimension of the stimulus.

Yadon *et al.* (2009) found that the Stroop effect negatively correlated with the P50 gating ratio, with those that exhibited a larger ratio (less inhibition) performing better on the Stroop task (reduced Stroop effect), indicating that they were more successful at inhibiting the irrelevant stimulus feature. Considering that the P50 is widely assumed to reflect inhibition, it is counterintuitive that a positive correlation was not found. Similarly, small and non-significant correlations between performance on the flanker task and sensory gating are typically found even though both tasks are proposed to measure a similar inhibitory deficit (Yadon *et al.*, 2009). The authors attribute this finding between gating and the Stroop task to the perceptual

load differences between high and low gaters. Those who have reduced sensory gating have less perceptual resources available to process distractors, and consequently they perform better on tasks that require inhibition of distractors. These results complicate theories linking sensory gating with cognitive interference, although further evidence based on other tests (e.g., the Simon test) should help confirm whether or not a relationship exists.

4.1.2. Executive Inhibition: Cognitive Control

The ability to hold an item in working memory and subsequently ignore it is a typical process associated with inhibition (Nigg, 2000). The process of inhibiting information that was once active within working memory, is measured by the latent inhibition paradigm, in which participants are pre-exposed to a class of stimuli while ignoring another class of stimuli. This serves to promote implicit learning of the ignored set of stimuli (Raschle *et al.*, 2001). In a subsequent task, the pre-exposed non-target stimuli become the target stimuli (Cohen *et al.*, 2004; Lubow & Gewirtz, 1995). However, due to these stimuli having been non-targets, performance on the subsequent task is poorer than in the pre-exposure task and compared to novel stimuli (Braunstein-Bercovitz & Lubow, 1998a; Escobar, Arcediano, & Miller, 2002; Kaplan & Lubow, 2011). Latent inhibition refers to this inability to re-learn previously non-target stimuli as target stimuli (Granger, Prados, & Young, 2012). A simple explanation for the effect is that the previously non-target items have been given low attentional weights and it takes time to overcome this (Cohen *et al.*, 2004; Lubow & Gewirtz, 1995; Pearce & Hall, 1980).

In the latent inhibition task, there is a concern that the critical test stimulus may just be eliciting a novel pop-out as a result of novel stimuli attracting more attention than old stimuli (Johnston & Hawley, 1994). Consequently, latent inhibition may actually reflect a facilitation effect for the non-pre-exposed stimuli rather than a deficit in performance for the pre-exposed stimuli. In response, Lubow and Kaplan (1997) created a method in which latent inhibition and

the novel pop-out effect could be measured independently. They found that reaction times were always faster for novel stimuli compared to old stimuli regardless of whether the old stimulus was familiar due to previously being the target or non-target. This implies that latent inhibition likely reflects a pre-exposure performance deficit due to a reduction in attentional allocation, in addition to a non-pre-exposure facilitation effect due to novel pop-out when the non-target stimulus has not previously been presented.

Another task that purportedly measures cognitive control is that of negative priming. Each trial in a typical negative priming task consists of a prime display followed by a probe display (Fox, 1995). During test conditions, the prime display will contain a distractor that the participant is explicitly told to ignore (Beech *et al.*, 1991). This contrasts with latent inhibition in which participants tend to learn through experience to ignore the distractor. The target during the probe display can be novel, the target from the prime display, or the distractor from the prime display (e.g. Park, Puschel, Sauter, Rentsch, & Hell, 2002). During a typical negative priming task, response latency during the probe display is longer when it is preceded by a prime display in which the distractor became the target (Moritz & Mass, 1997). During the prime display the representation of the distractor or the response to it is suppressed (inhibited), and thus when this distractor becomes the subsequent target, it is harder to reactivate that representation resulting in longer reaction times (Aron, 2007; Tipper, 2001). Conversely, if the prime display distractor is not suppressed (remains activated), it will facilitate responding during its presentation as the target in the probe display (positive priming; Dux & Marois, 2008). However, this effect can be long lasting (DeSchepper & Treisman, 1996), possibly indicating the involvement of episodic memory retrieval rather than inhibition (Neill, 1997). Thus, the conflict generated during incongruent prime and probe displays is due to the probe display failing to match up to the memory representation of the prime display (Logan, 2002; MacLeod, 2007; Tipper, 2001).

4.1.3. Executive Inhibition: Intentional Motor Inhibition

The distinction between automatic and intentional control was first suggested by Logan (1980), with the deliberate inhibition of a primary motor response to changing contextual cues is best demonstrated by the go/no-go task (Nigg, 2000). In this task, participants are required to make a response to a target stimulus and inhibit their response to a less frequently presented 'stop' stimulus (Kok, 1986). The more frequent 'go' stimuli cause the action of responding to become a prepotent response. This task involves sustained attention in addition to response control, as participants need to pay attention to both the target and the 'stop' stimuli, which do not appear simultaneously.

There are two proposed forms of response control, reactive and proactive (Aron, 2011). The former is a common form of response control in many inhibitory tasks including the go/no-go task. This reactive mechanism is initiated by the stop signal. It is the intentional inhibition of a currently activated response or goal as a result of new information (Nigg, 2000). Proactive inhibition is a way of anticipating the need to terminate a response before that need arises. This happens when a possible conflict is detected and all responses are paused until information regarding the next required response is provided. This can be illustrated in studies that compare randomised go/no-go trials with blocks of each type of trial. During randomised trials, participants are slower at responding but accuracy is not affected. This demonstrates a pre-emptive slowing of response in anticipation of a possible change in response type (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010).

A positive correlation has been observed between stopping error on the go/no-go task and P50 sensory gating (Yadon *et al.*, 2009), which may suggest that sensory gating is related to intentional motor inhibition at the response stage of the task. This interpretation would refute the claim that sensory gating is a pre-attentive process due to the requirement to attend to stimuli and select the appropriate response. However, this correlation may reflect the

sustained attention element of the go/no-go task and therefore support the opposite interpretation that sensory gating is pre-attentive. Issues with interpreting these results highlight the need for multiple tasks in determining the associated mechanisms with sensory gating.

4.1.4. Executive Inhibition: Oculomotor

Many of the executive inhibition tasks described above involve language or motor responses. There are tasks that involve simple ocular reflexes such as the antisaccade task in which participants must inhibit a reflexive response to the presentation of a stimulus. A typical antisaccade task requires the participant to move their gaze in the opposite direction to a presented stimulus (Hutton & Ettinger, 2006). In order to do this successfully, participants must inhibit the prepotent oculomotor response of directing their gaze towards a newly presented stimulus. The average error rate with this task, due to participants making a reflexive prosaccade, is around 20% (Ettinger *et al.*, 2003). With regards to sensory gating, a correlation has been found between antisaccade performance and sensory gating (Cadenhead, Light, Geyer, McDowell, & Braff, 2002). Others suggest that the two forms of inhibition are independent of each other, with sensory gating being a largely automatic, pre-attentional cognitive mechanism and oculomotor inhibition, as measured by the antisaccade task, being effortful and dependent upon attention (Braff & Light, 2004).

4.1.5. Attentional Orienting and Sustained Attention

Three separate anatomically and functionally defined attentional networks have been identified: orienting, alerting, and executive control (Fan, Fossella, Sommer, Wu, & Posner,

2003; Posner & Petersen, 1990). Fan, McCandliss, Fossella, Flombaum, and Posner (2005) devised the Attentional Network Task (ANT) in order to assess these types of attention (Posner & Rothbart, 2007). The task involves a cued reaction time task and a flanker task, and the efficacy of each network is assessed by the reaction time differences between conditions. Each trial may have a cue or no cue, which provides either temporal or spatial information about the target. The target then appears above or below a fixation cross with congruent or incongruent flankers either side of it. The difference between congruent and incongruent trials is considered a marker of the efficiency of the executive functioning network (Flanker task), while the difference between a temporal cue and no cue is claimed to reflect alerting ability. Finally, the difference between the trials with and without an accurate spatial cue is intended to provide a measure for orienting proficiency. The orienting network controls the ability to focus attention towards the source of specific sensory signals by way of identification and selection of sensory stimuli (Posner & Rothbart, 2007).

Wan, Friedman, Boutros, and Crawford (2008) found a positive correlation between sensory gating and performance on the ANT. Those with superior gating capacity demonstrated greater accuracy and quicker reaction time predominantly in the alerting portion of the task, suggesting that sensory gating is related to attentional vigilance and precision. The alerting network has also been associated with the continuous performance and vigilance tasks. These tasks measure the capacity to remain alert over a long period of time (Fan *et al.*, 2002) with the continuous performance task (CPT) directly measuring sustained attention (Nestor, Faux, McCarley, Shenton, & Sands, 1990). There are two main forms of this task, the CPT-single, which only requires the participant to respond when they see a target stimulus, and the CPT-AX or CPT-IP, which requires them to respond when they see the target stimulus but only when it is preceded by a cue stimulus (Lee & Park, 2006). Both variants of the task often take the form of a continuous stream of letters and participants respond when a pre-specified letter appears.

The ability to encode the relevant stimulus while ignoring the non-target stimulus, and maintaining the task instructions in working memory throughout the duration of the stream of stimuli is crucial to success on the CPT (Cohen, Barch, Carter, & Servan-Schreiber, 1999; Oades, 2000). Additionally, in the CPT-AX forms of the task, the cue stimulus must be maintained in working memory. Participants must control what information is selectively attended to and similarly what information is excluded from working memory (Rush, Barch, & Braver, 2006). When patients with schizophrenia are selected on the basis of relatively high or low P50 sensory gating ratios, those with the higher ratios (i.e., with reduced sensory gating) typically perform worse on the CPT than those with lower ratios (Erwin *et al.*, 1998), possibly due to increased susceptibility to distraction.

4.1.6. Top-down Modulation of Sensory Gating

The notion of attentional influences upon sensory gating, primarily the early P50 response, is a contentious issue within the literature. Many researchers claim that the P50 response to auditory stimuli is a pre-attentive, automatic process, and thus unaffected by attentional manipulations (Boutros *et al.*, 2004; Braff & Light, 2004; Freedman, Waldo, Bickford-Wimer, & Nagamoto, 1991; Jerger, Biggins, & Fein, 1992). Any such effects are not observed until later processing, which is reflected in the component N1 (Braff & Light, 2004; White & Yee, 1997). However, others have suggested that even components as early as P50, either the gating ratio or amplitudes, can indeed be affected by altering the capacity for sustained attention, or by directing attention towards the stimuli (Gjini, Burroughs, & Boutros, 2011; Rosburg, Trautner, Elger, & Kurthen, 2009; Yee *et al.*, 2010). The effects of attention on P50 may reflect top-down processing of sensory stimuli working simultaneously with the bottom-up processes. Support for top-down influences on sensory gating comes from research with patients and animals with lesions to the pre-frontal cortex. This research has demonstrated

that pre-frontal cortex damage impairs the ability to inhibit sensory information, specifically the ability to attend to relevant over irrelevant stimuli (Knight, Scabini, & Woods, 1989; Rosenkranz & Grace, 2001). Furthermore, developmental changes within the prefrontal cortex that lead to changes in attentional control may result in sensory gating improvements with age (Knight, Staines, Swick, & Chao, 1999; Marshall, Bar-Haim, & Fox, 2004). Further support for top-down influences on sensory gating has emerged from ERP studies which have found significant correlations between measures of frontal lobe dysfunction and sensory gating (Boutros *et al.*, 2009), as well as P50 generators within the frontal lobes (Grunwald *et al.*, 2003; Korzyukov *et al.*, 2007; Mears *et al.*, 2006).

4.2. The Present Study

In order to explore the cognitive functionality of sensory gating and provide a more comprehensive review of the possible underlying components, this correlational study tests participants' sensory gating alongside their performance on each of the tasks described above. It was predicted that sensory gating would correlate with several measures of inhibition, although detailed predictions could not be made with confidence due to unresolved issues in the literature. In this study, working memory and fluid intelligence have also been assessed in order to control for and explore potential top-down influences on sensory gating. Additionally, tests such as the CPT place substantial demands on working memory, raising the possibility that exploration of individual differences in psychometric intelligence may enable clearer distinction between task specific and more general cognitive factors associated with performance.

4.3 Design

A correlational design was employed whereby auditory sensory gating ratios were correlated with scores on each of the tests of inhibition (Stroop, Simon, latent inhibition, negative priming, go/no-go, switch, antisaccade, attentional network, and continuous performance). IQ (measured using Cattell's Culture Fair (CCF-IQ) Scale 2 form A, Institute for Personality and Ability Testing, 1973) and working memory capacity (measured using the automated-OSPAN; Unsworth, Heitz, Schrock, & Engle, 2005) differences were controlled for by conducting partial correlations. Participants completed the tasks in a pseudorandom order (the exception to full randomisation being that the switch task always immediately followed the go/no-go task). Auditory gating procedures can be seen in section 2.2.1., and behavioural procedures in section 2.3. For a full description of the methods see chapter two.

4.4. Results

A paired-samples *t*-test confirmed that the amplitudes for the first stimulus (mean = 1.33 μ V, SE = 0.14) was significantly larger than the amplitude for the second stimulus (mean = 0.97 μ V, SE = 0.14) ($t(49) = 5.1$, $p < .001$), which illustrates a group level sensory gating effect (see Figure 10A for the grand average waveform for stimulus 1 and 2, and Figure 10B for the individual distribution of the P50 response to stimulus 1 and 2). There was also a significant group level effect for all of the behavioural tasks, see Table 5.

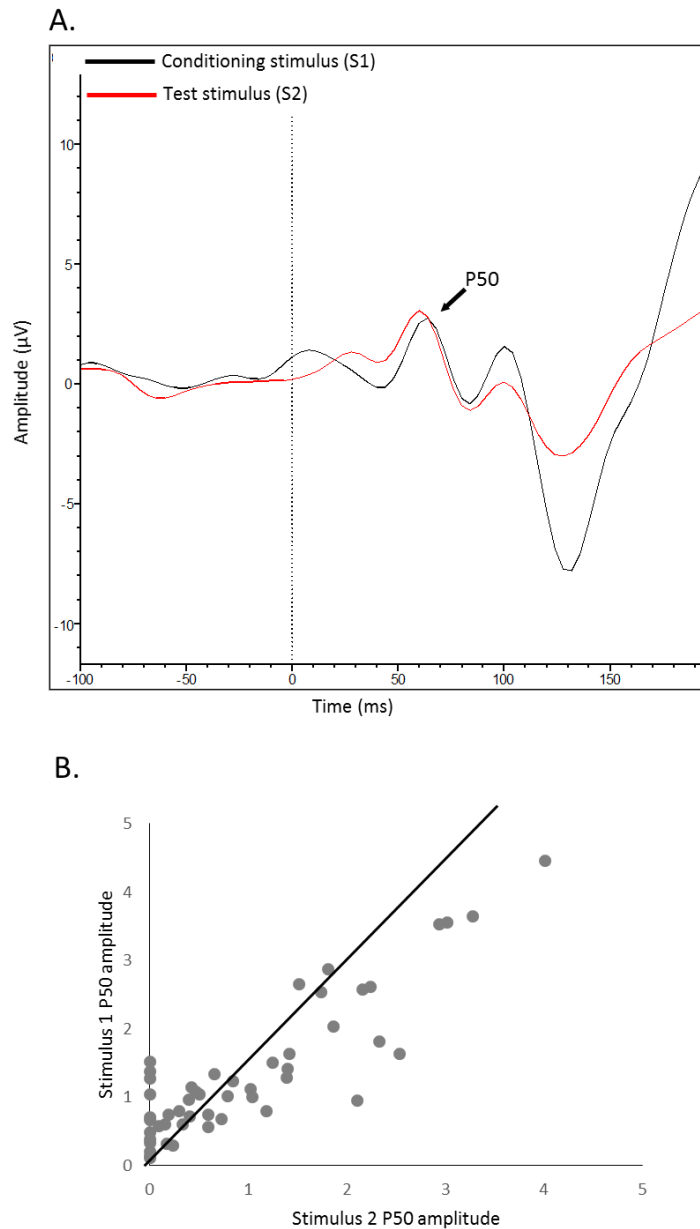


Figure 10. Panel A. Grand average EEG waveform in response to the presentation of the first and second stimulus at electrode Cz. Panel B. Scatterplot displaying the relationship between the P50 amplitudes for stimulus 1 and 2. The 45° line depicts the point at which there is no difference between the amplitudes. Points below the line illustrate individuals who demonstrated an attenuated P50 response to stimulus 2.

Table 5

Test information and descriptive statistics for all cognitive control measures used in Experiment two

Predictor variable	Test authors	Index and test of effect
Executive Inhibition: Interference Control		
<i>Stroop Effect</i>	Stroop (1935)	Mean incongruent RT (1009ms, SD = 262) was greater than mean congruent RT (934ms, SD = 211), $t(48) = 5.32$, $p < .001$
<i>Simon Congruency Effect</i>	Hommel (1993)	Mean incongruent RT (486ms, SD = 94) was greater than mean congruent RT (458ms, SD = 82), $t(44) = 4.45$, $p < .001$
<i>Conflicting (ANT)</i>	Fan <i>et al.</i> (2002)	Mean incongruent RT was greater than mean congruent RT (mean difference = 92.35ms, SD = 65.38), $t(44) = 8.85$, $p < .001$
Executive Inhibition: Intentional Motor Inhibition		
<i>No/No-Go Effect</i>	Rubia <i>et al.</i> (2001)	Mean percentage accuracy for go trials (not-responding, 98%, SD = 4) was greater than mean percentage accuracy for no-go trials (responding, 85%, SD = 18), $t(48) = 4.98$, $p < .001$
<i>Switch Cost</i>		Mean switch RT (513ms, SD = 111) was greater than mean non-switch RT (454ms, SD = 64), $t(48) = 6.26$, $p < .001$
Oculomotor Inhibition		
<i>Anti-Saccade Difference</i>	Brenner <i>et al.</i> (2001)	Mean RT to make anti-saccades (1738ms, SD = 1440) was longer than mean RT to make pro-saccades (871ms, SD = 492), $t(47) = 4.50$, $p < .001$
Executive Inhibition: Cognitive Control		

<i>Latent inhibition</i>	Lubow and Kaplan (1997)	Mean RT on pre-exposed trials (1331ms, SD = 456) was longer than mean RT on non-pre-exposed trials (1074ms, SD = 492), $t(20) = 3.76$, $p = .001$
<i>Negative Priming Effect</i>	Park <i>et al.</i> (2002)	Mean RT on ignored repetition trials (574ms, SD = 203) was greater than mean RT on neutral trials (490ms, SD = 157), $t(48) = 5.48$, $p < .001$

Sustained Attention

<i>Continuous Performance Accuracy</i>	Lee and Park (2006)	Mean accuracy to respond to target stimulus (97%, SD = 6) was greater than chance, $t(48) = 122.67$, $p < .001$
<i>Continuous Performance RT</i>		Mean time to respond to target stimulus was 523ms (SD = 14)
<i>Alerting (ANT)</i>	Fan <i>et al.</i> (2002)	Mean double cue RT (584ms, SD = 98) was greater than mean no cue RT (534, SD = 90), $t(44) = 8.69$, $p < .001$

Attentional Orienting

<i>Orienting (ANT)</i>	Fan <i>et al.</i> (2002)	Mean spatial cue RT (511, SD = 98) was faster than mean central cue RT (584, SD = 94), $t(44) = 6.66$, $p < .001$
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Covariates

CCF-IQ	Cattell and Cattell (1960)	Mean raw intelligence score was 35.12 (SD = 5.80)
<i>Automated OSPAN</i>	Unsworth <i>et al.</i> (2005)	Mean OSPAN absolute score was 39.06 (SD = 18.66)

Note. Only reaction times from trials with correct responses were used.

Using a bivariate correlation, a significant negative correlation was observed between the sensory gating ratio and CCF-IQ performance, suggesting that successful sensory inhibition is related to fluid intelligence. Additional significant negative correlations were found between the sensory gating ratio and the latent inhibition effect ($r = -.63$), the novel pop-out effect ($r = -.47$), the orienting component of the attentional network task ($r = -.38$), and accuracy scores on the CPT ($r = -.38$) (see Figure 11 depicting the correlations between sensory gating and CCF-IQ performance, CPT accuracy and latent inhibition). All other correlations were non-significant ($p > .05$). A summary of correlations between the attentional inhibition tasks and sensory gating can be seen in Table 6. While Figure 11 may indicate the presence of outliers driving this correlation, outliers were explored using the standardised residuals and extreme values: no data point was considered an outlier (all standardised residuals were between -1.96 and $+1.96$). To measure the difference in magnitude of these correlations, a series of Williams's t -tests were used following a Fisher's r to Z transformation. These results show that none of the correlations significantly differed from one another ($p > .05$), indicating that the magnitude of the correlations between each of the five tasks and sensory gating were similar.

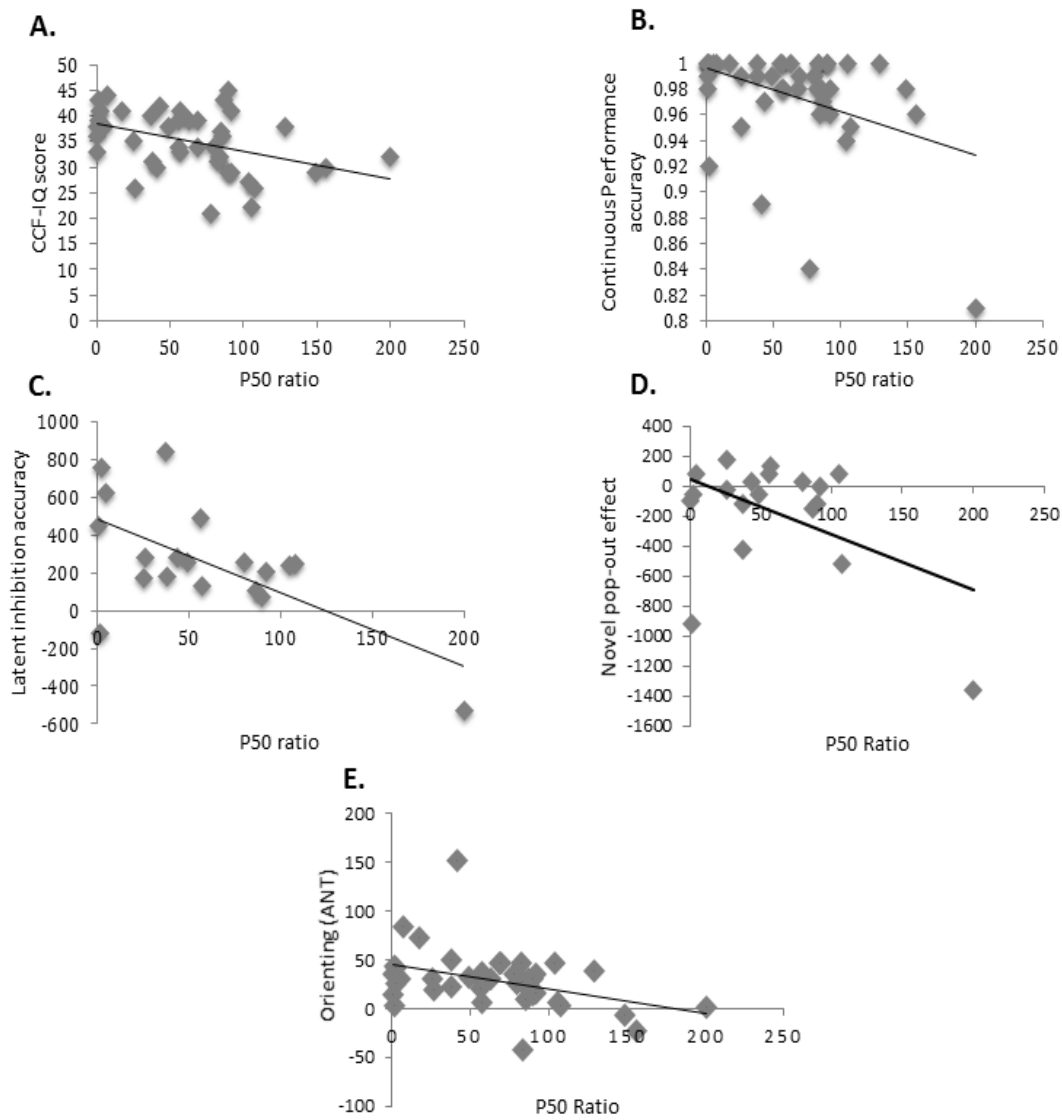


Figure 11. Scatterplots for significant correlations between cognitive performance measures plotted against the P50 ratio. Panel A. plots performance on the Cattell's Culture Fair measure of intelligence (CCF-IQ; max raw score is 46). Panel B. shows accuracy on the Continuous Performance Task, panel C. displays Latent Inhibition accuracy, panel D. displays the novel pop-out effect, and panel E. displays the orienting component of the attentional network task. Each panel shows a trend line reflecting the negative relationship in each instance.

Table 6.

Correlation coefficients from bivariate correlation between sensory gating and the measures of inhibition and psychometric tests.

Task correlations with sensory gating	Correlation coefficient (<i>r</i>)	<i>N</i>
<i>Executive Inhibition: Interference Control</i>		
Stroop	.06	43
Simon	.07	39
Flanker/executive control (ANT)	.04	41
<i>Executive Inhibition: Cognitive Control</i>		
Latent inhibition	-.63**	19
Novel pop-out	-.47*	19
Negative priming	.18	43
<i>Executive Inhibition: Intentional Motor Inhibition</i>		
Go/no-go	-.16	43
Switch	.16	43
<i>Oculomotor Inhibition</i>		
Antisaccade Task	-.15	43
<i>Attentional Orienting</i>		
Orienting (ANT)	-.38*	41
<i>Sustained Attention</i>		
Alerting (ANT)	.03	41
Continuous performance accuracy	-.38*	43
<i>Covariates</i>		
Intelligence: CCF-IQ	-.42**	43
Working Memory: OSPAN	-.23	43

Note. * sig. to .05, ** sig. to .01.

After statistically controlling for intelligence (as measured by CCF-IQ), correlations between the sensory gating ratio and both the novel pop-out effect and the orienting component of the attentional network task were no longer significant ($p > .05$). However, there remained a significant negative correlation between the sensory gating ratio and the latent inhibition effect ($r = -.62$), and the accuracy scores for the CPT ($r = -.58$). Again a William's t -test was conducted to explore the magnitudes of these two correlations. Neither the latent inhibition effect nor the accuracy score during the CPT correlated to a different degree with the sensory gating ratio ($Z = .15$, $p = .880$).

Working memory (as measured by the OSPAN) was also controlled for, resulting in comparable findings to that of CCF-IQ. The correlations between sensory gating and both the novel pop-out effect and attentional orienting were no longer significant, while the correlations between sensory gating and both latent inhibition ($r = -.63$) and continuous performance ($r = -.57$) remained significant. Again there was no significant difference between the magnitude of the correlation coefficients for latent inhibition and orienting ($Z = .22$, $p = .413$). These results were again similar when both fluid intelligence and working memory were controlled for together. Changes in the correlation coefficient when controlling for either/both fluid intelligence or working memory, can be seen in Table 7.

Table 7.

Correlation coefficients after partial correlation controlling for fluid intelligence (CCF-IQ) and working memory (OSPAN).

Task correlating with sensory gating	Bivariate correlation	Controlling for Cattell's	Controlling for OSPAN	Controlling for Cattell's and OSPAN
	Correlation coefficient (<i>r</i>)	Correlation coefficient (<i>r</i>)	Correlation coefficient (<i>r</i>)	Correlation coefficient (<i>r</i>)
Latent inhibition	-0.63**	-0.62*	-0.63**	-0.63*
Novel pop-out	-0.47*	-0.48	-0.43	-0.45
Orienting (ANT)	-0.38*	-0.38	-0.42	-0.37
Continuous performance	-0.38*	-0.58*	-0.57*	-0.56*

Note. * sig. to .05, ** sig. to .01.

4.5. Discussion

The present study explored the cognitive functionality of sensory gating, using auditory sensory gating and a battery of tests that tap different aspects of cognitive function. It was predicted that sensory gating would correlate with several measures of inhibition. The results demonstrate significant correlations between sensory gating and performance on the continuous performance and latent inhibition tasks. Correlations with other tasks, which also incorporated attentional inhibition, were weak and non-significant.

Higher sensory gating ratios were associated with reduced latent inhibition. Specifically, greater inhibition resulted in a larger detriment to performance when target stimuli in the test phase were non-targets during the pre-exposure phase. Latent inhibition occurs when repeated presentations of a stimulus without consequence results in that stimulus being

regarded as task-irrelevant. Subsequently, identifying that stimulus as the target in the following test phase is more demanding (Braunstein-Bercovitz & Lubow, 1998a; Escobar *et al.*, 2002). A primary feature of latent inhibition is that of selective attention whereby participants preferentially process stimuli that are deemed relevant to the exclusion of all other stimuli. Thus, limited attentional resources are focused upon aspects of the environment that are salient to the current task demands and goals (Granger *et al.*, 2012; Lubow, 1989). Essentially, the learned irrelevance must be overcome.

Evidence that the latent inhibition effect reflects processing of the non-target stimulus during the pre-exposure phase is supported when only the same stimulus at pre-exposure and test can elicit the latent inhibition effect, suggesting that some encoding of that particular stimulus (at pre-exposure) must occur (Lavie & Tsal, 1994). The encoding most likely reflects evaluation of stimulus relevance in order to prevent further attentional allocation to the non-target stimulus during the test phase.

Those with reduced latent inhibition (i.e., non-clinical high-psychotic participants) typically perform better on subsequent recognition and recall of the pre-exposed stimulus, despite a change in context (Beech *et al.*, 1989). A change in context normally eliminates the effects of latent inhibition in typical subjects. Taken together, this research suggests that latent inhibition is caused by both the encoding of the pre-exposed stimulus and the subsequent ability to inhibit that stimulus from further encoding through selective attention once it has been deemed task-irrelevant.

In addition to the relationship with latent inhibition, the present finding showed a sensitivity of sensory gating to accuracy on the CPT, with higher sensory gating ratio (indicative of reduced inhibition) associated with worse performance. This finding may reflect a failure of participants with higher gating ratios to attend to the relevant stimuli for sustained periods due to a difficulty in suppressing goal irrelevant distractor information. However, the single version of the task, as used in this study, is considered a measure of stimulus vigilance during sustained attention and encompasses limited, if any, suppression demand

(e.g., Halperin, Sharma, Greenblatt, & Schwartz, 1991; Nuechterlein & Dawson, 1984; van den Bosch, Rombouts, & van Asma, 1996).

The sensory gating and CPT procedures are structurally similar. Stimulus vigilance is measured in the single version of the CPT by presenting participants with an occasional target stimulus (to which they must respond) amongst a sequential stream of letters. Similarly, during the sensory gating task, participants were presented with a stream of identical auditory stimuli and were required to respond whenever an occasional different target stimulus was heard. The only obvious differences between the two tasks were that of different inter-trial intervals, input modality (which may indicate that sensory gating is not modality specific), and the use of identical rather than several different 'no response' stimuli in the sensory gating paradigm. The extent to which sensory gating is modality specific remains unresolved in the literature, but our findings are most consistent with a domain general view, in which gating operates across multiple input modalities. Nevertheless, further research will be required to resolve this debate. Putting aside the issue of input modality, both paradigms are closely similar in terms of task demands, and this conceptual similarity is likely to underpin the significant correlation between them. Additionally, even after the partial correlation in which CCF-IQ performance or the OSPAN score was the controlling factor, this correlation remained, which would be expected if they both entail similar task demands and additionally share some common underlying component independent of psychometric intelligence. Ceiling effects on the CPT limit the extent to which one can draw firm conclusions about the strength of the relationship with sensory gating, and the cognitive mechanism(s) underpinning both measures.

Negative priming did not correlate significantly with sensory gating, an unexpected finding given claims that it reflects the same underlying cognitive control mechanisms as latent inhibition (e.g., Nigg, 2000). This lack of correlation potentially provides support for the theory that negative priming does not reflect a component of inhibition but rather episodic retrieval processes (Neill, 1997).

Another difference between the negative priming effect and latent inhibition is the involvement of instruction. In negative priming, participants are informed about what is task-relevant and task-irrelevant prior to testing, whereas what is deemed task-irrelevant in the latent inhibition effect is 'learnt' through repetition. This assertion suggests that latent inhibition reflects an encoding stage at which the assessment of relevancy and saliency is conducted. This is similar to sensory gating paradigms in which participants are not informed that the second of the two stimuli is irrelevant.

It is proposed, therefore, that sensory gating reflects the identification of context specific irrelevance at the encoding (input) stage that is governed in part by goal-directed processes, and/or the subsequent ability to selectively attend to relevant stimuli based on the previous identification. Further research will be required to confirm whether sensory gating reflects both or just one of these mechanisms. With respect to proposed 'subcategories' of inhibition (Harnishfeger, 1995; Nigg, 2000), sensory gating may be related to the categorisation of task-irrelevance at the input stage as well as selective attention at the cognitive processing stage (cognitive inhibition). Consequently, sensory gating requires an element of top-down as well as bottom-up processing in order for task demands to influence selective attention. Although sensory gating is an early process, occurring at 50 ms post-stimulus onset, it is possible that top-down influences are in operation. Research indicates that top-down networks may be activated even before the presentation of stimuli (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999), during the expectancy period, and may continue to be active during the presentation of stimuli (Kastner *et al.*, 1999). It is this top-down processing that enables selective attention to relevant stimuli based on task demands (Pessoa, Kastner, & Ungerleider, 2003). The proposed neurological generators of sensory gating provide further support for these top-down influences. The fronto-temporal interaction model of sensory gating suggests that gating of basic stimulus properties may occur in the auditory cortex while additional or more goal-directed gating is more contingent upon prefrontal cortex (Jensen *et al.*, 2008;

Mears *et al.*, 2006; Oranje *et al.*, 2006; Tregellas *et al.*, 2007). Consistent with this model, deficits in sensory gating have been observed in patients and animals with prefrontal lesions (Knight *et al.*, 1999; Rosenkranz & Grace, 2001).

There was also a significant positive correlation between sensory gating and performance on CCF-IQ, a measure of non-verbal fluid intelligence (Cattell & Cattell, 1960). Research has suggested that correlations with intelligence may reflect the selection strategies employed during encoding (Cusack, Lehmann, Veldsman, & Mitchell, 2009). Those with higher intelligence encode the most relevant stimulus features. This is consistent with the proposed correlation between sensory gating and latent inhibition described above. Indeed, intelligence is also related to top-down goal-directed processing during selective attention (Duncan, 1995), and both intelligence and goal-directed behaviour are associated with activation of a fronto-parietal network (e.g., Colom, Karama, Jung, & Haier, 2010; Dumontheil, Thompson, & Duncan, 2011; Duncan *et al.*, 2008).

Several tasks failed to significantly correlate with sensory gating, including some measures of interference control, intentional motor inhibition, oculomotor inhibition, and attentional orienting. In the Stroop, Flanker, Simon, go/no-go, and switch tasks, there is a principal element of response competition and conflict resolution. Typically, there are either two opposing responses available, or there are stimuli that are incongruent with an automated/prepotent response, therefore requiring effortful overturning of that response tendency. In these tasks, then, the goal-relevant response occurs at the output stage of stimulus processing and may therefore be more related to behavioural inhibition than to the early processing reflected in sensory gating. This is not a feature of latent inhibition, as there are no competing responses or trials involving the congruency of target and response.

4.6. Conclusions

In summary, significant correlations were observed between sensory gating and i. latent inhibition and ii. accuracy on the CPT (but not other attentional inhibition tasks), after statistically controlling for differences in fluid intelligence and working memory. These findings suggest that sensory gating is associated with specific aspects of goal-directed attentional control. Fundamental to sensory gating is the identification of goal irrelevant information such that attention to that information is reduced relative to goal relevant information. Both top-down and bottom-up processes that occur at the initial encoding stage of stimulus processing underpin this ability. Additionally, sensory gating enables resistance to interference as well as early cognitive inhibition at the encoding stage compared to other inhibition tasks that arguably involve more cognitive and behavioural inhibition at the output/response stage.

Chapter 5

Experiment 3: Cognitive mechanisms associated with visual sensory gating

5.1. Introduction and rationale

This chapter replicates the procedures in chapter four for the visual modality, with the purpose of exploring the attentional inhibition components operating during behavioural task execution, and consideration of how these may relate to visual sensory gating. Attentional effects within the visual cortex are sometimes referred to as increasing the signal to noise ratio of the neuronal populations that process a particular stimulus or stimulus feature, resulting in the signal gain for that stimulus (Fischer, & Whitney, 2009). This has a facilitatory, tuning effect on the processing of a stimulus, but inhibitory functions may also be operating simultaneously or in sequence, in order to process a particular stimulus at the expense of other stimuli. Early research in animals did indeed find that the amplitudes of sensory evoked responses were augmented when attention was directed to a stimulus, suggesting facilitation, and were reduced when a stimulus was unattended, suggesting inhibition (Oatman & Anderson, 1977). Taken together, it is likely that visual processing requires a gating mechanism mediated by attention, which controls the information that is filtered in or out (Hillyard, Vogel, & Luck, 1998).

5.1.1. Visual ERPs and attentional inhibition

In terms of specific visual ERPs, several components have been found to be the mediators of attentional inhibition within both the striate and the extrastriate of the visual cortex (Slotnick *et al.*, 2003). Specifically, ERP and EMG recordings have found that the attentional effects within the extrastriate cortex occur around the same timeframe as the ERP P1 and

continue beyond this to components such as N1 (for review see Mangum & Hillyard, 1990). When Luck and colleagues (1994) investigated this, they found that rather than there being only facilitation, as reflected in an increase in amplitude for both components P1 and N1 in the extrastriate, the P1 component seemed to only show attenuation, and N1 exhibited only augmentation. This was also found in another spatial cueing task with an inter-stimulus interval (ISI) of 200-500ms, similar to the sensory gating ISI. During this research, there was a decrease in the P1 on invalid trials compared to neutral, suggesting that the P1 was modulated by the requirement to inhibit the invalidly cued attentional orientation. However, the component N1 exhibited no effect when comparing invalid and neutral trials, but did show an increase in negativity on valid trials compared to neutral (P1 showed no effects when comparing valid and neutral trials), suggesting that N1 was related to the facilitation effects that came with the valid cue (Hillyard, Mangun, Waldorff, & Luck, 1995).

There is less agreement with regards to the attentional modulation of the earlier ERP C1. Some research suggests that the C1 component, reflecting activity within the striate cortex, is unaffected by attentional selectivity (Anillo-Vento & Hillyard, 1996; Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Mangun et al., 1997), whereas others purport that the amplitude of C1 is enhanced when attention is directed towards a stimulus (Kelly, Gomez Ramirez, & Foxe, 2008; Somers, Dale, Seiffert, & Tootell, 1999). One explanation for this disagreement may be that the ERP C1 is modulated by attentional manipulations, but only in specific circumstances, such as tasks requiring stimulus discrimination (Gilbert, Ito, Kapadia, & Westheimer, 2000). Moreover, C1 has been shown to be affected by stimulus predictability (reduced response to more predictable stimuli) and stimulus relevance (more negative response) (Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; Stolarova, Keil, & Moratti, 2006). Attentional modulation has been linked to selective enhancements within the striate towards certain stimuli, which categorise inputs as relevant and in need of further processing (Lamme & Roelfsema, 2000), as well as the suppression of irrelevant stimuli in order to prevent further processing, and enable more proficient processing of the relevant stimuli (Hopf et al., 2006).

The components C1 and P1 are likely to both be involved in the attentional inhibitory process of stimulus processing (Slotnick *et al.*, 2003), with C1 modulations reflecting an early filtering mechanism, potentially controlled by top-down processes related to context and goals, and the component P1 reflecting additional or even 'back-up' filtering following processing in the striate (Rossi & Pourtois, 2012). This form of early inhibition in the striate may occur when perceptual load is high due to the narrowing of attention (reflected in a reduction of C1), however when the perceptual load is low, information is unintentionally processed, and thus increased inhibition is required at the level of the extrastriate, which is seen in the modulations of P1 (Oakley & Eason, 1990; Rauss, Pourtois, Vuilleumier, & Schwartz 2009). This unintentional processing is considered the consequence of spare attentional capacity 'spilling over' to include irrelevant stimuli, and so later filters processes are required in order to prevent these irrelevant stimuli from interfering with the relevant later on. Moreover, there is evidence for a feedback system occurring as soon as 10ms from extrastriate activation (Pascual-Leone & Walsh, 2001), from the extrastriate to the striate, in order to exert further control over attentional selectivity (Bullier; 2001).

However, much of this research has been conducted with the notion of stimulus driven modulation, thus it is worth noting the potential top-down, goal driven effects upon early visual processing. Although visual stimuli are processed in a hierarchical manner with increasingly complex features being addressed, the attentional system would require some form of bias derived from current goals and context in order to bias the visual processing stream towards processing that which is deemed relevant, salient etc. (Li *et al.*, 2004; Rauss *et al.*, 2011). This is in addition to attentional effects associated with perceptual capacity. It has been purported that the dorsal fronto-parietal network is involved in this top-down control, and can influence the earliest of processing within the primary visual cortex (Schwartz *et al.*, 2005). Indeed, research has shown top-down modulatory effects could be seen as early as 30ms after the initial activation within the striate (Foxy & Simpson, 2002; Lamme & Spekreijse, 2000).

5.1.2. Behavioural measures of attentional inhibition

There are several tasks in this study, which measure a variety of inhibitory functions. As described in the previous chapter, these tasks measure one or several forms of inhibition at different stages of information processing, including attending to a stimulus and stimulus discrimination at the encoding stage, suppressing no longer relevant information that has previously been encoded, and behavioural inhibition at the response stage. Kok (1999) first divides these tasks into passive, active, and focused attention paradigms, with passive tasks referring to those that do not require any overt behaviour, much like the original sensory gating paradigm. These tasks will not be discussed in this chapter as previous chapters have addressed the event-related potentials related to the passive task used during this research. Active tasks are those that do require overt behaviour, including active control over orienting, task-switching, go/no-go. Focused attention paradigms can be further divided into interference measures, where targets and non-targets are simultaneously presented (e.g., the flanker task, Stroop, negative priming, and latent inhibition), or measures of sustained attention, where targets and non-targets are successively presented, such as the continuous performance task. These tasks can modulate the amplitudes of the components P1 and N1, with such modulations occurring when a stimulus is either attended to or ignored/unattended. However, as discussed above, the component C1 may also be affected by such tasks conditions. A final sub-category of focused attention paradigms is the trial by trial focusing during spatial cueing measures, which can be measured in tasks such as the orienting and alerting components of the attentional network task. These tasks have also been known to alter the component P1, and again there is some debate regarding the modulation of C1 to tasks that require spatial orienting.

5.1.3. Active paradigms

Reflex suppression is considered to be an active paradigm which can occur when peripheral distractors are presented during active response tasks to target stimuli. In these situations, non-targets can reflexively attract attention and thus the processing of the target, and the related cortical response is reduced. Those who are better at inhibiting these distractors are thought to be more proficient at narrowing their attentional spotlight towards the target location only, and consequently their cortical responses are less affected by the presence of distractors (Macleod, 1991). This reflexive orienting to non-targets is not necessarily an overt movement of the eyes towards the distractors, but can be the covert shifting of attention if one's attention is not sufficiently focused upon the target stimulus (Kok, 1999). The control over a reflexive shift in attention is common in several tasks that include interference.

As well as the active control over reflexive shifts in attention, active tasks can also measure the inhibition of, or control over motor responses. This is typically evident in the go/no-go and switch paradigms. During the go/no-go task, there are two processes, making a response and inhibiting that response, that are competing at the response stage in a type of race, with the winning process being the one that ultimately controls the outcome behaviour. The stopping response has been linked to a complex connection of cerebral areas, including, but not limited to, the prefrontal cortex and the supplementary, premotor, and motor areas (Eimer, 1993; Kopp, Mattler, Goertz & Rist, 1996). Thus, it is unlikely that the visual sensory gating component measured in this research is related to such tasks, as these tasks require more processing than would typically be associated with 100ms post-stimulus onset. Indeed, the standard components associated with such tasks are the N2-P3 complex (Garavan, Ross, Murphy, Roche, & Stein, 2002).

Task switching is another active paradigm, during which participants are slower to respond when a task has just been switched compared to performance during a task when the previous trial required the same task set instructions. This control is purported to be the capacity to suppress the previously used task set in order to respond appropriately using the

new task set. Again this form of control is suggested to reflect executive control, or top-down functioning from involving the frontal lobes (Rogers & Monsell, 1995), and is consequently unlikely to be associated with the early processing linked to the components C1 and P1. Note that this suppression of a previous task set is similar but unrelated to the processes involved in latent inhibition. Latent inhibition requires the inhibition of previously learned, not explicitly told, associations between a stimulus and its relevancy, whereas task switching is the inhibition of task sets that are changed from trial to trial. However, this process may be related to what occurs during negative priming task used in this thesis (see section 2.3.6. for full procedure of the negative priming task used in this research) as the negative priming task does not have an explicit change in task instructions, rather there is a change from trial to trial. In fact, Kok (1999) also pointed out the similarities in the mechanisms employed during the switch task and negative priming.

5.1.4. Focused attention paradigms

Focused attention refers to the narrowing of the attentional field towards targets, while inhibiting the non-targets from being attended to and subsequently being processed. The simultaneous presentation of targets and non-targets in tasks demands the employment of mechanism(s) required for suppressing the distractors, or irrelevant stimulus features, while concurrently enhancing the processing of the targets, or relevant stimulus features. This is what is referred to as interference in chapter four. Tasks that require focused attention are the flanker, Stroop, Simon, Negative priming, and latent inhibition tasks. The flanker and Stroop tasks used in this study both require the participant to identify some aspect of the target stimulus to respond accordingly, and have been associated with frontal lobe functioning, indeed Posner has termed the flanker task the 'executive functioning' component of the attentional network task (Posner, 1980). Whereas tasks like the flanker task have interference from peripheral distractors (stimulus location based), the Stroop task interference comes from two features of the same stimulus (stimulus feature based). Thus,

the flanker task requires the identification of the target stimulus as well as the target stimulus location, which will employ more visual processing than just feature based discrimination, i.e. both the dorsal (stimulus location) and the ventral streams (stimulus feature) (Kramer *et al.*, 1994). However, the spatial distinction between the target and distractors in the flanker task may improve focused attention towards the target, but this is still not sufficient to allow the selective processing of only the target stimulus. In both these tasks, and the Simon, latent inhibition, and negative priming tasks, some of the features or stimuli that a participant has been instructed to ignore, will be encoded and thus require additional inhibition/suppression at a later stage, potentially the response stage (Barnhardt *et al.*, 2008; Desimone, & Duncan, 1995).

Although, there is this similarity amongst these tasks, negative priming and latent inhibition are not only employing the inhibitory mechanisms at the input and cognitive stage to reduce interference. In addition to these mechanisms, these two tasks also require the inhibition of previously used stimuli or stimulus features. During negative priming, one must respond to a previously irrelevant location even though the stimulus itself stays the same, whereas during the latent inhibition task, one must respond to a previously irrelevant stimulus, with the stimulus location changing with each trial. Thus there is an additional inhibitory requirement in these two tasks, as well as a constant change in stimulus location.

Focused attention can also be measured during tasks that do not present the target and non-target concurrently, but rather in succession. This is reflected in the continuous performance task. These tasks can be spatial in nature with the stimulus changing location with each trial, and such tasks typically result in enhancements of the early sensory components P1 and N1. As discussed earlier C1 is not always altered due to changes in spatial features. The non-spatial versions of such tasks, like the continuous performance task used in this study, tend to elicit more endogenous components which are more negative when attending to relevant stimuli, and more positive when suppressing the irrelevant stimuli (Alho, Woods, & Algazi, 1994; Hillyard *et al.*, 1995). This indicates that, much like the P1-N1 complex, there is a separate mechanism for the inhibition or non-

targets and the enhanced processing of targets, although this 'selection negativity' or 'selection positivity' tends to occur later than the components of interest in this research. However, greater neural responses in macaques have been seen in the primary visual cortex to stimuli that induce a stronger pop-out effect (Smith, Kelly, & Lee, 2007) which may be a factor in a continuous performance task that uses both neutral and salient stimuli, with salient stimuli eliciting larger responses.

The final sub-category of focused attention is spatial cueing, which allows for the exploration of attentional focusing on a trial by trial fashion using both voluntary and involuntary orienting. This is reflected in the orienting component of the attentional network task. During these paradigms, a cue is presented before the target stimulus which may or may not indicate the location of that stimulus. It has been found that when a target stimulus was previously cued there was an enhanced P1 response (Hopfinger & Mangun, 1998). Using a longer inter-stimulus interval to this previous study (200-500ms) (Hillyard *et al.*, 1995), there was a decrease in the P1 response on invalidly cued trials compared to neutral, when the cue resulted in the participant reflexively looking in the opposite direction and were required to voluntarily look towards the correct location once the target appeared. This finding suggests that the P1 component is affected by the need to inhibit the invalidly cued attentional orientation. However, the N1 showed no effect when comparing invalid and neutral trials, but did show an increased negativity on valid trials compared to neutral (P1 showed no effects comparing valid and neutral trials), suggesting that the N1 component is related to the facilitation effects that come with the valid cue. In addition to this, activity in the primary visual cortex has been shown to be enhanced for an attended target when it was previously cued, demonstrating a facilitation effect (Poghosyan & Ioannides, 2008).

5.2. *Present study*

The aim of Experiment three was to elucidate the cognitive mechanism that may be reflected in visual sensory gating. It was predicted that the sensory gating observed for component P1

would correlate with some of the behavioural tasks but not all. Based on the previous chapter findings, and the potential similar mechanism underlying both auditory and visual sensory gating, gating of component P1 may correlate with the latent inhibition and continuous performance task. However, the visual nature of the tasks used in both chapters may result in disparate findings between the two forms of gating. Some of the tasks described above may require forms of inhibition that are employed at later stages of visual processing and thus beyond the time frame of the P1 latency. One element in the literature is the notion of spatial modulation and how P1 can be affected by spatial alterations in either the stimulus location or the spatial attention of the participant, thus we may find some correlations with tasks that involve some aspect of spatial attention. Finally, with regards to early visual processing, as reflected in both components C1 and P1, it is unlikely that they will correlate with the same tasks due to both reflecting different stages in the visual processing stream. However, both have been shown to be augmented by relevant or salient stimuli. A second aim of this research was to compare the correlations observed for visual and auditory sensory gating to reveal any similarities the two may have and help further understand if the two mechanisms are qualitatively similar.

5.3. Design

A correlational design was employed whereby visual sensory gating ratios (amplitude of the response to the second stimulus/amplitude of the response to the first stimulus x 100; see section 2.2.4. for more details regarding EEG analysis) were correlated with scores on each of the tests of inhibition (Stroop, Simon, latent inhibition, negative priming, go/no-go, switch, antisaccade, attentional network, and continuous performance). See chapter two for full methods and section 2.2.2. for the visual sensory gating procedures and 2.3. for the behavioural tasks procedures. The antisaccade task was removed from this experiment due to access to appropriate equipment. Participants completed the tasks in a pseudorandom

order (the exception to full randomization being that the switch task always immediately followed the go/no-go task).

In order to confirm that the expected group level effects for each of the behavioural tasks were present, one repeated measures *t*-test was used for each of the tasks comparing the average reaction time/accuracy during the relevant conditions, for a summary of the conditions and dependant variables for each task see Table 8. Based on findings from chapter three, analysis for visual sensory gating primarily focused on the component P1 at electrodes Pz and Oz as this is where visual gating was more robust. Cluster electrodes were not used as lateralisation of the gating effect was not found and this method more closely matches the standard method for auditory sensory gating. In addition to this, component C1 was also examined at these electrodes as this component has a similar latency to that of P50 in the auditory paradigm and will help elucidate which, if any, visual components elicit comparable findings to auditory gating. To measure the group effect of visual sensory gating, four Bonferroni corrected one-sample *t*-tests were used with the value of 100. A bivariate correlation of the gating ratios for each component and electrode, and the behavioural task measures was used to explore the relationship between these measures. Note that corrections were not performed for multiple correlations due to the focus being more on the large effect sizes if these correlations, which is more informative than *p* values alone. Following this, three partial correlations were conducted to control for differences in IQ (measured using Cattell's Culture Fair (CCF-IQ) Scale 2 form A), working memory capacity (measured using the automated-OSPAN), and IQ and working memory together.

5.4. Results

All group level effects during the behavioural tasks were significant, see Table 8. Initial analysis using four Bonferroni corrected one-sample *t*-tests with the value of 100 ($p=.013$), indicated that successful sensory gating was observed at both locations for the component

P1 ($Pz - t(30) = -5.10, p < .001$; $Oz - t(30) = -3.18, p = .003$). To examine if there was a difference in this gating, a paired-samples t -test was conducted, revealing a difference in gating at the two locations that was approaching significance ($t(30) = 2, p = .054$), with more gating being observed at the electrode Pz, see Figure 12 for descriptives and the grand average waveform for both electrodes. There was no significant gating observed for the C1 component at either electrode site ($Pz - \text{Mean} = 86.36, SE = 8.9$; $Oz - \text{Mean} = 91, SE = 9.9$). These results are in keeping with those reported in chapter three.

Table 8

Descriptive statistics and group-level effects for all cognitive control measures used in experiment three

Predictor variable	Index and test of effect
<i>Stroop Effect</i>	Mean incongruent RT (983ms, SD = 205) was greater than mean congruent RT (849ms, SD = 136), $t(30) = 5.56, p < .001$
<i>Simon Congruency Effect</i>	Mean incongruent RT (477ms, SD = 76) was greater than mean congruent RT (434ms, SD = 69), $t(30) = 6.57, p < .001$
<i>Conflicting (ANT)</i>	Mean incongruent RT was greater than mean congruent RT (mean difference = 95.80ms, SD = 43.46), $t(30) = 8.54, p < .001$
<i>No/No-Go Effect</i>	Mean percentage accuracy for go trials (responding, 98%, SD = 0.02) was greater than mean percentage accuracy for no-go trials (not-responding, 79%, SD = 0.21), $t(30) = 5.06, p < .001$
<i>Switch Cost</i>	Mean switch RT (464ms, SD = 75) was greater than mean non-switch RT (419ms, SD = 59), $t(30) = 5.86, p < .001$
<i>Latent inhibition</i>	Mean RT on pre-exposed trials (1221ms, SD = 402) was longer than mean RT on non-pre-exposed trials (1021ms, SD = 424), $t(30) = 5.49, p = .001$
<i>Negative Priming Effect</i>	Mean RT on ignored repetition trials (507ms, SD = 102) was greater than mean RT on neutral trials (480ms, SD = 89), $t(30) = 3.13, p = .004$
<i>Continuous Performance Accuracy</i>	Mean accuracy to respond to target stimulus (98%, SD = 0.02) was greater than chance, $t(30) = 174.83, p < .001$
<i>Continuous Performance RT</i>	Mean time to respond to target stimulus was 414ms (SD = 45)
<i>Alerting (ANT)</i>	Mean no cue RT (581ms, SD = 77) was greater than mean central cue RT (552, SD = 75), $t(30) = 3.44, p < .001$

<i>Orienting (ANT)</i>	Mean spatial cue RT (505, SD = 74) was faster than mean no cue RT (581, SD = 77), $t(30) = 8.16, p < .001$
<i>Cattell's Culture Fair</i>	Mean raw intelligence score was 35.48 (SD = 4.51)
<i>Automated OSPAN</i>	Mean OSPAN absolute score was 35.94 (SD = 20.03)

Note. Only reaction times from trials with correct responses were used.

The latency of the components C1 and P1 were similar for both electrodes and thus two paired-samples *t*-tests were used for each component using pooled data from both electrodes. This was done to investigate any latency effects similar to that in chapter three. These showed that for component P1, the latency of the response to the first stimulus presentation (Mean = 137.29, SE = 4.84) was significantly slower than the response to the second stimulus presentation (Mean = 118.9, SE = 3.25; $t(30) = 4.83, p < .001$). This pattern was the same for component C1 however this did not reach statistical significance (S1 – Mean = 76.84, SE = 3.97; S2 – Mean = 72.1, SE = 3.56; $p = .069$). In order to explore a possible reason for gating for component P1 and not C1, a bivariate correlation was used with the amplitude response to the first and second stimulus presentation and the gating ratio. A correlation between the ratio and the S1 amplitude would suggest better gating is the result of increased processing of the first stimulus. Conversely, a correlation with the S2 amplitude suggest better gating is related to a smaller S2 amplitude and thus more inhibition of S2. Thus, a correlation between the ratio and S2 is more indicative of better inhibition (superior gating). The P1 gating ratio at both electrode sites was significantly correlated with the amplitude of response to the second stimulus but not the first (Pz – $r = 0.35, p = .050$; Oz – $r = 0.42, p = .024$). This indicates that successful gating was related to a smaller amplitude in

response to the second stimulus. These correlations were not observed for component C1 at either electrode site.

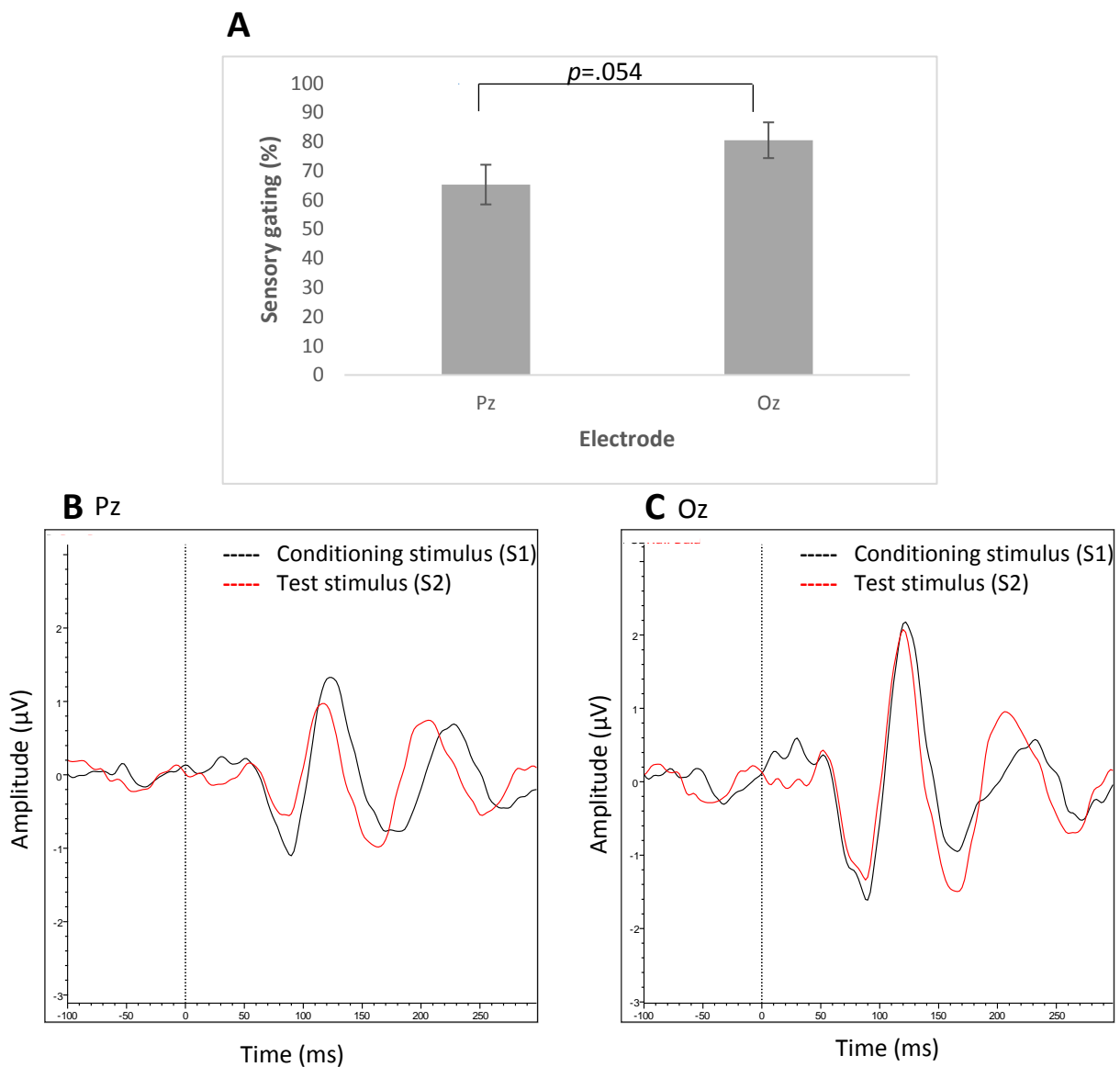


Figure 12. Panel A, average sensory gating ratio observed at electrodes Pz and Oz. Errors bars represent the standard error. Panel B and C, grand average waveforms for electrodes Pz and Oz respectively.

5.4.1. Component P1

A bivariate correlation was carried out with both the Pz and Oz sensory gating ratios for component P1. There were the same but fewer significant correlations between the Pz sensory gating ratio and the behavioural tasks compared to electrode Oz. Any significant discrepancies between Oz and Pz will be referred to throughout.

There was a significant negative correlation between the sensory gating ratio and latent inhibition, indicating that as the ratio increased (less inhibition), the latent inhibition effect decreased. In addition to this, positive correlations were observed between the sensory gating ratio, and the orienting component of the attentional network task and the continuous performance task reaction time when responding to salient stimuli. This suggests that a larger gating ratio (less inhibition) is related to an increased orienting proficiency and slower responding to salient stimuli. Scatterplots of these correlations can be seen in Figure 13. Using the William's *t*-test following a Fisher *r*-to-*Z* transformation, the magnitude of the correlation coefficients were compared resulting in no significant differences in magnitude between the three significant correlations ($p > .05$). A summary of the results can be seen in Table 9. Note that there was no significant correlation using electrode Pz for the continuous performance task. The ANT orienting score is the difference between the reaction time during non-spatially cued trials, and trials that provide a spatial cue. With this being said, the reaction time during each of these conditions was investigated separately, exploring the relationship of visual sensory gating with orienting towards a target stimulus with and without a spatial cue, rather than the amount a participant benefited from a spatial cue compared to no cue. The results of this post-hoc analysis showed no correlation between visual sensory gating and faster orienting towards a target stimulus with or without a spatial cue.

Table 9

Correlation coefficients from bivariate correlation between sensory gating and the measures of inhibition and psychometric tests. Component P1 at electrodes Pz and Oz.

Task correlations with sensory gating	Correlation coefficient (<i>r</i>)	
	Oz	Pz
<i>Executive Inhibition: Interference Control</i>		
Stroop	-.19	-.02
Simon	-.33	-.30
Flanker/executive control (ANT)	-.01	.10
<i>Executive Inhibition: Cognitive Control</i>		
Latent inhibition	-.52**	-.39*
Novel pop-out	.01	-.03
Negative priming	-.07	.10
<i>Executive Inhibition: Intentional Motor Inhibition</i>		
Go/no-go	.04	-.05
Switch	.24	.15
<i>Attentional Orienting</i>		
Orienting (ANT)	.53**	.38*
<i>Sustained Attention</i>		
Alerting (ANT)	.05	-.19
Continuous performance (neutral)	.32	.06
Continuous performance (salient)	.49**	.18
<i>Covariates</i>		
Intelligence: Cattell's Culture Fair	.23	.14
Working Memory: OSPAN	-.13	-.26

Note. * sig. to .05, ** sig. to .01.

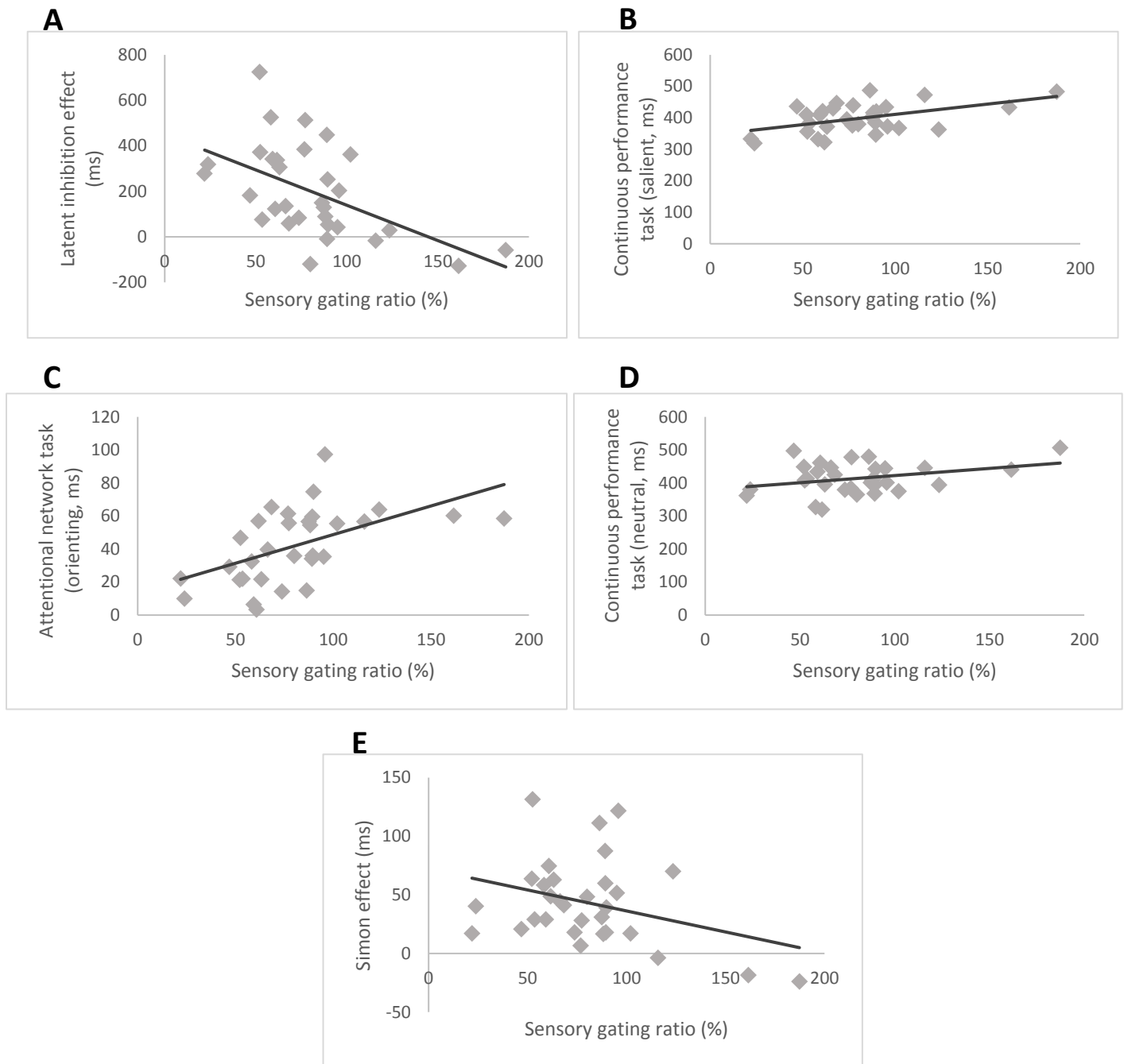


Figure 13. Scatterplots for significant correlations following a bivariate and partial correlation (component P1 and electrode Oz), adjusting for Cattell's Culture Fair score (fluid intelligence) and/or the OSPAN absolute score (working memory). Graphs a, b, and c are the significant correlations between the sensory gating ratio and the latent inhibition effect, reaction time to salient stimuli during the continuous performance task, and the orienting component of the attentional network task, respectively. Graphs d and e depict the relationship between the sensory gating ratio and the reaction time to neutral stimuli in the continuous performance task, and the Simon effect respectively. Note that the correlations represented in graphs d and e were only significant after adjusting for Cattell's Culture Fair score (CPT salient, Simon effect), and both the Cattell's Culture Fair score and the OSPAN absolute score (Simon effect).

Following this, several partial correlations were carried out adjusting for Cattell's Culture Fair score, the OSPAN absolute score, and both scores together. These results are summarised in Table 10 and William's t – tests confirm that there was no significant difference between the magnitudes of the correlation coefficients for the three behavioural tasks that correlated with sensory gating in the bivariate analysis. After adjusting for the Cattell's Culture fair score, there was a significant correlation between the sensory gating ratio and the continuous performance task (neutral) and the Simon effect. These correlations indicate that after adjusting for the effects of fluid intelligence, an increase in gating ratio is related to a slower reaction time to neutral stimuli, and a reduced capacity to respond quicker to congruent stimuli compared to incongruent. These results were only approaching significance when adjusting for the effects of working memory (CPT-neutral – $p=.09$; Simon – $p=.074$). Similar results were obtained when controlling for both CCF-IQ and the OSPAN. Scatterplots of these correlation are in Figure 13. Again using electrode Pz, there was no significant correlation with either the salient or the neutral aspects of the continuous performance task for any of the partial correlations.

Table 10.

Correlation coefficients after partial correlation controlling for fluid intelligence (Cattell's Culture Fair) and working memory (OSPAN). Component P1 at electrode Oz.

Task correlating with sensory gating	Bivariate correlation	Controlling for Cattell's	Controlling for OSPAN	Controlling for Cattell's and OSPAN
	Correlation coefficient (<i>r</i>)	Correlation coefficient (<i>r</i>)	Correlation coefficient (<i>r</i>)	Correlation coefficient (<i>r</i>)
Latent inhibition	-.52**	-.52**	-.52**	-.51**
Orienting (ANT)	.53**	.51**	.53**	.51**
Continuous performance (salient)	.49**	.51**	.48**	.49**
Continuous performance (neutral)	.32 (<i>p</i> =.075)	.37*	.31 (<i>p</i> =.09)	.36 (<i>p</i> =.056)
Simon effect	-.33 (<i>p</i> =.068)	-.45*	-.33 (<i>p</i> =.074)	-.47**

Note. * sig. to .05, ** sig. to .01.

5.4.2. Component C1

Although component C1 did not show any significant sensory gating, the same correlational analysis was still conducted with the behavioural tasks in order to explore differences between the later P1 component. As discussed in chapter three, C1 may not show significant gating due to the low perceptual load of the gating paradigm, however this does not negate a potential mechanism that is common between this component and behavioural tasks of attentional inhibition. The component C1 did not have the same behavioural task correlations as component P1, which is to be expected if there are indeed distinct, albeit related, mechanisms. As before there were the same but fewer correlations when using electrode Pz and so the subsequent results are those from electrode Oz. Following the

bivariate analysis, there was a significant correlation between the C1 gating ratio and the Simon effect ($r = -0.37$, $p = .039$), indicating that an increased gating ratio (reduced inhibition) is related to reduced ability to respond faster to congruent stimuli. In addition, there was also a significant correlation with the continuous performance task reaction time to neutral stimuli ($r = 0.37$, $p = .039$), demonstrating that an increase in ratio is related to slower responding to target stimuli. Finally, a significant positive correlation was observed with the alerting component of the attentional network task ($r = 0.39$, $p = .039$), with an increase in gating ratio being related to an increase in the capacity to respond faster when a temporal cue is presented. When investigating the reaction times during the conditions no cue and temporal cue independently, there were no correlations between these conditions and the gating measure. These results were identical to the partial correlations conducted, controlling for either CCF-IQ, the OSPAN absolute score, or both. There were no significant changes in the magnitude of the correlation coefficients compared to the bivariate correlation results. Additionally, using electrode Pz, there were no significant correlations between the C1 gating ratio and the Simon effect or the ANT alerting component.

5.5. Discussion

The first finding from this study was that significant sensory gating was only observed for the ERP P1 but not C1, which is consistent with the results found in chapter three. In addition to this, the results showed several correlations between the visual gating of the ERPs P1 and C1, and the behavioural tasks of attentional inhibition. This finding is in agreement with research showing that P1 is reliably altered in tasks that require the inhibition of unattended or to be ignored stimuli (Hillyard *et al.*, 1995), and C1 can be altered by attentional manipulations in specific contexts (Alink *et al.*, 2010; Kelly *et al.*, 2008).

A significant correlation was observed between P1 sensory gating and latent inhibition, with increased cortical inhibition being related to a larger latent inhibition effect. This will not be discussed in detail as this finding is the same as that found in the previous

chapter, using a measure of auditory sensory gating. It is possible that both forms of gating tap into similar early attentional processes, specifically, the processing of target and non-target stimuli during stimulus discrimination at the encoding stage, and the inhibition of the non-target stimuli during cognitive processing. Moreover, with regards to the hierarchical model of visual spatial attentional, this spatial processing occurs early on in the processing stream (as reflected in the component P1), and enhances the encoding of both target and non-targets as long as they occur within the attended location. It can be argued that during the visual search paradigm of the latent inhibition task, all locations are attended to until the target is found. In contrast to this finding, sensory gating of the component C1 was not correlated with latent inhibition. This is not surprising being that they are two different components, and this finding may indicate that P1 visual sensory gating is qualitatively more similar to P50 auditory sensory gating, a finding consistent with the results of chapter three. Moreover, it is important to remember that significant sensory gating was not observed for the component C1, and thus findings are likely to differ.

An additional correlation with P1 gating, again similar to the findings of chapter four, was the positive correlation with the continuous performance task. This experiment used both neutral and salient stimuli, and found that reduced gating was related to slower responding towards salient stimuli, and after controlling for fluid intelligence, slower responding to neutral stimuli. These correlations may reflect the sensitivity of P1 gating to attentional manipulations, since the CPT is a measure of sustained attention. However, as discussed in chapter four (section 4.5.), this may also be the result of the similarities between the experimental procedures for both the CPT and visual sensory gating paradigm. This would also explain why C1 gating also significantly correlated with the CPT.

In chapter four, the correlations similar to those above were the only ones to remain significant after partialling out the effects of fluid intelligence and working memory. Additional correlations found with P1 visual sensory gating were the orienting component of the ANT and the Simon task, with reduced gating reflecting better orienting proficiency, and a reduced capacity to respond quicker to spatially congruent stimuli, respectively. It is

surprising that reduced inhibition, as reflected by an increased gating ratio, was related to an increased ability to orientate towards the target stimulus faster when a spatial cue was presented. Post hoc analysis revealed that sensory gating was not related to simply orienting towards a target, but more specifically, the beneficial effect of a spatial cue. This indicates that it is not orienting per se that is related to visual sensory gating, but more likely a reduced capacity to inhibit non-target stimuli, resulting in faster encoding of the cue and thus a quicker response to that cue. A similar pattern of results was found for the component C1 and the alerting component of the ANT. An increase in gating ratio was related to faster responding when a temporal cue was given compared to the no cue condition. However, when exploring the reaction time to target stimuli with and without a temporal cue, there was no correlation between either condition and the C1 gating ratio. The correlation with the alerting component of the ANT, is again likely to reflect the benefit of a cue due to a decreased ability to inhibit non-target stimuli during the stimulus encoding stage.

With regards to the Simon effect, this occurs when spatially defined responses (left and right key press) are made to a non-spatial attribute of stimulus that continually changes its spatial location. Previous theories for the effect focused on the competition between the automatic route based on the spatial location of the stimulus, and the controlled route based on the content of the stimulus. These theories suggest that those who are better at inhibiting the automatic route prior to a response, perform better at this task, however the sequential dependency aspect of this task may suggest a more complex process. The sequential dependency effect provides evidence that the Simon effect is only observed when the previous trial is a spatially congruent trial (Praamstra, Kleine, & Schnitzler, 1999; Valle-Inclan, Hackley, & de Labra, 2002). When a previous trial is congruent (i.e. the the correct spatial response based on the stimulus content, coincides with the spatial location of the stimulus) the association between the stimulus features and location proves useful in making a correct response, i.e. the spatial route. Once this happens, one must overcome this learned association if the following trial is incongruent (Hommel, Proctor, & Vu, 2004; Wuhr & Ansorge, 2005). Consequently, if a trial is incongruent, this association is detrimental to

the response (the spatial route is no longer appropriate) and thus the association is not retained and no Simon effect is observed in the following trial. This implies that the Simon effect is not just about interference at the response stage, but also conflict with the previous response/association. In this respect, it is possible that visual sensory gating relates to the Simon effect for the same reason it does latent inhibition. Proficient sensory gating is beneficial for tasks that require the participant to inhibit a previous association during the encoding stage of stimulus processing. This correlation was also observed for the C1 component which may negate this theory due to the lack of a correlation between C1 and latent inhibition. Whereas the Simon effect is the consequence of trial by trial associations, latent inhibition has a more prolonged association period and potentially requires more effort to overcome. Therefore, C1 sensory gating may reflect a similar mechanism to that of P1 sensory gating, but only when the associations are easily overcome. Finally, the reason that this correlation, may not exist for auditory modality could be the spatial aspect of the task. The retinotopic layout of the visual V1 area, is spatial in nature, and thus potentially more sensitive to tasks that have a spatial element compared to the primary auditory cortex. Additionally, spatial aspects are known to be processed early in visual processing stream, which is reflected in the early components explored during this experiment.

5.6. Conclusions

This aim of this experiment was to explore different components of attentional inhibition, and how they relate to visual sensory gating. The correlations between visual sensory gating and latent inhibition and the Simon effect, suggests that visual gating is related to the encoding of relevant and irrelevant stimuli/stimulus features and the subsequent inhibition of previous associations regarding those stimuli. Once again this chapter found that while P1 visual sensory gating was observed, the gating of component C1 was not significant. In addition to this, there were more similarities between the correlations found with component P1 and those observed in the previous chapter with auditory P50 sensory gating. Taken together,

this provides further support that P1 sensory gating in the visual modality is qualitatively similar to P50 sensory gating in the auditory modality.

Chapter 6

Experiments 4 and 5: The sensitivity of auditory and visual sensory gating

6.1. Introduction and rationale

As defined in previous chapters, sensory gating is the reduction in the cerebral response to a second identical stimulus that typically occurs within 500ms of the first stimulus. One facet of this definition is the notion that the gating response is the brain's capacity to regulate its sensitivity to incoming sensory information, which in turn provides the basis for selective responding to important environmental stimuli (Davies *et al.*, 2009). The aim of this chapter was to further explore the function of sensory gating by investigating its sensitivity to experimentally manipulated stimulus change. This will help confirm whether or not sensory gating is primarily a mechanism that prevents the processing of irrelevant stimuli, or if it also acts to 'gate in' the relevant. If sensory gating is a pre-attentional mechanism designed to filter out all irrelevant information, i.e. filter out stimuli that are lacking additional information about the environment, then any and all changes to the second stimulus should elicit the equivalent cerebral response as the first. Moreover, if results are dependent on the type of stimulus change then this will provide more detailed knowledge of the limitations of the gating mechanism. This chapter explores some forms of stimulus changes in order to ascertain whether or not there is a limit to the sensitivity of the gating mechanism. In addition to this, previous chapters have discussed the existence of visual sensory gating and how it is potentially a qualitatively similar mechanism to auditory gating. This chapter will further examine this notion by assessing the similarities and differences in the sensitivity of each of these mechanisms.

One factor to explore regarding the sensitivity of sensory gating is what information is subsequently processed, as well as the information that is filtered out before further processing. Although sensory gating has been described as the ability of the brain to inhibit

or suppress incoming irrelevant information (Freedman et al., 1991), others have described it in vaguer terms, such as *the modulation of the cerebral response* (Braff & Geyer, 1990). This broader definition encompasses the capacity of the brain to 'gate in' the novel/salient, as well as 'gate out' redundant sensory information (Lebib et al., 2003). Boutros and Belger (1999) observed that the ERP P50 response was reduced for a second identical stimulus, but was augmented when the second stimulus was different to the first. The inhibitory function of sensory gating is explained by the neurons excited by the first stimulus inhibiting any subsequent stimulation of those same neurons. The 'gating in' response potentially occurs when a different set of not previously stimulated neurons are stimulated after the presentation of a non-identical stimulus. However, it must be noted that not all studies have found an augmented response to a second non-identical stimulus, and have instead found reduced but still significant gating (Mayer et al., 2009).

In light of this dichotomous notion of sensory gating, researchers have investigated the relationship between sensory gating during an oddball paradigm, during which a series of repetitive stimuli are randomly interrupted with a deviant stimulus. During a typical oddball paradigm, one would expect to observe the mismatch negativity (MMN) component in response to the deviant stimulus. This component reflects the cerebral response to stimuli which are novel in one or more perceptual feature, thus providing new or added significance. Sensory gating, as reflected in the attenuation of the component P50 has been linked to the MMN waveform, demonstrating a possible relationship between the gating in and out of stimulus information, and potentially indicating that these two mechanisms are not independent functions (Gjini et al., 2010; Kisley et al., 2004). If sensory gating reflects, or is related to, both the cerebral habituation (gating out) and disinhibition (gating in) to repeated or deviant stimuli, respectively, then it is prudent to explore the specific deviant perceptual features that will elicit an augmented response as opposed to attenuated.

With regards to auditory stimuli, an increase in the MMN waveform occurs when there is a qualitative change in the presented stimuli, that is, the intensity, frequency, spatial

locus, or duration of a stimulus (Näätänen, Paavilainen, Titinen, Jiang, Alho, 1993; Picton, Alain, Otten, Ritter, & Achim, 2000). Similarly, as well as being correlated with MMN, a change in stimulus intensity, frequency or pitch can also result in an increased P50 response (Boutros & Belger, 1999; Boutros et al., 1999; Boutros et al., 1995; Kisley et al., 2004). Conversely, later components such as N1 are more affected by the temporal characteristics of stimuli rather than the semantic. N1 sensory gating is related to changes in the inter-stimulus interval rather than qualitative changes (Cowan, 1995).

Visual evoked potentials are also augmented in response to stimulus changes. For instance, the C1 ERP, occurring at a similar latency as the auditory P50, is influenced by the spatial position of the stimulus in the visual field, however the P1 component is not (Clark et al 1995; Mangun, Hillyard, & Luck, 1993). In terms of stimulus relevance, stimuli appearing in the attended to location typically elicit a larger evoked response than that of stimuli in the unattended location (Zani & Proverbio, 2009). Although the standard sensory gating paradigm does not have explicit relevant and irrelevant stimuli, if we except relevance as being related to salient or novel information regarding the environment, then a second stimulus which is not identical to the first, could be described as relevant. Thus, we may expect to see the same augmented response of the visual ERPs during a gating paradigm. Later VEs have shown the same augmented response to location changes (Barnhardt *et al.*, 2008; Hillyard & Anllo-Vento, 1998), however some studies have demonstrated that this response is not always apparent for every VEP (Barnhardt *et al.*, 2008; Clark et al., 1995). Research has also shown that VEPs can be sensitive to changes in the content of a stimulus, such as colour and form (Proverbio *et al.*, 2010). Again this may not be the case for all VEPs, in fact some VEPs may be sensitive to spatial aspects of a stimulus while others respond to the content of a stimulus (Hillyard & Anllo-Vento, 1998; Hillyard & Münte, 1984). A possible explanation for the difference in sensitivity to the location and content of stimuli is that spatial attention occurs prior to attention based on features (Karns & Knight, 2009). Indeed, research has shown that visual ERPs are differentially affected by attention

manipulations based on the colour and the spatial aspects of a stimulus (Hillyard, & Münte, 1984).

In contrast to this research, Gawne and colleagues (2011) used a visual paradigm similar to auditory sensory gating, during which the second stimulus could either be in the same or a different location to the first stimulus, as well change in terms of colour/form. They found that the response to the second stimulus was gated out even when the second stimulus changed location and/or content, rather than being augmented as a result of stimulus changes. This research indicated that the sensitivity of sensory gating, as measured by ERPs, may be limited. The researchers suggested that these results may demonstrate that the VEP they explored (first positive peak, approx. P1) may portray the cortical activity of a large area in the striate cortex and thus visual stimuli that are presented within quick succession of each other will seemingly inhibit this area and thus elicit an attenuated response. Consequently, the VEP in their study may not be sensitive enough to detect changes in stimulus location and/or form and rather they only indicate that a stimulus occurred. This chapter has used the same stimulus changes as the research conducted by Gawne and colleagues in order to compare findings. These changes in the visual modality are colour/form using a red circle and a black and white checkerboard, and location by moving the stimulus from the top left to bottom left of the screen (or vice versa). Although a change in location may not be confounded, it must be noted that the change in form/colour includes more than one alteration and consequently limits conclusions that can be made regarding which one of these changes are responsible for any observed results.

6.2. Present study

In order to explore the sensitivity of sensory gating to stimulus changes, this chapter employs the standard auditory paradigm but with two types of stimuli rather than one, in

addition to changing the location of the stimuli. This allows for the comparison of the typical attenuated response to a second identical stimulus, with the response to a second non-identical stimulus. In addition to this, a comparable visual version of the task is used to explore any similarities or difference between the modalities. As previous research would suggest, an attenuated response should be observed for a second identical stimulus, and based on previous chapters, this response is expected to be found in both modalities, albeit less gating may be elicited in the visual modality. With regards to a change in stimulus form or location, research exploring the MMN waveform and the ERP P50 suggests that an augmented response will be found when the second stimulus is not identical to the first. However, different stimulus alterations may have different effects on each of the auditory ERPs associated with sensory gating. Again, these same pattern of results may be observed in the visual modality. However due to the topographic organisation of the striate cortex, earlier VEPs associated with this cortical region may in fact still elicit an attenuated response regardless of stimulus changes.

6.3. Experiment 4

6.3.1. Design

This was a 2x2x2 within-subjects design with the factors of stimulus modality (visual/auditory), stimulus type (same/different) and stimulus location (same/different). Each trial consisted of a conditioning and a test stimulus and thus the factor of stimulus type consisted of two types of stimuli for the first and the second stimulus, a checkerboard and a red circle (visual), or a beep and a click (auditory). Thus in the same stimulus type condition the two stimuli were either two checkerboards (two beeps) or two red circles (two clicks) and in the different stimulus type condition, the two stimuli were either checkerboard/red circle (beep/click) or red circle/checkerboard (click/beep). Additionally, the factor of stimulus

location consisted of two locations for the first and the second stimulus, top left and bottom left (visual), or left and right ear (auditory). Thus there were four conditions for both the visual and auditory experiments: same location and same stimulus (SLSS), same location and different stimulus (SLDS), different location and same stimulus (DLSS), and different location and different stimulus (DLDS). There were 40 trials per condition within each modality block and trials were presented in a random order. The visual and auditory sections of the study were counterbalanced across participants. Detailed methods can be found in chapter two.

As discussed in chapter 2, for this analysis, component P50 at electrode Cz was used for the auditory modality as this is the standard method within the literature. Moreover, chapter three confirmed that robust sensory gating can be observed at this electrode/component. A secondary analysis of the auditory component N1 was used throughout in order to see if any differences between the modalities was due to the latency of the components, with the auditory P50 occurring sooner than the visual P1. The auditory N1 latency is more similar to that of the visual P1. Results in chapter three and five have shown that visual sensory gating is more reliably observed for the component P1 and that this is found at electrodes Pz and Oz. Moreover, these previous chapters have shown that more gating is found at the Pz electrode compared to Oz. Consequently, this final chapter will focus on component P1 at electrode site Pz. To confirm that sensory gating was observed, a 2x4x2 repeated-measures ANOVA was conducted with the response amplitudes and factors modality (auditory, visual), condition (SLSS, SLDS, DLSS, DLDS), and stimulus (S1, S2). A 2x4 ANOVA using the gating ratios was then employed with the factors modality (auditory, visual), and condition (SLSS, SLDS, DLSS, DLDS), in order to investigate differences in the magnitude of gating.

Finally, a bivariate correlation was conducted using the gating ratios. This used the ratios for each condition within each modality (total of 28 correlations). As stated in previous chapters corrections were not performed for multiple correlations. Correlations were performed between modalities to help answer, as in previous chapters, if there is any

relationship between the two gating mechanisms and thus will continue to help elucidate the notion of a shared or separate mechanism. Within-modality correlations will help examine the relationship between conditions and thus support any findings that stimuli within two conditions have been similarly processed. For example, if the SLSS and SLDS conditions both exhibit gating and are also positively correlated, this may suggest that the gating mechanism has operated in the same way for the different conditions, which would show a lack of sensitivity the stimulus changes used in the SLDS condition.

6.3.2. Results

6.3.2.1. Successful sensory gating

The results of the 2x4x2 ANOVA to explore the presence of sensory gating revealed no significant effect of stimulus and no interactions with this factor. To explore this further, 2 separate 4x2 repeated measures ANOVAs were employed for each modality. These has the factors condition (SLSS, SLDS, DLSS, DLDS), and stimulus (S1, S2). The results for the auditory modality showed a significant effect of stimulus ($F(1, 28) = 31.48, p < .001, \eta_p^2 = .53$), with the response amplitude to stimulus 1 (Mean=1.98 μ V, SE=0.26) being larger than stimulus 2 (Mean=1.24 μ V, SE=0.16). There was also a significant interaction between stimulus and condition ($F(3, 84) = 8.26, p < .001, \eta_p^2 = .23$). To explore this interaction, four Bonferroni corrected paired-samples *t*-tests were conducted comparing the S1 and S2 amplitudes for each of the four conditions ($p = .0125$). These tests showed that significant gating was found for the conditions SLSS ($t(28) = 6.45, p < .001$) and SLDS ($t(28) = 4.41, p < .001$). These conditions also exhibited significant gating for the auditory component N1 (SLSS - $t(28) = 10.72, p < .001$; SLDS - $t(28) = 4.69, p < .001$). In the visual paradigm, the ANOVA revealed no significant effect of stimulus, nor significant interactions. In order to confirm the potential absence of gating in the visual modality, another four Bonferroni corrected paired-samples *t*-tests were employed for the four conditions ($p = .0125$). The

results of these tests showed that the condition of SLSS did exhibit significant gating ($t(28)=5.3$, $p<.001$), and the condition of SLDS was approaching significance ($t(28)=1.88$, $p=.07$).

6.3.2.2. *Within and between modality comparisons*

In order to investigate the differences and/or similarities between the gating exhibited in the two modalities, a repeated-measures ANOVA using the gating ratios ($S2/S1 \times 100$) was employed, with the factors modality (auditory, visual) and condition (SLSS, SLDS, DLSS, DLDS). The results reveal a significant effect of modality ($F(1, 25) = 7.3$, $p = .012$, $\eta^2 = .23$), with more gating occurring during the auditory modality (mean = 70.53, SE = 4.74) compared to the visual modality (Mean = 87.68, SE = 5.23). There was also a significant effect of condition ($F(3, 75) = 15.42$, $p < .001$, $\eta^2 = .38$), for which Bonferroni corrected pairwise comparisons confirm that more gating was found for the SLSS condition compared to all other conditions, and the SLDS condition elicited more sensory gating than the DLDS condition but not the DLSS condition, see Figure 14. No significant interaction was observed, indicating a similar effect of condition for both modalities. However, successful gating was only observed during two of the four conditions, and thus it may be misleading to average the gating across conditions in order to compare the amount of gating in each modality.

To verify these findings, a second 2x2 ANOVA (again using the gating ratios) was conducted with the factors modality (auditory, visual), and condition (SLSS, SLDS). These results also showed a significant effect of modality ($F(1, 28) = 18.48$, $p = .012$, $\eta^2 = .4$), with the auditory conditions exhibiting more gating (Mean = 50.77, SE = 3.75) compared to visual (Mean = 80.35, SE = 5.41), and a significant effect of condition ($F(1, 28) = 12.32$, $p = .002$, $\eta^2 = .31$), with more gating occurring during the SLSS condition (Mean = 54.3, SE = 4.32) compared to the SLDS condition (Mean = 76.82, SE = 4.64). Again, no significant interaction

was observed. See Table 11 for descriptive statistics of the sensory gating ratios and amplitudes for each condition and modality. Again these results were the same when comparing the auditory component N1 with the visual component P1. One difference occurred when comparing the differences for each condition, as the difference between the modalities for the condition SLSS was not significant. However, the trend for more gating to be observed during the auditory condition remained present.

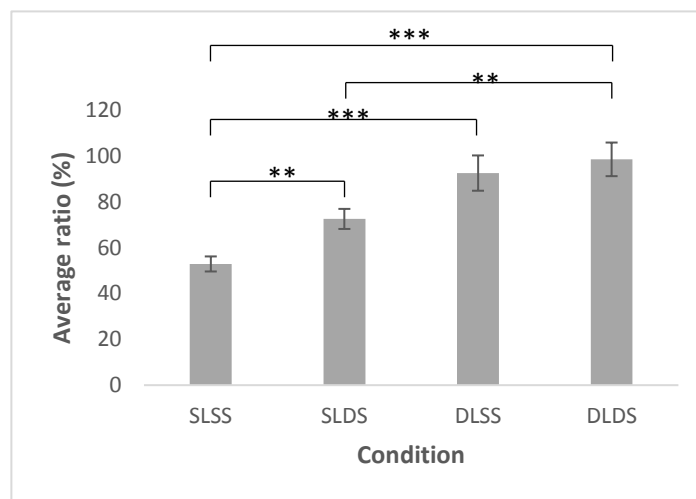


Figure 14. Average sensory gating ratios for each experimental condition for the visual (P1 and electrode Pz) and auditory (P50 at electrode Cz) modalities combined. Error bars represent the standard error. ** is sig. to .01 and *** is sig. to .001.

Table 11.

Averages and standard deviations for the ERP amplitudes and latencies, and the sensory gating ratio for each condition and modality.

Modality	Condition	Average S1 amplitude (uV) (SD)	Average S1 latency (ms) (SD)	Average S2 amplitude (uV) (SD)	Average S2 latency (ms) (SD)	Average Ratio (%) (SD)
Auditory (P50)	SLSS	2.13 (1.12)	54.32 (18.97)	0.82 (0.5)	50.17 (17.39)	42.28 (24.7)
	SLDS	2.06 (1.45)	55.93 (17.75)	1.15 (1.04)	51.86 (19.19)	59.27 (38.65)
	DLSS	1.74 (0.99)	56.52 (17.47)	1.31 (0.87)	53.56 (18.81)	85.5 (48.09)
	DLDS	2 (2.93)	57.21 (19)	1.68 (2.09)	58.41 (20)	101.59 (53.04)
Auditory (N1)	SLSS	6.84 (2.43)	118.45 (25.73)	4.03 (1.75)	109.17 (29.22)	59.38 (20.41)
	SLDS	6.5 (2.68)	114.1 (18.74)	4.51 (2.18)	108.86 (19.96)	71.66 (32.52)
	DLSS	6.49 (3.22)	117 (17.93)	5.99 (2.45)	114.45 (19.71)	102.85 (43.73)
	DLDS	6.73 (2.67)	110.14 (21.81)	5.81 (2.27)	110.93 (26.06)	99.18 (48.9)
Visual	SLSS	4.23 (1.86)	123.03 (20.23)	2.73 (1.9)	123.69 (25.94)	66.32 (33.31)
	SLDS	4.7 (2.9)	118.34 (32.78)	4.06 (2.72)	120.79 (35.02)	94.37 (44.58)
	DLSS	4.53 (3.35)	114.07 (25.88)	4.11 (2.56)	112.64 (26)	99.61 (54.4)
	DLDS	9.87 (28.77)	122.64 (25.35)	4.16 (1.99)	125.54 (28.37)	101.99 (47.91)

Note. Components used for the auditory paradigm are P50 and N1 at electrode Cz, and the visual component is P1 at electrode Pz. Absolute values used for the N1 amplitudes.

A bivariate correlation was used to identify the strength of relationships between sensory gating in the two modalities. The only significant correlations between the visual and auditory paradigms were between the auditory SLSS condition and the visual DLSS condition ($r=0.38$, $p=.049$), and the auditory SLDS condition with the visual DLDS condition ($r=0.46$, $p=.016$). All other between modality correlations were non-significant ($p>.05$). A second correlational analysis using the auditory component N1 found that there were no significant between modality correlations ($p>.05$). With regards to within modality correlations, a correlation was observed in the auditory modality which was approaching significance in the visual modality, whereby an increase in gating ratio during the DLSS condition was related to an increase in the gating ratio for the DLDS condition (auditory – $r=0.47$, $p=.009$; visual – $r=0.35$, $p=.08$). This was also observed for the auditory component N1 ($r=0.47$, $p=.038$). There was an additional correlation for the auditory paradigm using component N1, between conditions SLSS and SLDS ($r=0.39$, $p=.01$).

A bivariate correlation was then conducted between the gating ratios and the S1 and S2 amplitudes (16 in total). As discussed in previous chapters, a positive correlation between the ratio and the S2 amplitude indicates that better gating is related to the second stimulus being processed less. However, a negative correlation with the S1 amplitude suggests that the observed gating is more related to the first stimulus being processed more rather than better gating per se of the second stimulus presentation. Significant correlations were found between the sensory gating ratios and amplitude of primarily the S2 amplitude. Within the auditory modality, a significant correlation was found between the gating ratio and the S2 amplitude for the conditions that demonstrated successful sensory gating (SLSS – $r=0.64$, $p<.001$, SLDS – $r=0.61$, $p<.001$). This finding suggests that successful gating was related to the S2 amplitude being smaller than the first, rather than the S1 amplitude being larger to begin with. A significant correlation was also observed between the DLSS conditions ratio and the S1 and S2 amplitudes (S1 – $r=-0.38$, $p=.045$; S2 – $r=0.38$, $p=.040$), implying that those with a higher gating ratio demonstrated a smaller S1 amplitude as well as

a larger S2 amplitude. For the auditory component N1, the results revealed a similar pattern for conditions SLSS and SLDS, however for the conditions that did not demonstrate successful sensory gating, both conditions were significantly correlated with the S1 amplitude but not the S2 amplitude (DLSS – $r=0.69$, $p<.001$; DLDS – $r=0.68$, $p<.001$). In the visual modality, a comparable correlation between the SLSS ratio and the S2 amplitude was found ($r=0.59$, $p<.001$), as well as similar correlations between the DLSS ratio and the S1 and S2 amplitudes (S1 - $r=-0.35$, $p=.069$; S2 - $r=0.45$, $p=.014$). In addition to this, significant correlations were observed between the DLDS conditions and the S1 and S2 amplitudes (S1 – $r=-0.45$, $p=.016$; S2 - $r=0.49$, $p=.009$).

6.3.3. Discussion

This chapter aimed to explore the sensitivity of sensory gating and whether certain changes to the second stimulus in a standard sensory gating paradigm would elicit the same cerebral gating found in previous research when both stimuli are identical, or if an augmented response would be observed. The theory suggested by Braff and Geyer (1990) indicates that whenever two identical stimuli are presented within quick succession, the ERP response to the second stimulus is attenuated compared to the first. Moreover, when the second stimulus is not identical, this stimulus provides new information and consequently no gating occurs in order for this new information to be processed. In fact, an augmented response may be observed in this situation (Boutros & Belger, 1999). In addition to this, this chapter compared auditory and visual paradigms to explore further the potential shared or qualitatively similar mechanism involved in the two modalities.

The results from this experiment first demonstrated that, as expected, sensory gating was observed in both modalities when the first and second stimulus were identical. However, when comparing the either the auditory component P50 or N1 with the

visual component P1, there was less gating during the visual paradigm, which is consistent with the results found in previous chapters. The trend in results from both the auditory and visual paradigms suggest that when successful gating was observed, this was related to the response to the second stimulus being smaller, and independent of the S1 amplitude. Conversely, in many of the conditions in which successful gating was not found, this larger gating ratio was related to a smaller S1 amplitude to begin with, as well as a larger S2 amplitude.

In addition to the expected gating during the SLSS condition, significant gating was also observed when the stimulus content changed for the auditory paradigm and was approaching significance for the visual paradigm. These findings are consistent with previous research, which has also found successful auditory sensory gating, albeit reduced, in conditions when the second stimulus is qualitatively different from the first (Mayer *et al.*, 2009). This runs counter to the notion that an augmented P50 response would have been elicited by a second non-identical stimulus (Boutros & Belger, 1999; White & Yee, 2006). Moreover, Gawne and colleagues (2011) found successful visual sensory gating when stimulus content was altered in the same manner as this research. The reason for a non-significant result for the visual paradigm may indicate a difference in the gating mechanism. For example, perhaps VEPs are more sensitive to changes in the content of a stimulus, such as colour and form (Proverbio *et al.*, 2010), compared to auditory ERPs. However, the reduced gating in general may also explain this finding. As discussed in chapter three (section 3.4.), reduced visual gating may be a consequence of continuous visual stimulation throughout the study compared to the auditory modality which is not affected by additional stimuli outside of those used within the experimental procedure. If this is the case, then it is plausible that gating may have been significant in the condition of SLDS if participants' views were limited to the screen in front of them.

These findings suggest that sensory gating still occurs regardless of the perceptual features of a stimulus. However, as there was more gating when the stimulus and location

were both the same compared to only the location remaining the same, this implies that some of the altered stimulus features have been processed in the condition where only the stimulus type changes. This finding does support the theory of gating in as well as gating out information, however there appears to be a limit to the processing of changes at this stage. Although a significant difference was observed between the SLSS and SLDS conditions, no such difference was found between the DLSS and DLDS conditions. If a change in stimulus features still elicited some additional processing, then we would expect to observe a further reduction in gating or even augmentation in the DLDS condition. In fact, the correlations between the conditions DLSS and DLDS further imply that at this stage in stimulus processing, once the location of the stimulus is altered, no additional changes are processed. The fact that this study failed to find further changes in the gating ratio when both the location and the content changed, may indicate that the processing of changes in stimulus location supersedes that of changes in stimulus content. Indeed, during visual paradigms, a difference has been observed in the sensitivity to the location and content of a stimulus which has been attributed to spatial attention occurring prior to attention based on features (Karns & Knight, 2009). If spatial attention occurs first, then changes in the relevance (i.e. saliency) of a stimulus due to its location will be processed and subsequently gated in as a priority. Conversely, stimulus features are processed later and consequently some gating is still observed when the location remains the same, but no additional changes in processing are seen when the location changes.

With regards to the changes in stimulus location, this research found no significant gating in conditions where the location of the second stimulus was altered. This is in contrast to Gawne and colleagues (2011) who found successful gating even in conditions where the location changed. A potential reason for this is the inter-stimulus interval used in their study compared to the present research. Whereas they used a short 50ms ISI, this study used a 500ms ISI in order to allow for closer comparison with the auditory modality. Thus, perhaps 50ms is too fast for any additional processing to occur and for the stimulus to be identified as

novel, which is reflected in successful gating regardless of what has changed. Conversely, these results are in keeping with previous studies that show a reduction in gating or even augmentation of the second response due to stimulus changes, as a result of 'gating in' new information (Braff & Geyer, 1990). This sensitivity to location has also been observed in the visual modality, with later VEPs showing an augmented response to location changes (Barnhardt *et al.*, 2008; Hillyard & Anllo-Vento, 1998). The reason for a differential effect of stimulus type and location may be due to the order in which stimulus features are processed. Research that manipulated the spatial aspects of a stimulus, found that altering the location of an attended stimulus, augmented the response of several components at early at a positive deflection around 122ms regardless of the colour of the stimulus (Hillyard, & Münte, 1984). The effects of manipulating the colour of the stimulus were only seen when the spatial manipulations were more difficult. The procedures of experiment four are likely to reflect an easy spatial manipulation, as the location changes are easily discriminable. Consequently, the location of the stimulus is processed before that of the colour/form and this may explain why there is still gating during the change in stimulus type condition but not for the change in stimulus location. These results are also in keeping with fMRI studies, which investigate the effects of deviant stimuli on neuronal adaptation. As discussed briefly in section 1.3., fMRI adaptation studies observe a decrease in cortical activation when identical stimuli are presented in sequence. Moreover, with every subsequent presentation of an identical stimulus, activation decreases further. As with this chapters findings, when certain stimulus features are altered, this can reverse the adaptation effects, but only if the voxel being measured contains the neurons sensitive to the stimulus feature that has changed (Sawamura, Orban, & Vogels, 2006). Taken together, these results indicate that the mechanism of sensory gating is more sensitive to changes in stimulus location compared to stimulus content, and that this is potentially a shared trait for both the visual and the auditory modalities. Thus, it is surprising that fewer correlations were found between the two modalities. The only significant correlations between the modalities were found when the stimulus content conditions were the same, i.e. when the stimulus was the same for both

modalities or the stimulus was different for both modalities. This may suggest that the mechanisms are similar in terms of stimulus content processing, but diverge during spatial processing.

6.3.4. Conclusions

To conclude, significant gating was observed even when the content of a stimulus was altered. The reduction in gating compared to using two identical stimuli suggests that some additional processing has occurred when the stimulus features have been altered, however they have not been altered sufficiently to preclude gating. In contrast, changes to the stimulus location did result in no discernible sensory gating and thus the gating mechanism is potentially more sensitive to spatial changes compared to semantic ones. These results only partially validate the theory that sensory gating is a pre attentive process designed to filter out irrelevant and 'gate in' all relevant information, with spatial changes being deemed as relevant changes more so than semantic changes. The similar results found in the visual paradigm indicate that the mechanisms involved are qualitatively similar.

6.4. Experiment 5

6.4.1. Rationale

The results from experiment four indicate limitations in the sensitivity of sensory gating, suggesting that the mechanism is more sensitive to spatial changes compared to non-spatial changes. Other experimental manipulations that may alter the observed sensory gating are changes in attentional demands. Much of the research into auditory sensory gating refer to P50 sensory gating as a pre-attentional process (Adler *et al.*, 1992; Boutros & Belger, 1999;

Freedman *et al.*, 1991; Jerger *et al.*, 1992; Yee *et al.*, 2010), suggesting that attentional effects are not seen until later components such as N1 (Braff & light, 2004; White & Yee, 1997). The typical auditory sensory gating paradigm, as used in experiment four, is considered a passive task requiring no overt behaviours from the participant. This is often used to explore sensory gating due to the notion that P50 is an exogenous component and requires no mental operations from the participant, and simple sensory stimulation is enough to produce P50 and the gating effects of repeated presentations. This is in contrast to the later components such as P300 which are endogenous and require a cognitive task in order to be elicited (Boutros *et al.*, 2004). However, there is still some debate regarding the possible manipulation of the component P50 due to attention. Experiment five replicates experiment four (conducted on different participants to experiment four) but with the addition of a task implemented to further engage the participants and ensure that their attention is on the stimuli being presented. This task is described in more detail in chapter two. An infrequent, additional stimulus was presented during each paradigm (bell ring and blue square) to which participants were told to respond to by pressing a button on a response pad, thereby increasing the attentional requirements of the task compared to the passive version in experiment four. This, therefore, addresses the effects of attention on sensory gating as well as the effects that attention has on the sensitivity of sensory gating to changes in stimulus type and location. It may be possible that actively attending to the presented stimuli will increase the sensitivity of sensory gating to stimulus manipulations, allowing for increased processing of stimulus changes and thus reduced gating. However, if sensory gating is a pre-attentive process then the same results as experiment four should be found.

As sensory gating is primarily explored within the auditory modality, much research has already been conducted regarding the effects of attention. When attention was manipulated by having participants either discriminate between paired-stimulus intensities or the number of stimuli presented, the P50 sensory gating was unaffected (Jerger *et al.*, 1992). The effects of these tasks were only observed later for the N1 component. The same

task conducted later by White and Yee (1997) found the same results. Moreover, research using both scalp and intracranial recordings during the standard passive version and an active discrimination version of the sensory gating paradigm, also found that P50 was unaffected by attention (Rosburg *et al.*, 2009). In contrast to these studies, others have found a significant effect of attention on P50. When participants were required to selectively respond to specific stimuli the magnitude of sensory gating was reduced compared to the standard passive task (Guterman, Josiassen, & Bashore, 1992). Guterman and colleagues further found that the second P50 response was not attenuated at all when participants were instructed to count the occurrence of target stimuli. This research suggests that sensory gating is less likely when a subject's attention is focused upon the presented stimuli. In addition to this, focusing attention on the auditory stimuli was found to increase the amplitude of the S1 P50 response (although not the S2 response or the P50 gating ratio) (Gjini *et al.*, 2011). Finally, when patients with schizophrenia and control subjects were instructed to respond whenever a pair of stimuli were presented, and thereby directing attention to the second stimulus, the sensory gating ratio increased for both groups, indicating that attentional manipulations can interfere with sensory gating in healthy participants (Yee *et al.*, 2010).

Visual sensory gating has not been explored with regards to attentional manipulations, although research has been conducted on the effects of attention upon the amplitudes of the VEPs. When ERP responses are compared for stimuli that are explicitly attended to compared to stimuli to which attention has not been explicitly directed, the amplitude of components representing both the striate and extrastriate cortices increased (Clark & Hillyard, 1996; Slotnick *et al.*, 2003; Somers *et al.*, 1999; Zani & Proverbio, 2009). Functional imaging and magnetoencephalography (MEG) recordings have also indicated enhancement of activity towards stimuli that are attended to and attenuation of responses to unattended or irrelevant stimuli (O'Conner, Fukui, Pinsk, & Kaster, 2002; Poghosyan & Ioannides, 2008). In fact, increasing the attentional load has shown to further reduce the C1

and P1 responses successively to unattended stimuli possibly as part of a dual inhibitory mechanism (Rauss *et al.*, 2009). Poghosyan and Ioannides investigated both the auditory and visual modalities and found the same results in the primary auditory and visual cortices at latencies as early as P50 and C1. In contrast to the evidence suggesting that attention can influence the cortical response to stimuli, other research suggest that these effects are only seen later extrastriate regions of the visual cortex as reflected in the P1 response, rather than as early as C1 (Clark & Hillyard, 1996; Gonzalez *et al.*, 1994; Heinze *et al.*, 1994). This finding may be related to lower load conditions, during which attentional modulation does not occur until further down the visual processing stream at P1. Simply using an active task rather than a passive one, may not be enough to elicit attentional modulations of C1 (Fu, Fedota, Greenwood, & Parasuraman, 2010).

6.4.2. Design

For each modality, a 2x2 within-subjects design was employed with the factors of stimulus type (same/different) and stimulus location (same/different). The same four conditions were used as in experiment four. The only change to the experiment was the addition of a third stimulus type, which appeared randomly throughout the study with a total of 20 appearances. For the auditory experiment this was a bell ring, and for the visual, a blue square. This stimulus always appeared on its own and without a second test stimulus presentation. Again trials were randomized. For a detailed description of the methods see chapter two. Different participants completed the auditory and visual paradigms to reduce fatigue experienced during the longer experiment four and help increase attentional capacity. The same electrodes and components were explored as in experiment four, with components P50 and N1 at electrode Cz for the auditory modality, and component P1 and electrode Pz for the visual modality.

Similar analysis as experiment four was conducted. For each modality, a 4x2 repeated measures ANOVA was employed using the response amplitudes, with the factors condition (SLSS, SLDS, DLSS, DLDS) and stimulus (S1, S2). Once the presence of successful gating was ascertained, an ANOVA was conducted using the gating ratios to compare the magnitude of gating observed across and within the modalities. This employed the within-subjects factor of condition (SLSS, SLDS, DLSS, DLDS) and between-subjects factor of modality (auditory, visual). Once conducted for the primary components of P50 (auditory) and P1 (visual), this was repeated using the auditory component N1 to ascertain whether or not any differences between the modalities were due to the difference in latency between P50 and P1. Following this two bivariate correlations were employed using the gating ratios in order to investigate the relationship within and between modality gating (28 correlations), and between the ratios and the S1 and S2 amplitudes (16 correlations). Consistent with previous chapters, correlations were not corrected for with a focus primarily on the large effect sizes.

6.4.3. Results

6.4.3.1. Successful sensory gating

The results of the auditory 4x2 ANOVA revealed a main effect of stimulus ($F(1,7)=9.42$, $p=.018$, $\eta^2=.57$), with the response amplitude to stimulus 1 (Mean=1.84 μ V, SE=0.20) being significantly larger than the response to stimulus 2 (Mean=1.0 μ V, SE=0.24), indicating that gating was observed overall for the modality. There was no significant interaction between stimulus and condition, however four Bonferroni corrected paired-samples t -tests ($p=.0125$) comparing the response amplitude to stimulus 1 and 2 for each of the conditions showed that significant gating was only observed for the conditions SLSS ($t(7)=5.75$, $p=.001$) and SLDS ($t(7)=3.13$, $p=.010$). There was no significant difference between the first and second

stimulus response amplitudes for the conditions DLSS and DLDS ($p > .0125$). Comparable results were seen with the auditory component N1, showing a significant main effect of stimulus ($F(1,7)=11.29$, $p=.012$, $\eta^2=.62$), which following four corrected t-tests was significant in the conditions SLSS ($t(7)=3.62$, $p=.008$) and SLDS ($t(7)=4.35$, $p=.003$). Similar results were seen for the visual modality, with the 4x2 repeated-measures ANOVA also revealing a main effect of stimulus ($F(1,9)=17.68$, $p=.002$, $\eta^2=.66$), with the response to stimulus 1 (Mean=6.83 μ V, SE=0.69) being significantly larger than stimulus 2 (Mean=5.02 μ V, SE=0.46). There was also a significant interaction between stimulus and condition ($F(3, 27)=7.77$, $p=.001$, $\eta^2=.46$), with four Bonferroni corrected paired-samples t -tests ($p=.0125$) comparing the response amplitude to stimulus 1 and 2 for each of the conditions, revealing significant gating only for conditions SLSS ($t(9)=5.62$, $p<.001$) and SLDS ($t(9)=3.7$, $p=.005$). For descriptives see Table 14.

6.4.3.2. Within and between modality comparisons

Using the gating ratios, a between-subjects ANOVA was conducted to explore the differences between visual and auditory gating. A significant effect of modality was found ($F(1,16)=9.92$, $p=.006$, $\eta^2=.38$), showing more gating was observed during the auditory paradigm. However, four Bonferroni corrected pairwise comparisons, comparing the difference in each condition between the modalities, indicated that this significant difference in modality was only evident in the SLSS condition ($p=.006$), for which the auditory paradigm demonstrated more sensory gating compared to the visual modality. In no other condition was there a significant difference in gating ratio between the two modalities. When comparing modalities using the auditory component N1, no significant differences were observed for any condition between the two modalities. (See Table 12 for amplitude and ratio descriptive statistics for all conditions for each modality).

To determine the differences within each modality (as different participants completed each paradigm), and avoid more gating within the auditory modality having a disproportionate effect on the results, two separate ANOVAs were employed with the factor of condition (SLSS, SLDS, DLSS, DLDS). This revealed a significant effect of condition within the auditory ($F(3, 21)=4.8$, $p=.011$, $\eta^2=.41$) and the visual ($F(3, 27)=6.86$, $p=.001$, $\eta^2=.43$) modalities. Bonferonni adjusted pairwise comparisons (a total of 6 comparisons) indicated that within the auditory paradigm, the SLSS condition showed significantly more sensory gating than the DLDS condition ($p=.049$ following adjustment). No other differences were significant and no significant differences were found between the conditions for the component N1. In the visual paradigm, six corrected pairwise comparisons revealed that the condition SLSS demonstrated significantly more gating than the conditions DLSS ($p=.027$ following adjustment) and DLDS ($p=.007$ following adjustment). See Figure 15 for a summary of these findings.

Table 12

Averages and standard deviations for the ERP amplitudes and latencies, and the sensory gating ratio for each condition and modality.

Modality	Condition	Average S1 amplitude (μ V) (SD)	Average S1 latency (ms) (SD)	Average S2 amplitude (μ V) (SD)	Average S2 latency (ms) (SD)	Average Ratio (%) (SD)
Auditory (P50)	SLSS	1.97 (0.78)	49.25 (10.1)	0.51 (0.6)	45.25 (17.76)	24.2 (23.3)
	SLDS	1.59 (0.87)	53.63 (9.38)	0.68 (0.33)	49.38 (14.37)	49.55 (31.34)
	DLSS	2 (1.38)	52.63 (14)	1.08 (1.26)	47.75 (15.81)	62.07 (62.17)
	DLDS	1.81 (0.59)	55.75 (13.5)	1.74 (1.38)	51 (12.96)	102.2 (76.96)
Auditory (N1)	SLSS	8.6 (3.73)	121.38 (19.38)	4.29 (1.6)	109.5 (11.3)	56.09 (25.2)
	SLDS	8.21 (2.99)	113.25 (9.63)	4.74 (2.12)	112.75 (14.13)	58.24 (16.14)
	DLSS	8.01 (3.68)	103 (36.89)	5.89 (1.58)	112.38 (11.56)	82.27 (27.6)
	DLDS	7.94 (3.65)	113 (21.27)	6 (1.99)	105.89 (8.9)	84.57 (32.15)
Visual	SLSS	6.88 (2.4)	141.3 (32.9)	3.68 (1.67)	134 (26.19)	54.1 (17.02)
	SLDS	7.35 (2.9)	141.6 (22.46)	4.8 (2.45)	144.2 (22.42)	66.81 (27.39)
	DLSS	7.55 (2.95)	143.3 (24.24)	6.65 (2.64)	139 (27.46)	89.71 (17.28)
	DLDS	5.55 (1.74)	148.1 (25.49)	4.93 (1.8)	137.6 (14.62)	93.77 (32.71)

Note. Components used for the auditory paradigm are P50 and N1 at electrode Cz, and the visual component is P1 at electrode Pz. Absolute values were used for the N1 amplitudes.

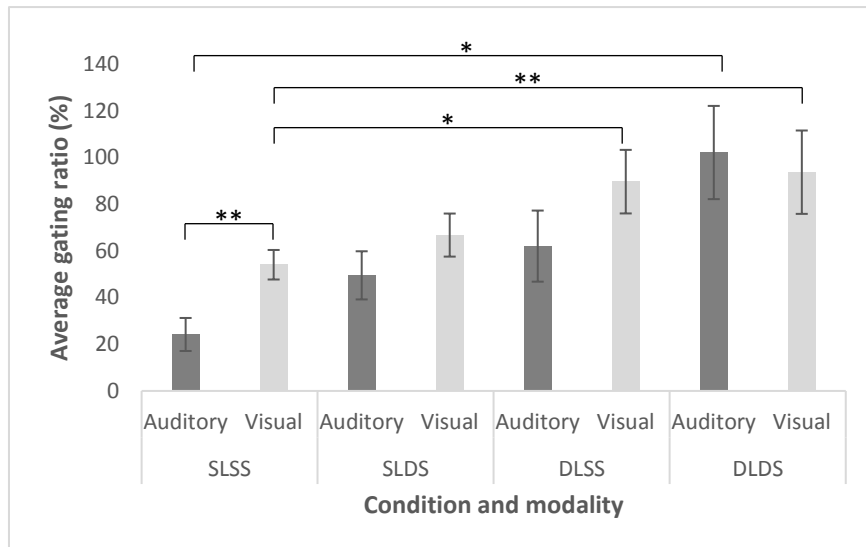


Figure 15. Average sensory gating ratios for each experimental condition for the visual and auditory modalities (auditory component P50). Error bars represent the standard error. * is sig. to .05 and ** is sig. to .01. The result demonstrating a significant difference between the visual and auditory modalities for the SLSS condition was obtained from the between subjects ANOVA. All other results are from the one-way ANOVA conducted for each modality separately.

The bivariate correlations for this study revealed fewer correlations between the sensory gating ratio and the component amplitudes compared to the previous study. However, some of the same correlations were found to be significant. A significant correlation between the gating ratio and the S2 amplitude in the SLSS condition was found, for both the auditory ($r=0.92$, $p=.001$) and the visual paradigms ($r=0.64$, $p=.046$). Additionally, a correlation between the DLDS ratio and S1 amplitude was found for the auditory paradigm only ($r=0.83$, $p=.011$). For the auditory component N1 the ratio for condition DLSS also correlated with the S1 amplitude ($r=0.79$, $p=.020$). All other correlations were nonsignificant ($p<.05$) with small effect sizes.

6.5. Comparison between experiments 4 & 5

A one-way ANOVA was conducted using the gating ratios, with the grouping variable of experiment (4 or 5), in order to establish if there were any significant differences in the amount of sensory gating observed in each study. This was only conducted for the conditions which demonstrated successful sensory gating, SLSS and SLDS. Although the studies had unequal sample sizes, the Levenes test for homogeneity of variance was nonsignificant for all conditions ($p > .1$). A summary of these results can be seen in Figure 15. None of the ratios were significantly different, however the difference between the SLSS conditions in the auditory paradigm was approaching significance ($p = .055$), as was the difference between the SLDS conditions in the visual paradigm ($p = .075$). These results indicate that there is a trend for more sensory gating during the second study. To explore this trend in more gating during experiment 5, a final one-way ANOVA was conducted using the response amplitudes with the factor of experiment (4, 5), and the amplitudes to stimulus 1 and 2 for the conditions SLSS and SLDS for both modalities as dependant variables. Again the Levenes test showed that the assumption of homogeneity of variance had not been violated. The results show that in the visual modality, the response amplitude to the first stimulus presentation was significantly larger in experiment 5 for the conditions SLSS ($F(1) = 14.01$, $p = .001$) and SLDS ($F(1) = 6.24$, $p = .017$).

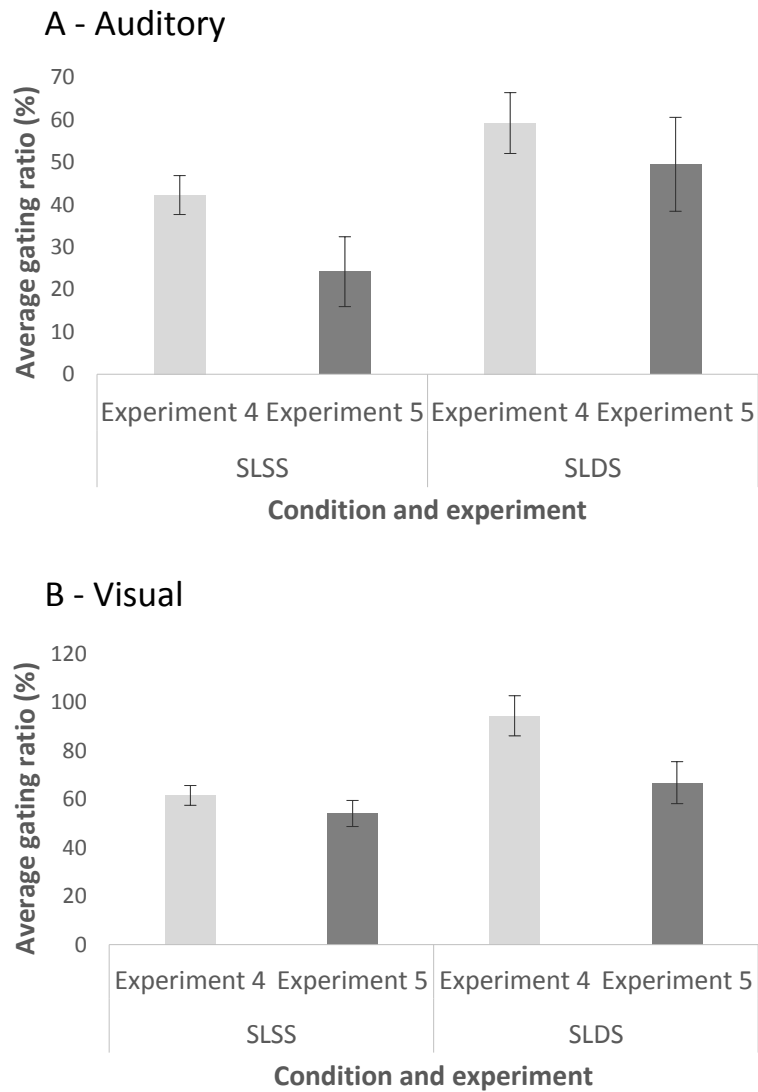


Figure 16. Panel A summarises the auditory results from the between-subjects ANOVA comparing the magnitude of the average sensory gating observed during experiments four and five for component P50. Panel B depicts the same results for the visual paradigm. Only the conditions which demonstrated successful sensory gating were included in the analysis. Error bars represent the standard error.

6.6. General discussion

The results from experiment five support the findings from the previous experiment in terms of more gating being seen in the auditory versus the visual modality. However, the magnitude of this difference was not the same (i.e., there was no longer a significant

difference in modality for the SLDS condition). This is most likely a result of there being significant gating for the visual condition of SLDS in experiment five, whereas this condition in experiment four did not reach significance. This is potentially due to the increased attention in experiment five having a larger impact on the visual modality compared to the auditory modality, and thus the amount of gating observed in each modality is converging in experiment five.

Another similarity between the two results is the trend in the amount of gating seen in each condition. In both experiments the data shows that the gating ratio observed at the SLSS condition is significantly lower than the ratio in the conditions where the location of the stimulus changed. Although not significant for every electrode and component, the ratio during the SLDS condition also appeared smaller than that of the two conditions that have a change in stimulus location. This paired with the fact that successful gating was observed in the same two conditions for both experiments, supports the idea that sensory gating is more sensitive to a change in location than a change in stimulus features, with sensory gating no longer occurring when the location changes. Results showed that there was no change in the cortical response to the second stimulus compared to the first stimulus in conditions during which the location changed from S1 to S2. This indicates that once the location of the second stimulus has changed, the processing of that stimulus is equal to that of the processing for the first, implying that the change in stimulus has been detected and processed as a novel stimulus.

In contrast to this, both experiments also showed a trend for the SLSS to elicit more gating than the SLDS condition. Although this was less apparent in experiment five, which did not show a significant difference between these conditions, within the visual modality or for the auditory component N1. This discrepancy may be the result of fewer participants and the between-subjects design resulting in even fewer participants in each modality. Despite this, the data suggests that more gating occurred when both the stimulus content and location remained the same compared to when the location remained the same but the stimulus

features changed, implying that sensory gating is sensitive to a change in stimulus features, however not to the same degree as stimulus location. This indicates, that at this early stage of information processing, a change in stimulus features is detectable, however the attenuation, albeit reduced attenuation, of the P50/P1 cortical response indicates that these changes are not recognised as a novel stimulus. As mentioned earlier, this increased sensitivity to spatial changes compared to non-spatial changes may be the result of spatial features being processed before that of non-spatial features.

A notable difference in findings between the two experiments is that there was a trend for more gating in experiment five compared to experiment four. Although these differences were only ever approaching significance it is perhaps still worth noting that in the two conditions combined, where successful sensory gating was observed, there was an average gating ratio of 37% and 60% for the auditory and visual modalities in experiment five, whereas experiment four had average auditory and visual gating ratios of 51% and 80%. This implies that the active task employed in experiment five focused attention more towards the stimuli, which resulted in modulation of the sensory gating mechanism, in the way of an increased proficiency to gate out. This runs counter to previous research that suggest that attending to the stimuli will increase the gating ratio (Guterman, *et al.*, 1992; Yee *et al.*, 2010). One explanation for this for the visual modality, is that the proficiency of sensory gating did not improve with increased attention, rather the processing of the first stimulus improved and thus resulted in the observed decrease in the sensory gating ratio. For the visual modality, in the conditions for which successful gating was found, there was also a significant increase in the P1 amplitude to the first stimulus presentation in experiment five compared to experiment four. If there was a significant decrease in S2 this would support the notion that more proficient gating had occurred as the second response was reduced even further. However, in this study, the decrease in sensory gating ratio for experiment five was likely the result of an increase in the processing of the first stimulus rather than an increase in the inhibition of the response to the second stimulus. An increase

in the P1 response is a common finding in the literature when attention is directed towards the stimulus (Clark & Hillyard, 1996; Slotnick *et al.*, 2003; Somers *et al.*, 1999; Zani & Proverbio, 2009). The reason that this same result was not found for the auditory modality may be validation that sensory components before approximately 100ms do not demonstrate this increased response with an increase in attention (Braff & light, 2004; White & Yee, 1997). However, there were also no significant differences between experiments four and five when comparing the auditory N1 ratios. This, and the fact that there was a trend for auditory gating to improve with increased attention still suggests that earlier components may be sensitive to attentional manipulations, although the attentional manipulations in the study were not sufficient to produce a significant change. Taken together these finding indicate that attentional manipulations differentially affect the visual and auditory modality.

A further observation is that although in experiment five there was a tendency for successful sensory gating to be the result of a decrease in the S2 response rather than an increase in the S1 response, there were fewer of these significant correlations in comparison to experiment four. A potential explanation may be the reduced number of participants and the between-subjects design further reducing the number of participants within each modality. This may have simply reduced the power, rendering it difficult to identify statistically meaningful relationships. As well as fewer, albeit similar, findings regarding the within modality correlations, the correlations between the modalities were no longer present in experiment five. This could also be a consequence of reduced power, however because there were no significant relationships, rather than fewer, this may provide further evidence that the addition of a task to direct attention to the stimuli, may have affected the visual and auditory modalities in a different manner.

6.7. Conclusions

This chapter aimed to explore the sensitivity of auditory and visual sensory gating with regards to stimulus changes and attentional changes. The findings of both experiments taken together indicate that sensory gating is not as Gawne and colleagues (2011) suggested, in that the early cortical processing simply denotes the existence of a stimulus, providing no information regarding its content and location, and thus is unaffected by changes in such. On the contrary, the current research implies that sensory gating is in fact sensitive to changes in both location and stimulus content. However, the processing of spatial features is a priority and thus a more pronounced effect on gating is seen when the location is altered compared to the stimulus features. In fact, once the location has changed significant gating no longer occurs. In addition to this, these effects are consistent across both modalities, suggesting that both visual and auditory sensory gating is again a qualitatively similar mechanism. Finally, when an active version of the task is used to increase the attention participants must give towards the stimuli, there is also an effect upon the level of gating observed, with a trend for more gating compared to the passive paradigm. This effect was more prominent within the visual modality, with the addition of a larger response amplitude to the first stimulus presentation, suggesting that visual gating may be more sensitive to attentional manipulations.

Chapter 7

General discussion

A principal aim of this thesis was to examine the modality-specificity of sensory gating. With much of the existing literature focused on auditory sensory gating, this thesis explored whether a similar function exists in the visual modality, and subsequently compared these findings with auditory sensory gating. In order to establish whether a shared or unrelated mechanism operates across modalities, we compared three aspects of visual and auditory gating, 1) the latency and surface scalp location of the gating observed, 2) the associated cognitive mechanism, 3) the sensitivity of gating to stimulus and attentional changes.

Chapter three set out to establish whether or not visual sensory gating could be reliably measured, with a primary focus on the latency and electrode position at which maximal sensory gating may be observed. A secondary aim was to explicate the similarities and/or differences with auditory sensory gating, in order to establish whether or not these gating mechanisms characterise unrelated processes, or a cross-modal shared mechanism. We measured the first three prominent ERPs in both modalities, at nine electrodes spreading from the vertex towards the occipital sites. The findings indicated that more sensory gating could be observed in the auditory modality, and within this modality, gating was maximal at the central locations. Moreover, gating was found at all three auditory components, and was not maximal for the component P50. Within the visual modality, sensory gating was consistently observed in just one component, P1, and this was more prominent at locations further back compared to auditory gating. Finally, this chapter found no robust correlation between the two modalities, indicating separate mechanisms. However, similarities between the intra-modality correlations and latency effects suggests that they may be qualitatively similar.

The aim of chapter four was to investigate the underlying cognitive mechanism that may reflect the mechanism of auditory sensory gating. This was accomplished by comparing the sensory gating efficacy with 11 behavioural tasks that recruited a range of attentional inhibitory mechanisms. Mechanisms that ranged from inhibiting non-target/irrelevant stimuli/stimulus features from entering working memory at the encoding stage of stimulus processing, to reducing conflict at the behavioural response stage. After accounting for the effects of fluid intelligence and working memory, we found that performance during the latent inhibition and continuous performance tasks were correlated with auditory sensory gating. We therefore concluded that auditory sensory gating was related to the cognitive process/es of 1) encoding relevant and irrelevant stimuli or stimulus features, in order to categorise these stimuli and 2) gating in or out these stimuli based upon this categorisation. Furthermore, the correlation with the measure of fluid intelligence and the goal-directed requirement of the above tasks suggests an element of top-down control is exerted upon the sensory gating mechanism.

Chapter five replicated the methods in chapter four using the visual analogue of the sensory gating task. When exploring components C1 and P1, again we found that more gating was observed for the P1 ERP. With regards to the behavioural tasks, the same correlations were found with the latent inhibition and continuous performance tasks. Additional correlations were revealed between visual sensory gating and the Simon task and ANT orienting. Consequently, visual sensory gating, as reflected by component P1, is also related to the partial encoding of all stimuli in order to categorise and filter accordingly. The similarities with, not replication of, chapter four again indicates a functionally separate but qualitatively similar mechanism for the auditory and visual modality.

Finally, chapter six explored the sensitivity of visual and auditory sensory gating with regards to stimulus and attentional changes, i.e. the type of stimulus alterations required for a perceived change in relevance/saliency, in order to alter the magnitude of sensory gating. We changed the content and/or location of the second stimulus and found that sensory

gating in each modality was sensitive to both types of stimulus alterations. Moreover, spatial features appear to be processed earlier and subsequently a change in location is prioritised over a change in stimulus content. The addition of a small task to increase the attention given towards the stimuli, altered the magnitude of sensory gating, with a more pronounced effect in the visual modality.

7.1. Theoretical contributions

7.1.1. The existence of visual sensory gating

Previous research regarding sensory gating, has paid particular focus to the auditory modality, with gating being observed at the three MLAEPs, P50, N1, and P2 (Boutros *et al.*, 1999; Rentzsch *et al.*, 2008). This bias is likely due to the wealth of research on schizophrenia and a sensory gating deficit, with auditory hallucinations being more common in the disorder compared to visual (Mueser *et al.*, 2009). Although this bias may be of use in such research, in order to achieve a comprehensive understanding of the gating mechanism, one must explore it with regards to all sensory modalities and search for commonalities and/or differences that may further elucidate its properties. This thesis is the first work to investigate visual sensory gating in conjunction with an auditory analogue, employing multiple lines of enquiry (electrophysiological characterisations, associated cognitive function(s), and sensitivity).

The first major finding of this thesis was the reliable observation of visual sensory gating. The only other studies to make a direct comparison between visual and auditory gating, produced conflicting findings. Adler and colleagues (1985) found gating for the auditory modality but not for visual, when using similar electrode sites and components as this thesis. One reason for the discrepancy with our results may be that participants were instructed to close their eyes throughout the visual paradigm. Although this may ensure that

visual stimulation is restricted to stimuli within the experimental procedure, this will increase the power of the alpha frequency band within the EEG trace, and potentially mask the similarly low frequency components (Cardenas *et al.*, 1997). Conversely, a study that found comparable results to this thesis, Oranje and colleagues (2006), observed successful gating for both modalities. A study that explored the same components for both modalities rather than focusing on the ERPs appropriate to each modality. The waveforms elicited by each modality are not entirely comparable, with the first major VEP, C1, having no fixed polarity, unlike the auditory P50. Moreover, each sensory system processes stimuli at differing speeds, thus to compare the activity at the same latency, and imply that the same underlying mechanism occurs at this latency, is misleading. Additionally, the fact that the authors focused on electrode Cz for both modalities implies an expectancy of a shared cross-modal mechanism, counter to the findings of this same research suggesting that each modality has a different primary cerebral source but with a converging mediating source.

The specific findings from experiment one showed that although auditory gating was observed at most electrode sites and for all components as expected (excluding the occipital sites), visual gating was only consistently found for the component P1 at the parietal and occipital sites. These results are consistent with research that also found gating for P1 (Gawne *et al.*, 2011; Gjini *et al.*, 2008), although these studies this focused only on the occipital electrodes. A surprising result was that gating was not also found for the component N1 at the P and O electrode sites (Barnhardt *et al.*, 2008).

Experiment one in this thesis is the only research to the author's knowledge, which has explored multi-modal sensory gating by analysing findings at three separate components specific to each modality, while also focusing on numerous electrode sites from the vertex towards the occipital lobe. These findings may contribute to future research investigating visual sensory gating by providing details of the most reliable component and location to observe such gating. Although auditory gating is typically associated with the component P50 at electrode Cz, gating in the visual modality is best examined at a later

latency (P1 – 100ms) and further towards the occipital lobes around the primary visual cortex. With these results in mind, it seems unlikely that the gating observed for each modality reflects a single cross-modal mechanism. However, the similarities regarding the latency effect (response to second stimulus occurs earlier than the response to the first stimulus), and within-modality correlations (correlations between the different locations for each component), implies some commonalities between each process. Further comparisons between the modalities will be discussed later.

7.1.2. Cognitive relevance of sensory gating

To further explore sensory gating across modalities, and to understand the potential underlying cognitive mechanism(s) associated with this neurophysiological measure, experiments two and three examined the relationship between auditory and visual sensory gating with numerous behavioural tasks. Due to broad models of ‘inhibition’ and the heterogeneity of tasks labelled as inhibitory (Kramer *et al.*, 1994; Yadon *et al.*, 2009), it is constructive that these experiments used as many as 11 behavioural tasks. Indeed, as expected, not all of the behavioural tasks correlated with either auditory or visual sensory gating. The inclusion of more tasks also serves to address possible non-inhibitory mechanisms that may be related to sensory gating. Although research has been conducted on several of the tasks used in this thesis with VEPs, there has yet to be a study using a visual paired-stimulus paradigm to explore these tasks and sensory gating specifically. These studies are similar to that of Yadon and colleagues who also investigated the relationship between auditory gating and four cognitive tasks, however this research, as discussed, used a broader range of cognitive tasks, controls for fluid intelligence and working memory, and replicates this method for the visual modality. It is surprising that the same correlations were not observed (for either modality) between this research and that of

Yadon, with their findings implying a dissociable relationship between auditory gating and the Stroop and go/no-go tasks.

One main finding to emerge from these experiments is that both the auditory and visual sensory gating paradigms significantly correlated (after accounting for the effects of fluid intelligence and working memory) with latent inhibition and the continuous performance task. These results may validate the notion of related mechanism and a converging mediating cortical source as discussed above. The fronto-temporal interaction model implies that although the temporal lobes are the main source of auditory sensory gating, a major contributing source are the frontal lobes (Korzyukov *et al.*, 2007). In keeping with this, Oranje and colleagues (2006) found that when comparing a paired-stimulus paradigm using either an auditory or visual stimulus for S1 (S2 was always auditory), there was a common frontal source for both modalities. Moreover, the VEPs independent of gating research have been found to originate primarily from the striate and extrastriate regions but have a frontal generator (Foxe & Simpson, 2002; Fu *et al.*, 2009; Proverbio *et al.*, 2010). Although these findings provide the basis for a possible common mechanism, this thesis did not explore the activity within the frontal lobe and consequently such definitive conclusions cannot be made. It would be beneficial for future research to replicate the experiments in this thesis while measuring electrical brain activity with a dense array of electrodes. This would highlight any common activation patterns between the two modalities.

Although there were similarities between the auditory and visual findings, within the visual experiment, the component C1 did not share this correlation with latent inhibition. It is unsurprising that the C1 and P1 components do not reflect the exact same mechanism, considering the different generators (striate and extrastriate respectively) of these components and their differential modulations to task demands. Indeed, the several components during auditory sensory gating also do not share the same behavioural indices. If C1 reflects early inhibition when cognitive load is low, and P1 reflects 'back up' inhibition when cognitive load is higher (Oakley & Eason, 1990), then this discrepancy with latent

inhibition may result from the task involving a high enough degree of cognitive load, that early striate inhibitory processes were not sufficient. The fact that gating in both the visual components shared a correlation the Simon task may support this. It is possible that the Simon task and latent inhibition share a common process of inhibiting previously learnt associations, with the Simon task being lower in cognitive load and subsequently related to the gating of component C1 as well as P1.

Previous research exploring auditory sensory gating and cognitive mechanisms are inconsistent with the findings presented in this thesis, reporting a negative correlation with the Stroop task and a positive correlation with the go/no-go task (Yadon *et al.*, 2009). The authors attributed this discrepancy to the different perceptual load associated with these tasks. However, it is perhaps surprising that tasks such as go/no-go were associated with sensory gating. The main mechanism of the go/no-go task is that of conflict resolution at the response stage of information processing, which is much later in the stimulus processing stream than one would expect an early sensory gating mechanism to relate to. This is supported by research showing that later components (N2 and P3) tend to be associated with this task (Garavan *et al.*, 2002). Other research has also found a correlation with auditory sensory gating and the CPT (Erwin *et al.*, 1998), which the authors explained based on the increased susceptibility of poor 'gaters' to distracting stimuli. This thesis also found a significant correlation between the CPT and both auditory and visual sensory gating. However, it is more likely the common task demands (sustained attention) of the CPT and sensory gating paradigms explicates this correlation as inhibition of distractors is not an apparent process with the CPT. Indeed Halperin and colleagues (1991) suggest that there a minimal suppression demands with the CPT, and that the task more likely reflects stimulus vigilance during sustained attention.

Taken together, the results of experiment two suggest that sensory gating reflects the process/es of early encoding of all stimuli in order to categorise these stimuli based on relevance/salience, and the subsequent inhibition of stimuli deemed irrelevant. If we include

the commonalities between latent inhibition and the Simon task, the results of experiment three may help narrow this suspected underlying process further. As both these tasks share the process of inhibiting previous stimulus/response associations, sensory gating potentially reflects the mechanisms just described, but more specifically the relevance of these stimuli is based on previous stimulus associations. However, this interpretation may be misleading as the Simon task did not correlate with auditory sensory gating. This may result from visual and auditory gating reflecting similar but not the same underlying mechanism, or perhaps the spatial and visual characteristics of the Simon task drives the correlation in the visual but not the auditory paradigm. It would be interesting for future studies to address this question with the inclusion of more auditory behavioural tasks. Future research might also investigate the proposed associated cognitive mechanism in more depth, with more tailored paradigms to tease apart the encoding and cognitive inhibition aspects. Finally, it would benefit the understanding of the gating of each of the ERPs if EEG recordings were used throughout the behavioural tasks too. For example, the tasks whose behavioural indices correlated with P1 sensory gating may also show a correlation with gating and the modulation of P1 during those same tasks.

A principal difference between the two experiments, was that auditory gating correlated with fluid intelligence, however the visual did not. Again, this may suggest that the two modalities do not have the same associated cognitive mechanism. However, this may also be the result of the different number of participants used in each experiment (auditory – 43, visual – 31). To check whether our non-significant correlation between visual sensory gating and CCF-IQ was due to a lack of statistical power, a post hoc power analysis was conducted with power ($1 - \beta$) set at 0.80 and $\alpha = 0.05$, two-tailed. This revealed that in order to detect an effect size of 0.23, the sample size would have to increase to 146. A William's *t*-test found no significant difference between the magnitude of the correlation coefficients between auditory and visual sensory gating and CCF-IQ. Another difference between these experiments was that time taken for each participant to complete all the tasks. Participants

during experiment two were given several days to complete the entire study, allowing for more intra-individual variability on the performance during each of the tasks. Most of the participants during experiment three completed the study over the course of one day and thus intra-individual variability with regards to mood, alertness etc. becomes less of an issue. The reason for study completion over fewer days was to reduce the number of people failing to complete the entire study. It would be beneficial to repeat this study using both the visual and auditory sensory gating paradigms with the same group of participants.

7.1.3. Sensitivity to stimulus changes

Experiments two and three confirm that sensory gating is related to selective tasks of attentional inhibition, and more specifically, tasks that involve the processing of all stimuli and the subsequent filtering out of the irrelevant. With this in mind, it is prudent to explore how sensitive the sensory gating mechanisms are to a change in stimulus relevance.

Experiment four explored this question using a similar visual paradigm to that of Gawne and colleagues (2011), with the exception of a longer ISI in order to make a more like for like comparison with the auditory gating paradigm. This paradigm allowed for the exploration of the effects of stimulus changes on sensory gating, although this study was limited to changes in stimulus location (spatial) and changes in form/colour (qualitative).

It was hypothesised that certain stimulus changes may still elicit sensory gating, but that stimuli that change in both dimensions would likely lead to an augmented response to the second deviant stimulus presentation. This was based on previous research that demonstrated significant augmentation rather than attenuation when the second stimulus was different to the first (Boutros & Belger, 1999; Kisley *et al.*, 2004; White & Yee, 2006). The results from experiment four (replicated in experiment five) showed that when the stimulus deviated from the first in terms of qualitative features, there was still significant

sensory gating, albeit reduced compared to two identical stimuli. However, unlike previous research, changes to stimulus location or changes in location and form did not result in augmentation as expected, rather no significant difference was found between the responses to the first and second stimulus presentation. This being said, others have also found either no difference, or significant but reduced gating even in conditions where the second stimulus is not identical to the first (Gawne *et al.*, 2011; Mayer *et al.*, 2009). The conflicting findings in the literature are likely due to the heterogeneity of the experimental designs, specifically the way in which stimuli are altered. With respect to the study conducted by Gawne and colleagues, the same stimuli and stimulus changes were used in experiments four and five, however their study found significant gating in all conditions unlike this study which found no gating following a change in stimulus location. This is likely due the shorter ISI used by Gawne. Furthermore, this research went further by not only employing these manipulations on visual stimuli, but also on auditory stimuli in order to investigate these manipulations on the more common modality of gating in the literature. As a result of these findings, it is purported that sensory gating is sensitive to changes in stimulus location and form, however more so to changes in stimulus location. Although other authors have found a larger increase in the gating ratio (augmentation), this experiment found that sensory gating is sensitive to changes in the qualitative features and location of a stimulus, which supports previous auditory gating research. Additionally, these findings are supported by previous research into the visual modality, suggesting a sensitivity of the VEPs to changes in stimulus colour, form, and location, with a priority to detect changes in location (Hillyard & Munte, 1984; Karns & Knight, 2009; Proverbio *et al.*, 2010).

As experiment four was based on the study by Gawne and colleagues (2011), it is surprising that we did not reach the same conclusion that the gating mechanism is not sensitive to stimulus changes. This is likely the result of significant differences between the methods and analyses. Whereas this thesis aimed to use a visual paradigm that would allow for a like for like comparison with the auditory gating procedure, and thus used an ISI and ITI

of 500ms and 6-8s respectively, the study by Gawne and colleagues used much shorter intervals (47ms and 500-750ms). The result of this is that their shorter timings allowed for much less stimulus processing to have occurred, which is why they would have found no additional processing of the second stimulus.

7.1.4. The effects of attention on sensory gating

After establishing that there are limits to the sensitivity of sensory gating, the aim of the final experiment of this thesis was to explore the previous findings in the context of an attentional manipulation. While experiment four used the passive version of the sensory gating procedure, experiment five used an active version by including an easy selective attention task. The effects of increasing attentional awareness during an auditory sensory gating paradigm is a contentious issue within the literature, with some claiming that gating of the earliest component is immune to attentional manipulations, while the later components (after 100ms) are susceptible to these changes (Adler *et al.*, 1992; White & Yee, 1997). However others claim all components to be affected by attention (Guterman *et al.*, 1992). To date, there has been no research regarding visual sensory gating and changes in attention, but studies looking at the VEPs have found similarly conflicting results (Anllo-Vento & Hillyard, 1996; Di Russo *et al.*, 2003; Proverbio *et al.*, 2010). The findings from this thesis contribute to the literature on auditory sensory gating, but more importantly, address the issue of attention in the visual modality.

The first result of experiment five was the replication and further validation of the findings from experiment four, with the same pattern of successful gating observed over the four conditions. One difference was that visual sensory gating showed significant gating at both electrode locations (Pz and Oz) during the SLDS condition. In fact, although only ever approaching significance, there was a trend for more gating overall in experiment five. This

is counter to the previous research that suggests when there are effects of attention, an increased attentional awareness of stimuli decreases the magnitude of gating. However, in experiment five there was a larger visual P1 amplitude in response to the first stimulus, which would explain the increase in gating ratio. These results can be explained by the effects of attention increasing the processing of the first stimulus, similar to the effects seen with attended compared to unattended stimuli (Clark & Hillyard, 1996; Slotnick *et al.*, 2003), rather than an increase in gating per se. If there was a genuine increase in sensory gating, we would expect to see a significant decrease in the response to S2 rather than an increase in the response to S1. Despite mechanisms underlying the attentional effect, there were more differences for the visual modality compared to auditory, indicating that visual gating may be more susceptible to attentional manipulation. Finally, this result was not replicated for the auditory modality. Although there was the same trend for increased gating in experiment five, there was no significant difference between the S1 or S2 amplitudes. This may appear to validate the notion that the earliest of the auditory components is unaffected by attentional changes unlike the later components. However, when exploring the auditory N1 component (a similar latency to the visual P1), a similar results were observed. This may further suggest that the visual modality was more susceptible to changes in attention, although these changes seem to increase the processing of the first stimulus rather than increase the magnitude of gating.

In experiments four and five, the visual component P1 was used to measure the magnitude of sensory gating. Although this decision was implemented on the basis of experiments one and three failing to demonstrate reliable gating using the component C1, this would have been difficult to measure in experiments four and five due to sensitivity of C1 to the spatial location of the stimulus. As a result of the retinotopic organisation of the primary visual cortex, stimuli presented to opposite regions of the retina will elicit opposite polarities (Di Russo *et al.*, 2002; Rauss *et al.*, 2011). Stimuli presented to either part of the visual field will activate the geometrically opposite neurons and thus the observed VEP is of

the opposite polarity. Consequently, with a change in stimulus location being a condition of these experiments, it is likely that the component C1 would have been undetectable in the average waveform, which would have included stimuli presented to both the upper and lower visual field. In addition to this, conditions in which the stimulus changed location would have been distorted.

7.1.5. A qualitatively similar mechanism across auditory and visual modalities

The principle aim of this thesis was to explore the commonalities and differences between auditory and visual sensory gating in order to ascertain whether or not these functions were separate or distinct. First, the differences between auditory and visual gating will be addressed, differences which may indicate that these mechanisms are unrelated. The two forms of gating were not observed in comparable electrode locations or at similar latencies. Auditory gating can be observed in more locations and at more time points, but as with previous research, this gating is reliably found at the electrode Cz around 50ms post stimulus onset. Visual gating however, is only consistently observed later, after 100ms post stimulus onset, and is more pronounced at the central-parietal and central-occipital locations. It is surprising that the visual component C1 did not elicit successful gating in any of the experiments, a component which is arguably more comparable to that of the auditory P50. As discussed above, this finding may be the result of the changing polarity of the C1 component when a stimulus changes location. In the experimental designs of this thesis, either the stimulus changed location and thus may have averaged out the C1 response, or the stimulus was presented in the centre of the screen, and most likely the centre of the participant's visual field, which may have also resulted in a smaller C1 component with no distinct polarity. Future research may want to replicate the experiments in this thesis but with an experimental design more suited to capturing the C1 component. In addition to this, a

task with low perceptual load demands is less likely to elicit inhibition within the striate (C1), and rather the extrastriate (P1 and N1) is required for early perceptual filtering (Desimone & Duncan, 1995; Rossi & Pourtois, 2012). The sensory gating paradigm is a task with low perceptual demands and subsequently these experiments were unable to detect gating within the striate as reflected in the component C1. This being said, it may not be possible to increase the demands of the sensory gating tasks, as studies which have done just that have found a reduction in gating due to this increased demand (Jin & Potkin, 1996; Moran *et al.*, 2012).

Other differences found in this thesis include correlations between visual gating and the Simon task and varying forms of cueing during the ANT, which were not observed for auditory gating. Moreover, only auditory gating significantly correlated to the measure of fluid intelligence. Again, these differences may imply two unrelated gating mechanisms. However, the correlations between visual gating and the Simon task and ANT (orienting and alerting) are potentially a consequence of the spatial nature of these tasks and the shared modality with the visual form of the sensory gating paradigm. The difference in fluid intelligence is more of an indication that visual and auditory gating are not the exact same process. As Oranje and colleagues (2006) found that visual and auditory gating shared a mediating frontal source, it is unexpected that both versions of gating did not relate to intelligence scores. As discussed above, it would be beneficial for future research to replicate experiments two and three using a dense electrode array in order to evaluate any common frontal sources.

A final difference between the modalities is the amount of gating observed in each of the experiments of this thesis. There was consistently more gating during the auditory paradigm compared to the visual whenever a direct comparison could be made. Even in experiment five, which found a larger increase in visual gating when an active version of the task was used, there was still significantly more gating elicited during the auditory paradigm. An explanation given for this in chapter three, is that during the auditory study, participants

only form of auditory stimulation is that of the stimuli presented during the experiment, whereas during the visual paradigm, participants can view the surrounding area in their periphery. Indeed during the long ITI it is also possible that the participants' attention was focused elsewhere due to the lack of visual stimulation on the screen in front of them. As discussed, an increase in sensory stimuli reduces sensory gating (Jin & Potkin, 1996; Moran *et al.*, 2012).

Although these differences, which suggest that the underlying mechanism of visual and auditory sensory gating do not originate from the same cortical source, there are several similarities. In experiment one, there was a consistent effect on the latency of the response to the second stimulus. Thus, despite gating being observable at a different location and time, this effect on latency does indicate a potentially similar process is involved. Moreover, this latency effect was only found for the components and electrodes which most reliably elicited successful gating. A second finding from experiment one, found for both the visual and auditory modality, was the within-modality correlations, with each component correlating with the same component at the other electrode locations. The findings from experiment one do indicate a comparable sensory gating process for both modalities.

In addition to these mechanistic parallels observed between the components P50 (auditory) and P1 (visual), these components also shared a correlation with performance during the latent inhibition and continuous performance tasks. Both modalities were also affected similarly by perceptual and spatial stimulus changes, a result found in two separate experiments (four and five). These findings and the concept of a shared mediating frontal source advocate for a functionally separate but qualitatively similar mechanism underlying both visual and auditory sensory gating. It would be beneficial to explore somatosensory gating in a similar manner as presented in this thesis, in order to ascertain if this conclusion is supported with an additional modality.

7.2. Final conclusions

By comparing the two modalities in each experiment, this thesis has a) examined sensory gating in the visual modality, an area which is considerably lacking in the current literature, b) helped elucidate the issue of a cross-modal gating mechanism or related but functionally separate process, and c) explored the underlying process reflected in the neurophysiological measure of gating, counter to previous research which used gating as simply a measure of inhibition with limited consideration of more detailed function(s). A chief finding of this thesis is whereas auditory sensory gating may be observed after 50ms post stimulus onset at electrode Cz, in order to observe a comparable visual gating process, one must use electrodes further towards the occipital lobe and at a later latency (100ms post stimulus onset). This thesis builds on previous research conducted by Oranje and colleagues (2006), suggesting two distinct and one converging cortical generators of visual and auditory sensory gating. As a result of the numerous comparable findings for both the auditory and visual gating paradigms, this thesis has revealed that, both electrophysiologically and functionally, there is not one cross-modal gating mechanism that functions to gate information from multiple modalities, rather there are analogous mechanisms associated with each of the primary sensory areas.

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Appendix

Glossary of abbreviations

ANT	The Attentional Network Task (Fan <i>et al.</i> , 2002). Includes the measures: orienting, alerting, and executive function.
CCF-IQ	Cattell's Culture Fair (Institute for Personality and Ability Testing, 1973). A measure of fluid intelligence.
CNS	Central nervous system.
CPT	Continuous Performance Task (Lee & Park, 2006).
DLDS	Different location, different stimulus. One of the experimental conditions during experiments four and five. The second stimulus to be presented was in a different location with different perceptual features compared to stimulus 1.
DLSS	Different location, same stimulus. One of the experimental conditions during experiments four and five. The second stimulus to be presented was in a different location but the identical stimulus type as stimulus 1.
EEG	Electroencephalogram. A way of measuring the changes in cerebral electrical activity from the scalp.
ERP	Event-related potential. The amplitude change/deflection, as measured using EEG, in response to a particular event.
fMRI	Functional magnetic resonance imaging. A neuroimaging technique that measures the changes in cerebral blood flow.
ISI	Inter-stimulus interval.
ITI	Inter-trial interval.

MEG	Magnetoencephalography. A neuroimaging technique that measures the magnetic field changes within the brain.
MLAEP	Mid-latency auditory evoked potential. Specific event-related potentials produced by auditory stimulation. Occurring from 50-200ms post-stimulus onset.
MLERP	Mid-latency event-related potential. A general term for event-related responses that occur between 50-200ms post-stimulus onset. Can be applicable to any modality.
MMN	Mismatch negativity. A specific evoked response referring to the negative deflection elicited in response to deviant stimuli.
NOV	A condition in the latent inhibition paradigm referring to the use of novel targets and distractors in the test phase.
NPE	A condition in the latent inhibition paradigm referring to the novel pop-out effect. The target in the pre-exposure phase becomes the distractor in the test phase, and the test phase target is novel.
PE	A condition in the latent inhibition paradigm referring to previous exposure. The target and distractor stimuli in the pre-exposure phase swap roles in the test phase
S1	Stimulus 1 in the sensory gating paradigm.
S2	Stimulus 2 in the sensory gating paradigm.
SLDS	Same location, different stimulus. One of the experimental conditions in experiments four and five. The second stimulus presented was identical to the first in perceptual features but had changed location.
SLSS	Same location, same stimulus. One of the experimental conditions in experiments four and five. The first and second stimuli presented were identical and in the same location.

VEP Visual evoked potential. A type of evoked response specific to that which is elicited by visual stimulation.