# Suppressive and Inhibitory Interactions in Human Vision and their Functional Role in the Perception of Number Sets

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I dedicate this thesis to

the memory of my father

Eddie Jastrzebski 1951-2010

-- a critical thinker

Abstract

Number sense – the ability to discriminate between 'fewer' and 'more' objects beyond the range of counting is present from infancy (six months), and is the cornerstone of arithmetical and mathematical cognition. However, much remains to be understood about the brain processes that underlie number sense and numerosity processing. Hence, the chief aim of this research was to ascertain whether there was a relationship between the mechanisms involved with the removal of unessential visual information (sensory filtering) and numerosity processing. This was achieved by means of surround-masking, a psychophysical protocol well documented to modulate sensory filtering resources. This thesis comprises four main sections. Section one is a psychophysical investigation into the effects of surround-masking on numerosity comparison judgements, where task performance was varied by differences in central and surround stimulus contrasts. Section two consists of cognitive assessment tasks from the Wechsler Adult Intelligence Scale (WAIS-IV); Ravens Advanced Progressive Matrices; and a series of computerised tasks that measured speeded magnitude comparison judgements, and true/false judgements of arithmetical statements. Section three comprises a magnetoencephalographic (MEG) study that examined the spatial and temporal response signatures associated with surround-masking of numerosities. Finally, in order to examine the electro-magnetic response signatures for attentional enhancement and attentional suppression (selective attention) during numerosity comparison judgments, section four consists of a second MEG study where participants underwent another psychophysical task that gauged these processes. Essential findings abstracted from all four experiments were a positive correlation between WAIS-IV arithmetical sub-test scores and response times (RTs) for MEG surround-masking comparison judgements under high contrast centre/high contrast surround conditions. From these findings, poor arithmetical ability is suggested to be associated with anomalous neural inhibitory mechanisms. The MEG analyses further revealed that modulations in sensory load via surround-masking and stimulus saliency recruited high-order attentional resources when making numerosity comparison judgements – possibly in relation to motor response and error monitoring. It was concluded that poor numerosity judgement performance could be attributed in part, to an anomaly of inhibitory processing mechanisms that serves to remove the noise in incoming visual information.

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Declaration of originality

I, Nicola Renata Jastrzebski, solemnly declare that this PhD dissertation is my own work and to the best of my knowledge, contains no materials previously published or written by another person. I also declare that this thesis contains no materials in part or in whole that have been accepted for the award of any other degree or diploma at Swinburne University or any other educational institution. I also declare that the intellectual content of this thesis is my own work, except to the extent that assistance from others in the project's design and conception is acknowledged. Information derived from the published work of others has been fully acknowledged where appropriate through in text referencing, and in the bibliography.

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# Part 1

# Introductory Overview

## 1.0. Overview

The central topic of this dissertation concerns the question about how mechanisms within the visual system involved with removal of unessential visual information (sensory filtering) contribute toward the perception of numerosity, or the ability to make accurate approximations about the perceived number of elements too numerous to count (non-symbolic numerosity sets). It was also of interest to examine performance on numerosity comparison judgement tasks, and the functional quality of sensory filtering mechanisms in relation to schizotypal traits within non-clinical populations. Sensory filtering mechanisms, and their contribution in making numerosity comparison judgements, were examined through surround-masking, a psychophysical paradigm known to 'swamp' sensory filtering resources, and in the context of selective ignoring of highly salient, yet irrelevant visual information.

The neurophysiological mechanisms involved with making numerosity judgements are not yet fully understood, and there is much controversy surrounding the theoretical frameworks that offer explanation of the attentional and perceptual processes recruited during its execution (see Anobile, Cicchini, & Burr, 2016 for an extensive review on current theories of numerosity processing). Hence, the central topic of this dissertation is important because it adds a new understanding of one of the many mechanisms recruited during numerosity perception, revealing a relationship between sensory filtering and numerosity perception that has not been reported elsewhere.

When making comparison judgements of large non-symbolic numerosity sets, the visual system has been argued to capitalize on statistical descriptors such as the mean, variance, and median of the perceptual set in order to glean the most relevant stimulus properties (Chong & Treisman, 2003; Ross & Burr, 2010). Through such observations, it has been argued that this numerosity extraction process occurs early on in the visual processing hierarchy, and that incoming information about the perceived number of elements is in itself "a primary sensory attribute" or a psychophysical property of perception (Burr & Ross, 2008). From this, there has been a long-standing debate about whether numerosity perception is a numerically or perceptually driven process.

The prevailing numerically-driven account posits that numerosity processing is executed through an innate awareness of magnitude difference that is uninfluenced by psychophysical properties of the display such as for example, luminance (Pinel, Piazza, Le Bihan & Dehaene, 2004; Piazza et al., 2010; Piazza, Izard, Pinel, Le Bihan & Dehaene, 2004). The perceptually driven account however, argues that the perceived number of elements is influenced by non-numerical visual parameters such as surface density and diameter of dot arrays, which serve as cues as to whether elements are numerically larger or smaller (Gebuis & Reynovet, 2012; Szücs, Nobes, Devine, Gabriel & Gebuis, 2013).

The ability to make non-symbolic numerosity judgements is severely compromised in those with developmental dyscalculia (DD), a specific learning disorder in the acquisition of arithmetic skills despite normal intelligence (Ansari & Karmiloff-Smith, 2002). For example, visual estimation ability of pre-adolescent children with pure DD have demonstrated numerosity estimation psychophysical thresholds comparable to neurotypical 5 year old children (Piazza et al., 2010). Poor arithmetic reasoning, a prominent characteristic of DD, has also been linked with schizotypal personality disorder – as ascertained by neuropsychological assessment (Mitropoulou et al., 2005; Trotman, McMillan, & Walker, 2006; Weiser et al., 2003), and more recently autism spectrum disorder (Aagten-Murphy, Attucci, Daniel, Klaric, Burr & Pelicano, 2015; Meaux, Taylor, Pang, Vara & Batty, 2014).

The aetiology of DD is not fully understood, however, it has been proposed that it may be partly characterised by a functional defect of the dorsal visual pathway (Sigmundsson, Anholt, & Talcott, 2010), or a developmental anomaly of temporal and parietal cortices (Ansari & Karmiloff-Smith, 2002). It was of particular interest to ascertain the effect of swamping of sensory filtering resources (through surround-masking) on the ability to make accurate non-symbolic numerosity judgements of neurotypical observers. If numerosity comparison judgements are impaired by surround-masking, then it may be inferred that poor non-symbolic numerosity processing may partly be explained by aberrant sensory filtering mechanisms.

In order to conceptually integrate the notion of sensory filtering with the perception of number sets, it is necessary to elucidate the concepts integral to the ideas of the dissertation that are (1) the suppressive mechanisms involved with surround-masking, (2) integration and segregation of cortical networks in the course of development, (3) non-symbolic comparison judgements and schizotypal traits in non-clinical populations, (4) neurocognitive models of selective attention and sensory load of visual perception.

### 1.1. Suppressive mechanisms involved with surround masking

Earlier surround-masking experiments have demonstrated that high contrast peripheral stimuli had a deleterious effect upon contrast discrimination judgements of centrally presented textures (Xing & Heeger, 2000). The perceptual disturbances induced through surround-masking, result as elevated psychophysical thresholds during contrast matching judgements of stimulus patches embedded within the surround annulus mask(Xing & Heeger, 2000, 2001). That is, high contrast surround stimuli have an illusory effect upon apparent contrast, where in the presence of the surround, the contrast of the centrally presented target appears lower than a contrast matching reference patch without a surround (Chubb, Sperling & Solomon, 1989).

The cortical responses to surround masking has been characterised as BOLD suppression of striate cortex (V1) – putatively a reflection of horizontal (cortico-cortico) interactions which occur by extra-classical receptive field (RF) modulation or surround suppression (Zenger-Landolt & Heeger, 2003). The inhibitory mechanisms of surround suppression in V1 have been characterized as a change in peak-amplitude of evoked responses as a function of surround contrast via MEG recordings (Ohtani, Okamura, Yoshida, Toyama, & Ejima, 2002) . To elaborate further, high contrast surrounding stimuli have an attenuating effect upon evoked response amplitudes at latencies around ~90ms. An increase in response amplitude was observed for trials in which the high contrast surround was absent. These findings show some similarity with ERP investigations into visual working memory (WM) capacity that found between-group differences in peak amplitudes for the electrophysiological signatures of filtering task-irrelevant distracters (Fukuda & Vogel, 2009, 2011; E Vogel, McCollough, & Machizawa, 2005; Edward Vogel & Machizawa, 2004) – observers with poor WM capacity demonstrated greater peak-amplitudes than those with high WM capacity which was interpreted as reflecting functional efficacy of signal gating resources.

Considered as a whole, it would seem that the mechanisms involved with surround suppression and sensory filtering are not mutually exclusive, as they are both modulated strongly by the physical properties of perception such as high contrast gain (Albrecht et al., 2003; M Carandini, 2004; Edden, Muthukumaraswamy, Freeman, & Singh, 2009). Indeed, one of the visuo-perceptual anomalies observed in schizophrenic populations is poor motion direction discrimination under high contrast conditions (Tadin et al., 2006), which has been argued to be a functional consequence of defective RF surround suppressive mechanisms – attributed to deficient GABA concentrations (Tadin et al., 2006; Yoon et al., 2010).

### 1.2. Integration and segregation of cortical networks in the course of development

It has been previously suggested that learning and cognitive development processes occur by interdependently related mechanisms, which involve the problem of reducing input error and encoding the most statistically probable physical properties of perceptual context (Friston 2005; Friston & Price 2001; Johnson & Munakata, 2005) . Functional specialization may be conceived in terms of the gradual establishment of specific connections between cortical and sub-cortical regions in the course of learning and cognitive development (Friston & Price 2001; Johnson, 2001).A complementary process that occurs in the course of this increasingly specialized pattern of connectivity between cortices has been referred to as functional segregation (Friston 2005; Friston & Price 2001; Johnson & Munakata, 2005). The mechanisms, by which functional segregation has been posited to occur, are through synaptic pruning (down-scaling) of unessential inter-regional connections (Johnson & Munakata, 2005). Synaptic pruning of redundant cortico-cortico connections is demonstrated in experience-dependent modifications in plasticity, such as in the inhibitory signalling counterpart of long-term potentiation (LTP), or Hebbian learning (Rozas et al., 2001; Wilson, Ty, Ingber, Sur, & Liu, 2007). Context dependent modifications in plasticity or visual perceptual learning (VPL) have been widely evidenced through fMRI as a prominent reduction of BOLD signal in visual areas through the course of learning (Gál et al., 2009; Mukai et al., 2007; Sasaki, Nanez, & Watanabe, 2010; Schwarzkopf, Zhang, & Kourtzi, 2009; Yotsumoto, Watanabe, & Sasaki, 2008). This learning dependent reduction in BOLD signal is thought to be a reflection of cortical sharpening (Gál et al., 2009; Mukai et al., 2007) – a functional component of one of the mechanisms involved with predictive coding (Friston 2005; Friston, 2005; Friston & Price 2001; Tsodyks & Gilbert, 2004).

One of the more short term or immediate features of predictive coding and cortical sharpening is signal gating (gain attenuation) of statistically redundant input, which is largely mediated by GABA (gamma amino-butyric acid) dependent neural processes such as synaptic depression (Rao & Ballard, 1999; Rothman, Cathala, Steuber, & Silver, 2009; Schwartz & Simoncelli, 2001). That is, gain attenuation via synaptic depression has a functional role in the formation of a given neural circuit (or network) – this is achieved through the minimization of variability between input signal and the tuned response (Dosher  & Lu 1998; Rao & Ballard, 1999; Schwartz & Simoncelli, 2001; Tsodyks & Gilbert, 2004). The course of functional specialization for any given behaviour or high order cognitive representation, depends critically upon the efficacy of neural-code timing mechanisms involved with inhibitory gating or predictive coding at a sensory level (Johnson, 2011) .

It is worth noting that some of the perceptual and cognitive deficits associated with atypical neurodevelopment have been argued as attributable to an imbalance in the excitatory and inhibitory signalling ratio within cortical micro-circuitry (Baroncelli et al., 2011). The phenotypes of neurodevelopmental disorders Autism and schizophrenia are characterised by a deficiency of inhibitory connections that gate plasticity of excitatory/pyramidal micro-circuits (Baroncelli et al., 2011; Gonzalez-Burgos & Lewis, 2008). The functional consequences of defective inhibitory circuits are likely to have a deleterious impact upon the aforementioned mechanisms in the distributed coordination of temporal coding signatures that reduce signal prediction error within large scale (i.e. cortico-cortical) circuits (Uhlhaas & Singer, 2010).

### 1.3. Non-symbolic comparison judgements and schizotypal traits in non-clinical populations

Poor motion sensitivity in schizophrenia (Tadin et al, 2006) has also been observed in children with DD (Sigmundsson, Anholt, & Talcott, 2010) . From this, it may be argued that the poor non-symbolic comparison judgements in arithmetic learning impairments may be a consequence of developmentally anomalous RF inhibitory mechanisms, where such visuo-perceptual disorders (i.e. dorsal stream vulnerability) have been evidenced to occur with attentional deficit hyperactivity disorder (ADHD), Williams syndrome and Turners syndrome – developmental disorders noted to be associated with poor spatial and arithmetical reasoning (Ansari, Donlan, et al., 2007; Simoncelli, 2003; Van Herwegen, Ansari, Xu, & Karmiloff-Smith, 2008).

Schizotypy, or schizotypal personality disorder is characterized by a cluster of traits common to schizophrenic individuals such as ideas of reference, magical thinking, paranoia, and severe social anxiety in the absence of psychosis (Mitropoulou et al., 2005; Trotman et al., 2006; Weiser et al., 2003). This DSM axis-II disorder nonetheless, shares many of the cognitive impairments found in schizophrenia, only with less severity (Weiser et al., 2003). For example, cognitive ability assessment of schizophrenic, schizotypal, and demographically matched controls have revealed that schizotypal individuals showed significantly lower WAIS-arithmetic and WAIS-similarities sub-test scores than the demographically matched control group, however, showed significantly better performance than the schizophrenic group (Weiser et al., 2003).

In a later investigation into the cognitive performance profile of schizotypy, it was once again found that WAIS arithmetic sub-test scores of schizotypal adolescents at high risk of psychotic illness were significantly lower than the control group, where poorer performance on this WAIS sub-test correlated with the severity of negative symptoms (Trotman et al., 2006). Like schizophrenia, the cognitive performance profile of schizotypal personality disorder has been associated with poor spatial working memory, episodic memory, and processing speed, with poor spatial working memory postulated as the underlying core of cognitive deficits in schizophrenia spectrum disorders (Mitropoulou et al., 2005). Given these associations between schizotypal personality disorder, poor spatial reasoning and arithmetical ability, it was of interest to further examine the relationship between each of the schizotypal traits and cognitive performance in the normal population via the schizotypal personality questionnaire (Raine, 1991) and the Wechsler adult intelligence scale (WAIS-IV).

### 1.4. Neurocognitive models of selective attention and sensory load of visual perception

According to the load theory of selective attention (Lavie, 2005; Lavie et al., 2004), there are two mechanisms by which visuo-perceptual load are driven – (1) sensory-driven or bottom-up selection of task-relevant stimuli, where high perceptual load facilitates the exclusion of task-irrelevant distracters (2) top-down attentional control in the maintenance of filtering out task-irrelevant distracters with low perceptual load. Both top-down and bottom-up mechanisms proposed by load theory are not functionally independent of one another however – it is rather the case that these components of selective attention are recruited under certain conditions of perceptual load.

Recently, load theory was generalized onto the attentional processes that occur during enumeration (counting 5 to 8) and subitization (rapid counting 1 to 4) via a series of dual-task experiments that varied in attentional load (Vetter, Butterworth, & Bahrami, 2008, 2010). This dual-task paradigm comprised a primary task that entailed colour detection of centrally presented targets, and the secondary task of enumeration (high attentional load) or subitization (low attentional load) of peripheral high contrast elements that ranged from 1 to 8 amid low contrast distracters. Observers undertook three main experimental blocks that varied in attentional load – the primary and secondary task in combination with one another, and the primary task then secondary task individually. The main aim of these experiments was to determine whether subitization was a truly ‘pre-attentive’ mechanism as proposed by earlier investigators (c.f. Trick & Phylyshin, 1994). Essentially, as attentional load increased – by means of undergoing the primary and secondary task together, there was a steep decrease in the accuracy of subitization and enumeration ability. These findings were concluded to indicate that subitization was unlikely to be a pre-attentive mechanism.

The rationales of the Vetter et al., (2008; 2010) investigations were novel in that the notion that load theory was generalised onto numerical cognition processes for the first time. However, one potential caveat within the experimental design was likely to have confounded the effects of attentional load from perceptual load. As noted earlier, stimuli from the secondary task comprised high contrast target elements that ranged from one to eight amid low contrast distracter elements surrounding the primary task. The objective of the secondary task was to indicate how many target elements surrounded the primary task stimuli. Given that the target elements to be subitized or counted were of high contrast, it was conceivable that the stimuli had a saturating effect upon sensory gating rather than attentional resources. This potential confound was not corrected for. Indeed, the stimulus configuration for the secondary task was not unlike that of surround-masking, particularly when observers were required to enumerate seven or eight elements. Therefore, while these investigations were novel, it was not possible to conclude from their main findings that subitization of peripherally presented elements was vulnerable to attentional load, given that perceptual and attentional load were not distinguished from one another. Hence, one of the aims of this research was to disambiguate the effects of attentional from perceptual load, and to observe whether contrast gain saturation had a deleterious effect upon numerosity comparison judgements. The mechanisms of contrast gain saturation and perceptual load are described with detail in the following chapter.

## 1.5. Research questions, aims and hypotheses

The psychophysical experiments described here measured only two of the many aspects of perceptual load – the first by means of high contrast visual stimulation (surround-masking), and the second via feature based selective attention. The surround masking experiments involved the saturation of signal gating resources in LGN and V1 (Freeman, Durand, Kiper, & Carandini, 2002; Solomon, White, & Martin, 2002; Webb et al., 2005), whereas the 'numerosity filtering' experiment recruited inhibitory mechanisms involved with transient and feature-based selective attention in order to suppress or ignore task-irrelevant numerosity sets (Andersen & Müller, 2010; Carrasco, 2011; Zhang & Luck, 2009).

It was of particular interest to examine individual differences in arithmetical ability of adults, and whether these variations were associated with the functional quality of attentional and sensory suppression during comparison judgements of non-symbolic numerosities. Given that groups of individuals with schizotypal personality disorder (SPQ) and autism spectrum disorder (ASD) show mathematical difficulty (Aagten-Murphy et al., 2015; Meaux et al., 2014; Mitropoulou et al., 2005; Trotman et al., 2006; Weiser et al., 2003), it was also of interest to investigate whether SPQ and AQ traits within the typically developing (TD) population correlated with numerosity estimation performance. In order to explore these possibilities, the experiments were divided into four sections, where each section addressed key aims and research questions.

### 1.5.1. The surround-masking of numerosity (psychophysics part 1)

As earlier noted, surround-masking induces high sensory load that results in poor contrast discrimination of centrally presented texture patches among neurotypical observers ( Xing & Heeger, 2000, 2001; Zenger-Landolt & Heeger, 2003). By these observations, the aims of experiment 1 (section 1) were to ascertain whether the deleterious effects of surround-masking upon contrast discrimination were generalizable onto numerosity comparison mechanisms. That is, does surround-masking have the same disruptive influence over the sensory process for numerosity comparison as it does whilst making contrast-matching judgments? Experiment 1 was designed to answer this research question, which comprised a psychophysical design with variations in surround contrast (high/low), centre contrast (high/low), and numerosity (fewer/more dots). If the high contrast surround has a disruptive effect upon the ability to estimate the difference between fewer and more elements, one may infer that numerosity comparison mechanisms are susceptible to sensory load, and that the proficiency of numerosity comparison judgments depends upon the functional quality of inhibitory gain control mechanisms.

### 1.5.2. Measurement of SPQ/AQ traits and cognitive assessment of arithmetical ability (Part 4)

The extent of schizotypal and autistic traits for each participant was measured by the SPQ (Raine, 1999) and the AQ (Baron-Cohen, Wheelright, Skinner, Martin & Clubley, 2001). These questionnaire items were randomly combined and undertaken online. In a separate session, the Ravens Advanced Progressive Matrices (RAPM) test was administered in order to evaluate the non-verbal IQ of participants, followed by the WAIS-IV vocabulary, forward, backward, sequencing and arithmetical sub-tests. Finally, participants underwent a set of computerised tasks that assessed arithmetical ability and reaction times of magnitude comparison judgements. It was of particular interest to determine which SPQ/AQ traits correlated with the cognitive domains assessed, and what sort of correlation existed between them.

Given that the neuropsychological profile of schizotypal personality disorder has been characterised by poor arithmetical ability (Mitropoulou et al., 2005; Trotman et al., 2006; Weiser et al., 2003), it was hypothesised that participants with high SPQ scores would display significantly poorer performance in the WAIS-IV arithmetical sub-test, arithmetic true/false judgement task, and symbolic number comparison task than participants with low and average SPQ scores. In terms of AQ scores and neuropsychological assessment, it was hypothesised that participants with high AQ scores, particularly those with high attention to detail, would show better performance on the arithmetical/mathematical tasks than those with low or normal AQ scores in light of the literature that has suggested high AQ individuals show superior performance in mathematics (Baron-Cohen, Wheelright, Skinner, Martin & Clubley, 2001).

### 1.5.3. Magnetoencephalographic response properties associated with surround-masking of numerosity (part 5)

The psychophysical experiments outlined in section 1 were customised slightly so that MEG recordings could be obtained for the physiological responses associated with surround-masking of numerosity comparison. From inspection of the findings from section 1 (psychophysics) – that that the high contrast centre and high contrast surround had a disruptive effect upon numerosity comparison performance, it was hypothesised that significant sensor clusters would be localised to occipital and parietal regions of the sensor array. That is, event related field (ERF) responses were expected to be maximal within occipital regions given that contrast gain saturation mechanisms have been shown as driven by LGN and V1 (Carandini, 2004; Zenger-Landolt & Heeger, 2001). More specifically, it was hypothesised that the neuromagnetic signature for sensory gain control (most optimal under high contrast centre/high contrast surround conditions) would be characterised as lower (attenuated) ERF peak amplitude than the neuromagnetic signature for receptive field (RF) facilitation (most optimal under low contrast centre/low contrast surround conditions) within occipital and parietal sensors.

### 1.5.4. Sensory load modulations of numerosity comparison judgements via feature based selective attention (Number filtering, part 6)

Section four was a MEG investigation into the effects of stimulus saliency on attentional selection during numerosity judgements. Unlike the surround-masking of numerosity experiments, the non-symbolic sets to be compared were presented simultaneously, and were distinguishable by differences in luminance. To elaborate, the psychophysical design of the final experiments were segmented into eight conditions that varied in background luminance (black/zero and grey/low); target numerosity (fewer or more dots); luminance of target and distracter dots (high/bright and low/dim); and contextual congruency (e.g. more bright target dots amid fewer dim distracter dots (congruent)/fewer bright target dots amid more dim distracter dots (incongruent)). The objective of this task was to indicate whether the cued set of target dots were fewer or greater in numerosity than the distracter dots. It was of special interest to determine whether there were ERF response differences in the attentional selection of salient and attentional suppression of irrelevant stimulus features during numerosity comparison judgements. From this, it was hypothesied that numerosity comparison judgements of contextually incongruent stimuli (e.g. fewer high luminance target dots amid more low luminance distracter dots) would be substantially more difficult to make than comparison judgements of contextually congruent stimuli (e.g. more high luminance target dots amid fewer low luminance distracter dots). The neuromagnetic signature for such cognitive interference was hypothesised to occur within occipital-temporal sensors (Andersen & Müller, 2010; Fukuda & Vogel, 2009; 2011).

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# Part 2
# Literature Review:

# The Micro and Macro Structural Dynamics of Suppressive Mechanisms, and their Functional Relationships With Visual Attention

# Abstract

The configuration of an organised and coherent percept is subject to a myriad of external factors that compromise the fidelity of incoming information. One such contributing factor toward perceptual noisiness is reduction in signal to noise ratio (SNR) of visual input relayed from lateral geniculate nucleus (LGN) to the primary visual cortex (V1). The computations involved with perception require the dynamic coordination of attentional enhancement in the selection of contextually relevant information, and also the inhibition of noisy input. The functional contribution of early inhibitory mechanisms for perceptual processing and visual attention is non-trivial and complex, as there is more than one variety of inhibition within the visual system. Hence, the aim of this literature review was to firstly outline these differences in inhibitory responses that occur in the early visual system, and to describe their associated psychophysical properties. Following this, the activity dependent and genetic aspects of inhibition and sensory filtering will be detailed, in combination with the most recent computational models that have posited inhibitory mechanisms as an essential component of perceptual noise exclusion, predictive coding, and sensory gain attenuation processes. The genetic aspect of inhibition will be discussed because of its contribution toward the development of sensory filtering circuits via the regulation of inhibitory neurotransmitter GABA. From recent psychophysical and neuroimaging empirical literature, the functional contribution of sensory filtering/perceptual noise exclusion for selective attention and cognitive development is reviewed in answer to one of the main research questions of this dissertation that was: how might poor sensory filtering mechanisms and weak inhibition impair the ability to make numerosity estimation judgements?

## 2.0. Introduction

In order to comprehend the functional significance of sensory filtering and its contribution towards learning, attention and cognitive development, it is necessary to describe some of the physiological response properties that characterise it. Sensory filtering, the removal of redundant afferent visual information, occurs mainly at 3 different levels of neural organisation – the synapse (Rothman, Cathala, Steuber, & Silver, 2009); the cortico-thalamic or cortico-geniculate relay (Angelucci & Sainsbury, 2006; Callaway, 2004),and by intra-cortical inhibition of horizontal connections that overlap neighbouring extra classical receptive fields (ECRFs) in V1(Carandini, 2004). At the synaptic level of organisation, sensory filtering has been proposed to occur by means of GABA-ergic inhibition, where interneurons such as fast spiking basket cells hyperpolarise excitatory pyramidal cells in V1 by their pre-synaptic contacts (Bartos, Vida, & Jonas, 2007; Markram et al., 2004). At the macrostructural level of neural organisation such as the cortico-thalamic or geniculo-striate relay, sensory filtering occurs by means of inhibitory feedback onto visual afferents (i.e. magnocellular, koniocellular or parvocellular input) from either the thalamic reticular nucleus (TRN) onto lateral geniculate nucleus (LGN), or through cortico-thalamic feedback from layer 6 of V1 onto LGN (Angelucci & Sainsbury, 2006; Sherman, 2005).

Some of the visual perceptual anomalies associated with schizophrenia have been associated with poor motion discrimination during high contrast visual stimulation, arguably attributed to weakened inhibitory surround mechanisms of receptive fields (RFs) in LGN and V1 (Tadin et al., 2006). The RF suppression of geniculo-striate cells during high contrast visual stimulation may be conceived as a functional component of sensory filtering or contrast gain saturation (Albrecht, Geisler, & Crane, 2003; Bonin, Mante, & Carandini, 2005; Henrie & Shapley, 2005). In the instance of schizophrenia and autism, the patho-physiologies of sensory filtering are likely to be attributed towards GABA (gamma amino butyric acid) deficiency, where the functional consequences of such neurochemical offsets are likely to cause pervasive disturbances in the excitatory/inhibitory (E/I) balance of synaptic microcircuits (Baroncelli et al., 2011; Gonzalez-Burgos & Lewis, 2008; Yoon et al., 2010).

The focus of this chapter is to describe in depth some of the mechanisms involved with gating redundant visual input, and its functional contribution towards selective attention, learning, and cognitive development. Some of the central issues of discussion will be the molecular, genetic or activity dependent processes associated with inhibitory signalling within the primate and non-primate visual system, and its influence over predictive coding within neuronal microcircuits involved with perception. Also central to discussion will be the distinct forms of inhibition that occur at each level of the visual hierarchy, and the functional contribution for each distinct inhibitory mechanism towards sensory filtering of perceptually irrelevant visual input. Finally, this chapter will include a review of some recent neuroimaging investigations into the neuromagnetic, electrophysiological and metabolic properties related to GABA mediated inhibition within the human visual system. Such physiological markers are characterised by disturbances in perceptual organisation and sensory gain control of highly salient yet irrelevant input (sensory filtering) in autistic and schizophrenic populations.

## 2.1. The origins and mechanics of inhibition

At the most rudimentary level, visual sensory information is carried, gated or amplified by the RF properties to which thalamic and cortical neurons are respectively tuned (Alitto & Usrey, 2003). The organisation of RF properties within the geniculo-striate relay is varied and depends largely upon the stimulus features to which a neuron is tuned. In LGN for example, the excitatory/inhibitory segments of an RF are organised by a concentric centre/surround structure that falls into 2 functional classes – on centre/off surround and off centre/on surround (Wurtz & Kandel, 2000). The RF responsiveness of on and off centre cells in LGN depends on stimulus spatial frequency and luminance contrast. At any one visual field eccentricity of this topographically mapped nucleus, the parvocellular RFs respond to relatively higher spatial and lower temporal frequency (Wurtz & Kandel, 2000). Magnocellular RFs respectively, can be activated at low luminance contrast, low spatial and high temporal frequencies (Wurtz & Kandel, 2000). For the magnocellular channel in particular, the inhibitory segment of an RF (extra classical RF) and its magnitude of suppression is greater than koniocellular or parvocellular LGN inputs (Solomon, White, & Martin, 2002). The most robust suppressive effects of magnocellular ECRFs have been observed to occur at high Michelson contrast – evidenced by a reduction in peak firing rates of magno cells as contrast increases (M Carandini, 2004). Stronger suppressive fields of magnocellular over parvocellular inputs may be partly explained by a higher density of GABA-ergic interneurons in magnocellular layers of LGN than parvocellular (Montero & Zempel, 1986). In LGN, 3 main inhibitory phenomena have been described – (i) contrast response saturation, (ii) surround masking and (iii) size tuning. Surround masking induces RF inhibition by means of high contrast peripheral stimulation (i.e. high peripheral sensory load) whereas RF inhibition increases as the size tuning and diameter of high contrast surround masking stimuli widens (M Carandini, 2004).

In V1, the organisation of RF response properties to stimulus features is more diverse and complex than that of the centre/surround structure of cells in LGN (Wurtz & Kandel, 2000). The RF structures of cells in V1 fall into 2 classes, which are simple and complex – each with unique tuning properties to stimulus features. Simple cells for example, possess an elliptical RF structure with a discrete on (excitatory) and off (inhibitory) segments that flank a bar shaped centre with an orientation selective axis (Carandini, 2004; Wurtz & Kandel, 2000). The RFs of complex cells are selective to features such as motion direction and orientation, however do not possess the spatially segregated off and on and excitatory segments of simple cells. The majority of the RF responses from complex cells are determined by pre-synaptic input from simple cells (Wurtz & Kandel, 2000).

Although the cells in V1 and LGN possess distinct RF physiological properties, they nonetheless interact in dynamic coordination during the encoding and elimination of afferent information as part of perceptual organisation and sensory filtering (Albrecht et al., 2003; Alitto & Usrey, 2003; Fitzpatrick, 2000). The RF inhibitory response mechanisms that occur through high-contrast surround masking for example, are driven by early and late temporal ECRF signatures, characterised by contrast saturation in LGN (early) and orientation specific surround suppression via collinearly aligned centre and surround gratings (late) in V1 (M Carandini, 2004; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005).

The effects of surround masking on discrimination judgements for psychophysical properties of visual perception, have been well described by primate electrophysiological and psychophysical literature throughout the last 5 decades (Albrecht et al., 2003; Carandini, 2004). Surround masking has been widely demonstrated to have a deleterious impact upon discrimination judgements of motion direction (Tadin & Lappin, 2005; Tadin, Lappin, Gilroy, & Blake, 2003) and perceived luminance contrast (Xing & Heeger, 2000; Zenger-Landolt & Heeger, 2003). The functional consequences of surround masking have been argued to exert capacity limits upon sensory filtering or signal gating resources in LGN and V1 by means of response saturation at high contrast (Albrecht et al., 2003). Surround masking then, may be a valuable implement in the systematic study of sensory filtering and perceptual inefficiencies.

### 2.2. Activity dependent and genetic processes involved with inhibition and sensory filtering

The synaptic configuration of RF inhibitory microcircuits in V1 and LGN over developmental time is likely to be shaped and moulded through experience dependent modifications in neural plasticity and gene expression via sensory experience (B. Lu, Wang, & Nose, 2009). The genetic transcription factors associated with experience dependent inhibition in the visual system are brain derived neurotropic factor (BDNF) and glutamic acid decarboxylase (GAD) – a rate limited enzyme involved with synthesis of GABA (Lu et al., 2009). The calcium ($Ca^{2+}$) dependent second messenger involved with genetic expression of glutamatergic synaptic plasticity also plays a functional role in signalling for gene transcription of BDNF promoter IV, that in turn contributes to gene transcription of GABA synapse formation (Wilson & Sur, 2011).

Mouse model investigations into the functional consequences of gene-targeted disruption of inhibitory neurotransmission have enabled much insight into the pervading disturbances that characterise developmentally anomalous sensory filtering mechanisms. For example, through subtle mutation of a $Ca^{2+}$ responsive element that binds the second messenger protein CREB (calcium response element binding) to BDNF promoter IV, Hong, Mc Cord and Greenberg (2008) observed a cascade of deleterious effects upon experience dependent mechanisms during the regulation of inhibitory synaptic development in mouse visual cortex. That is, mutation of CREB-binding sites in V1 resulted in a defect of BDNF promoter IV gene transcription – a part of the neuronal response machinery for activity dependent calcium influx. Following a 14-day dark rearing period, wild type control and CREB-mutant mice underwent 90 minutes of light exposure in order to activate sensory experience dependent expression of BDNF. Compellingly, the 20-fold increase of BDNF promoter IV mRNA observed in visual cortex of control mice was reduced by ~75% in CREB-mutant mice.

Hong et al., (2008) used electrophysiology to examine the functional consequences of reduced $GABA_A$ and GAD-65 expression over V1 inhibitory microcircuits in CREB-mutant mice electrophysiologically, and observed a significantly lower frequency of miniature inhibitory post-synaptic currents (mIPSCs) in CREB-mutant neurons as compared to control mice. The amplitude of mIPSCs in CREB-mutant neurons was moreover significantly greater than control mice. This was argued to reflect a developmental offset in the neural mechanisms for sensory experience dependent inhibition in visual cortex. Overall, gene targeted disruption of BDNF transcription machinery has been widely demonstrated to manifest as a pervasive perturbation in the regulation of inhibitory synaptic strength, so as to induce a homeostatic offset in the excitatory/inhibitory balance of gating plasticity, resulting in increased excitability of V1 neurons (Abidin, Eysel, Lessmann, & Mittmann, 2008; Burrone & Murthy, 2003; Hong et al., 2008; Wilson & Sur, 2011).

One of the most striking physiological features associated with gene-targeted disruption of GABA-ergic inhibition in mouse V1, is a marked absence in neuronal response saturation (Hong et al., 2008) and prolonged discharge in extra-cellular single unit recordings (Hensch et al., 1998) evoked by luminance sensory stimulation. One of the possible causes of this defect in sensory gating is a reduction in axonal branching of basket interneurons, and GABA-ergic synapses on peri-somatic regions of pyramidal cells (Abidin et al., 2008; Chattopadhyaya et al., 2007). Such microstructural defects not only impact the previously mentioned synaptic gain control mechanisms that attenuate signal intensity, but they also disrupt the temporal coordination of predictive coding pattern signalling between neuronal ensembles in V1 (Miles, 2000; Tsodyks & Gilbert, 2004).

In humans, this same homeostatic offset in sensory experience inhibition, or excitatory/inhibitory balance of gating plasticity in V1, has recently been evidenced psychophysically and *in vivo* through magnetic resonance spectroscopy (MRS). For example, it was demonstrated psychophysically that following 150 minutes of monocular deprivation, the perception of dichoptically rivalrous stimuli (binocular rivalry) was twice as apparent within the previously occluded eye, where the perceived contrast of stimuli to the deprived eye was much greater than the non-deprived eye by a factor of 1.36 (Lunghi, Burr, & Morrone, 2011). An increase in apparent contrast was indicative of amplification in signal gain within the deprived eye (Lunghi et al., 2011). This amplification in sensory gain and increase in perceived contrast following 150 minutes of monocular deprivation was recently evidenced to be a functional reflection of decreased resting GABA in V1 through MRS (Lunghi, Emir, Morrone, & Bridge, 2015).

There are several developmental and neuropsychiatric illnesses that are characterised by lowered concentrations of cortical GABA, such as high functioning autism, schizophrenia, and bipolar affective disorder (Baroncelli et al., 2011; Behrendt & Young, 2004; Torrey et al., 2005; Peter J. Uhlhaas & Singer, 2010; P. Uhlhaas et al., 2009). Also, post mortem investigations have revealed that the most prominent neurochemical marker for schizophrenia, bipolar disorder and autism was significantly reduced gene expression of GAD-67 in parietal and anterior cingulate cortex compared to control brains (Fatemi et al., 2002; Torrey et al., 2005).

In humans, GABA deficiency resulting from reduced GAD-67 expression has been postulated to greatly impair the functional quality of temporal coordination and synchronisation of neuronal encoding signatures involved with signal gating, plasticity, and perceptual organisation (Peter J. Uhlhaas & Singer, 2010; P. Uhlhaas et al., 2009). As evidenced by magnetoencephalography (MEG), gamma band oscillations (30-200 Hz) have been noted as a functional reflection of GABA mediated inhibition in V1 (Muthukumaraswamy, Edden, Jones, Swettenham, & Singh, 2009). In schizophrenia and autism, the gamma power spectra of visually evoked and induced oscillations have been observed to be significantly lower than in neurotypical observers (Peter J. Uhlhaas & Singer, 2010). It has been suggested that weakened gamma oscillatory activity may be a physiological marker for a pervasive defect in $GABA_A$ mediated synchronisation of cortico-cortico networks (Gonzalez-Burgos & Lewis, 2008; Lewis, Hashimoto, & Volk, 2005; P. J. Uhlhaas & Singer, 2007). Anomalous network synchronization is likely to have an adverse effect upon low-level mechanisms involved with the relay of visual sensory input or coordination of temporal coding patterns as part of experience dependent plasticity, perceptually salient stimulus selection, and predictive coding of input statistics as part of perceptual organisation (Uhlhaas et al., 2009).

**2.3. Computational models of predictive coding and sensory gain attenuation of redundant afferent information**

Experience dependent plasticity, as part of the development in excitatory and inhibitory microcircuits, may be conceived as the most rudimentary component of learning (Ghose, 2004). There has been much literary debate concerning the sensory processes that contribute to the RF tuning mechanisms of environmental and sensory context – does the learning of perceptual representation arise through the amplification of contextually relevant stimulus features or the suppression (gating) of task irrelevant and redundant information?(Ghose, 2004; Tsodyks & Gilbert, 2004). According to the hierarchical predictive coding hypothesis of Rao and Ballard (1999), RF suppressive phenomena of neurons in V1 and LGN plays a functional role in the elimination of feed-forward signal error, and the prevention of statistically redundant input relayed to high order extra-striate areas. The functional architecture of the predictive coding model is characterized by a hierarchically structured relay comprising of feedback pathways that carry high order predictions about temporal coding patterns in sensory areas and conversely, feed-forward relays that carry information about residual errors between high order statistical prediction, and neuronal responses to input. Higher order visual areas such as V2 or V5 for example, serve as predictive estimators that correct feed-forward residual errors in lower order visual areas such as V1 or LGN. The critical aspect of the predictive coding framework in the context of sensory filtering is that the minimisation of residual error in feed-forward signalling is mediated by extra-classical RF (inhibitory) phenomena such as end-stopped surround suppression.

A more recent development of the predictive coding model from Spratling (2011), provides a functional account of the physiological response mechanisms that occur in V1 and LGN, as a course of error minimisation between sensory input and feedback predictions. Essentially, intra-cortical inhibition, a suppressive phenomenon in V1 that occurs either by horizontal or by cortico-cortico feedback, was represented as the instrument by which the aforementioned predictive feedback minimises feed-forward signal error. These intra-cortical inhibition simulations that occurred as a result of error prediction feedback, were generated (or induced) via high contrast surround masking and contrast gain saturation.

Intra-cortical inhibition, through the combination of V1 surround suppression and LGN contrast gain saturation, has been mathematically modelled as a process named divisive gain normalisation (Albrecht et al., 2003; M Carandini, 2004; M. Carandini, Heeger, & Senn, 2002; David, Vinje, & Gallant, 2004; Rothman et al., 2009; Schwartz & Simoncelli, 2001; M. W. Spratling, 2011). Divisive gain normalisation in neuroinformatic modelling has been widely applied to simulate or explain an array of suppressive phenomena in the geniculo-striate relay, including cross-orientation inhibition (Carandini et al., 2002), surround suppression (Carandini, 2004) and thalamo-cortical synaptic depression (Carandini et al., 2002; Rothman et al., 2009). It has also served as a computational framework to explain the physiological mechanisms by which predictive feedback minimises the variance in neuronal firing patterns following contrast gain saturation (Albrecht et al., 2003; Carandini, 2004; Schwartz & Simoncelli, 2001).

So far, in this chapter, a sound number of biologically plausible computational models have been developed that provide a functional explanation of RF inhibitory mechanics involved with feed-forward error minimisation at a synaptic level of neural organisation. However, one question that remains is: how does the visual system generate a coherent percept via the regularity of statistical descriptors from afferent input? To answer this question, it is first of all necessary to describe the notion of input statistics in the context of how the geniculo-striate relay encodes and gates sensory input. This is by no means a trivial problem, as there is a continuous deluge and diversity of physical properties arriving in the visual pathways at almost every instant (Carrasco, 2011).

Statistical descriptors of psychophysical properties are conceived in terms of frequency, variance and mean of any given stimulus feature per unit of time or space (Ariely, 2001). The noisiness or error inherent in the feed-forward signal is moreover statistically represented as the variance of neuronal firing patterns or temporal coding signatures in response to sensory input (Albrecht et al., 2003; Schwartz & Simoncelli, 2001). Greater variance in the coding properties of feed-forward neurons would therefore result in a reduction of SNR, or a more ambiguous reconstruction of the perceptual representation (Lu & Dosher 2008; Lu & Dosher 1998; Z.-L. Lu & Dosher, 1999). The minimisation of variance in neuronal firing may hence depend upon the functional quality of dendritic inhibition (M.W. Spratling & Johnson, 2001) . In the context of perceptual disorders, such as in autism or schizophrenia, it may be well to speculate that prediction error feedback mechanisms may be functionally aberrant, compared to neurotypical populations. The most likely mechanism underlying the aberrant prediction error feedback may be a developmentally anomalous inhibitory system by as earlier mentioned, a deficiency of BDNF promoter IV and GAD-67 transcription.

**2.4.What functional role does sensory filtering play in selective attention?**

Considering the theoretical framework of the predictive coding hypothesis, sensory filtering may be considered as a mechanism by which input-coding error is minimised by high-order feedback signalling from extra-striate areas. But what are these feedback prediction errors modulated by? Biophysical computational modelling has postulated that selective attention is the means by which predictive feedback signalling suppresses or filters out perceptually noisy input (Spratling, 2008; Spratling & Johnson, 2004). Undoubtedly, the suppression of contextually irrelevant input is not the only mechanism that contributes to the functional orchestration of selective attention. It is most likely to occur through a combination of excitatory feedback that serves to amplify feature saliency, and intra-cortical inhibition in V1, to filter out noise or task irrelevant distracters (Carrasco, 2011; Spratling & Johnson, 2004; Spratling, 2008).

The cortical dynamics of neural facilitation and suppression via feature-based selective attention has been observed empirically using steady state visually evoked potentials (SSVEP). Andersen and Müller (2010) for example, noted temporally distinct SSVEP responses for attentional enhancement (neural facilitation) and task-irrelevant distracter exclusion (suppression) during cued attentional shifts to either red or blue superimposed random dot kinematograms (RDKs). Observers were required to detect any motion coherence of the cued RDK colour (targets), while ignoring the simultaneously presented RDKs that served as distracters. The SSVEP data were acquired through electroencephalographic (EEG) recording, with stimulus response amplitudes being greatest in a cluster of occipital electrodes. There were a number of compelling SSVEP response characteristics, that were modulated by selectively attending and ignoring RDK stimulus features. Firstly, the sign of the SSVEP response amplitudes were distinguished by facilitative and suppressive mechanisms of feature based selective attention. That is, the SSVEP amplitude sign when attending to the cued RDK stimulus was positive, and commenced approximately 220ms following cue onset. Respectively, suppression of unattended or task-irrelevant stimuli was characterised by a negative SSVEP response that occurred approximately 360ms post cue.

The functional implications of Andersen and Müller’s (2010) findings not only suggest that the cortical dynamics of feature based selective attention comprise distinct temporal components in the enhancement and suppression of feature input, it also suggests a likely electrophysiological marker for a sensory filtering mechanism of selective attention in sensory areas of human cortex. That is, the electrophysiological signature for suppression in V1 at least, may partly be characterised by a negative deflection of evoked response amplitudes to statistically redundant visual input.

The distinction between facilitative and suppressive response properties of selective attention have also been evidenced to possess a central/peripheral spatial organisation in visual cortex, where the current source distribution in response to peripheral distracter exclusion in occipital cortex appears to be characterised by a focal excitatory zone with increased current source density and an inhibitory zone surrounding this (Hopf et al., 2006). While the previously discussed investigations both examined the electrophysiological signatures of excitation and inhibition in lower order visual areas during selective attention, it is imperative to note that these experiments were operationalized differently. Hopf et al., (2006) observed the inhibitory surround characteristics of selective attention via covert serial search, Andersen and Müller (2010) on the other hand measured the effects of filtering task-irrelevant distracters through feature based selective attention.

The findings of these investigations fall in line with the theoretical assumptions of the biased competition hypothesis (Desimone & Duncan, 1995), that posits the locus of attentional enhancement is a capacity limited process, where by neurons compete among each other to encode the deluge of afferent with the greatest salience. The “winning” features that fall onto a neurons RF facilitative zone are enhanced to form a contextually relevant representation of perceptual gestalt, as the RF inhibitory regions suppress or filter out the “losing” features.  Sensory filtering, therefore, may be viewed as a functional component of selective attention. It may be inferred that it minimises resource-limited competition occurring between neurons in sensory areas such as V1 through intra-cortical inhibition, as excitatory feedback serves to enhance the salience and context of perceptual and cognitive representation (Spratling, 2008; Spratling & Johnson, 2004).

## 2.5.The functional role of filtering in cognitive development

As discussed earlier, learning at the most rudimentary level of neural organisation involves the combination of strengthening and eliminating synaptic connections that form the microcircuits to relay, amplify, attenuate and gate sensory input (Tsodyks & Gilbert, 2004). Synaptic depression mediated by GABA-ergic inhibition – serves to suppress or attenuate afferent information that is uninformative about the context or relevance of a given perceptual representation (Carandini et al., 2002; Rothman et al., 2009; Schwartz & Simoncelli, 2001; Tsodyks & Gilbert, 2004). These mechanisms however relate to the low order processes associated with experience dependent plasticity in sensory cortex, which is not very informative about the more widespread modifications that occur as part of the learning process of high order and abstract cognitive representation.

Gal et al., (2009) nonetheless, observed via fMRI that learning to ignore task-irrelevant distracters within the organisation of a perceptual set was accompanied by an attenuated BOLD (blood oxygen level dependent) response in V5 as a result of learning. Specifically, following training on a motion direction discrimination task of 2 overlapping dot fields, one being task-relevant and the other being task-irrelevant, observer BOLD responses were found to be differently modulated by task-relevant and task-irrelevant motion direction. Learning induced responses for task-relevant motion direction was characterised by an increase of BOLD magnitude within V1. Learning to suppress task-irrelevant motion direction however was characterised by a significant reduction of BOLD response magnitude compared to pre-training baseline in V4, V2, V3a and V5. These findings suggest that the suppression (or filtering) of task-irrelevant information might provide a functional contribution towards the mechanisms involved with learning representational sets.

Another fMRI investigation into learning dependent changes in cortical activation patterns across time, also demonstrated an attenuated BOLD response in selective attention networks following training on a contrast discrimination task (Mukai et al., 2007). To elaborate, as compared to pre-training BOLD activation, task learning dependent changes were observed as significant reduction in BOLD magnitude of intra-parietal sulci (IPS), frontal eye fields (FEF), supplementary eye fields (SEF) and Brodmann areas 18 and 19 – visual association areas in occipital cortex. There was a sub-group of observers in this study, however, who failed to demonstrate this post-training BOLD reduction within this cortical network – that was argued to be a functional consequence of non-learning.

It is reasonable to ask at this point, how do learning associated BOLD deactivations within the cortical networks supporting selective attention relate to sensory filtering of contextually irrelevant stimulus features?
Previously discussed fMRI investigations (Gál et al., 2009; Mukai et al., 2007) both concluded that learning dependent BOLD attenuation of visual attention areas might be a functional reflection of changes occurring in RF tuning properties as their response selectivity becomes increasingly tuned to the target features. This process, which has been named cortical-sharpening, might then be an inhibitory mechanism that eliminates input redundancy in sensory areas, and concomitantly narrows the functional specialization of high order attentional areas in the developmental course of learning (Gál et al., 2009; Mukai et al., 2007).

### 2.6.How do poor sensory filtering mechanisms and weak intra-cortical inhibitory mechanisms impair the ability to make number comparison judgements?

Mukai et al., (2007) noted that a small group of observers who participated in their visual perceptual learning experiment, did not demonstrate a post-training BOLD reduction within attentional network cortices. This effect was postulated to reflect non-learning, but raises the question of whether these non-learning effects were attributed to a functional anomaly of suppressive mechanisms associated with contrast gain attenuation (divisive normalisation)? If so, how would this functionally compromise the ability to make estimation judgements of non-symbolic numeric perceptual sets?

There is ample psychophysical evidence that suggests when making more/less judgements of numerosity sets, the visual system capitalises upon statistical properties within the display in order to glean the most representative input within the percept (more/less), rather than attend to the individual items of which they are comprised (Ariely, 2001; Burr & Ross, 2008; Chong & Treisman, 2003; Gallistel & Gelman, 2000). That is, observer accuracy of more/less judgements might be determined by the mean of target elements against their respective background distracter ratio (Ariely, 2001), and by their scalar variability – characterised by the signal distribution within sensory input (Gallistel & Gelman, 2000). The scalar variability within a numeric perceptual set might then be conceived of in terms of external noisiness, where greater element variability results in a greater representational ambiguity (Gallistel & Gelman, 2000).

How does the visual system minimise the scalar variability (or external noisiness) inherent within non-symbolic number sets? This question may be partly answered through psychophysical evidence that has indicated the efficacy by which observers estimate the mean target set of elements (i.e. orientation average), may depend partly on the number of sample elements employed within the display (Dakin, 2001). That is, when the texture density of a visual display is held constant, and its radius and number of elements co-vary, internal noise estimates (psychophysical thresholds) have been shown to decrease as the number of sample elements increase (>64). This greater number of elements within a display was argued to enhance the sampling density mechanisms the visual system recruits in order to relay the most informative input of the visual percept as signal variance (noise) increases (Dakin, 2001).

Individual differences in internal noisiness when making non-verbal estimation judgements may be quantified as a psychophysical threshold via the Weber fraction ($w$) – the proportion of error within the sum of estimation judgement responses (Gallistel & Gelman, 2000; Halberda, Mazzocco, & Feigenson, 2008; Piazza et al., 2010). Observers with poor non-verbal number acuity such as those with developmental dyscalculia have demonstrated significantly elevated estimation judgement thresholds compared to neurotypically-developed controls (Piazza et al., 2010). One is tempted to relate high numerosity estimation thresholds seen in some individuals to the functional quality of internal noise exclusion mechanisms, a property that has often been conceptualised as sensory filtering (Lu & Dosher 2008; 1999).

## 2.7. Conclusion

While one cannot conclusively relate psychophysical thresholds to the functional quality of sensory filtering mechanisms, it is parsimonious to draw together associations between the existing notions on sensory filtering mechanisms (as discussed in this chapter) and what functional influences they may have upon psychophysical performance for numerosity comparison judgements. The main association, it would seem, is that the sensory filtering and numerosity comparison of number constructs, share a common conceptual framework structured around the notion that generating a perceptual gestalt is achieved through the elimination of noisiness or uninformative visual information. Both sensory filtering and numerosity comparison mechanisms rely on statistical sampling processes that take the mean and variance of the most rudimentary and recurring features of a percept in order to organise a coherent representation (Ariely, 2001; Burr & Ross, 2008; Chong & triesman, 2003; Dakin, 2001; Gallistel & Gelman, 2000; Rao & Ballard, 1999; Schwartz & Simoncelli, 2001).

In summary, the neural mechanisms for enhancement and suppression of incoming sensory information is a computationally expensive process that is prone to considerable signal encoding error including variance in neuronal firing patterns, RF sampling errors and temporal coding signature lags (Albrecht et al., 2003; Z.-L. Lu & Dosher, 1999; Simoncelli, 2003). In excess, such neural inefficiencies are likely to induce a cascade of perceptual distortions that offset the functional quality of selective attention, learning mechanisms and cognitive development. Hence, the functional role of sensory filtering in the reliable configuration of contextually relevant perceptual set representation should not be underestimated. Sensory filtering, is likely to be a hierarchically organised and sensory experience dependent process, where top-down feedback prediction signals from higher extra-striate areas are derived from a feed-forward relay that carries information about the physical properties of the environment by means of statistical sampling of the most representative stimulus features (David et al., 2004; Spratling, 2011; Spratling & Johnson, 2004).

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# Part 3
# The Effects of Surround-masking on Numerosity Comparison: Psychophysics

Abstract

The process of numerosity comparison involves the discrimination of magnitude between two distributions or perceptual sets that vary in numerosity, where one set will always possess more or fewer elements than the other. Here, it was demonstrated that by psychophysically imposing limits upon the mechanisms that mediate sensory and perceptual noise exclusion, the ability to make numerosity comparison judgements became severely impoverished in observers with no developmental or psychiatric disorders. Under conditions of high contrast stimulation of the peripheral visual field, observers became significantly more impaired in a centrally presented numerosity comparison task, compared with low contrast peripheral stimulation. Moreover, the centre and surround contrasts of the stimuli appeared to affect the accuracy of discrimination judgements differently. Observers were more accurate in the discrimination of more elements when the surround contrast was low and the background luminance of the central region containing the elements was dark (black centre). Conversely, accuracy was severely impaired during the discrimination of less elements when the surround contrast was high and the background luminance of the central region was mid contrast (grey centre). It may be inferred from these findings that differences in numerosity comparison may depend upon the functional quality of low-order suppressive mechanisms in lateral geniculate nucleus and primary visual cortex that filter statistically redundant afferent information. Therefore, it was conjectured that poor numerosity comparison commonly observed in developmental dyscalculia – an arithmetical learning disorder despite normal intelligence, may relate to pervasive developmental anomalies in the elimination of unessential visual information.

# 3.0. Introduction

Surround-masking is a phenomenon whereby peripheral visual stimulation at high sensory load deleteriously affects perceptual discrimination. Examples include discrimination of texture regions (Dakin, Carlin, & Hemsley, 2005; Xing & Heeger, 2000, 2001), tilt of line bars or Gabor elements (Polat & Norcia, 1996; Van Der Smagt, Wehrhahn, & Albright, 2005), and awareness of motion direction (Tadin & Lappin, 2005; Tadin, Lappin, Gilroy, & Blake, 2003). Such perceptual inefficiencies produced by surround-masking are likely influenced by low-order inhibitory mechanisms such as surround suppression in lateral geniculate nucleus (LGN) or intra-cortical inhibition in V1 and extra-striate regions (Carandini, 2004; Carandini, Heeger & Senn, 2002; Shapley, Hawken & Ringach, 2003). One of the earliest (and most influential) investigations into the effects of surround-masking revealed that the apparent contrast of a central texture region became much lower to observers when enveloped by a high contrast surround (Chubb, Sperling, & Solomon, 1989).

The Chubb et al., (1989) investigation spurred further inquiry into the relationship between induced perceptual inefficiency and inhibitory gain control during the attenuation of redundant visual information. For example, Xing and Heeger (2000) replicated the findings of the Chubb et al. (1989) surround-masking experiments, and further noted that a low contrast annular grating had a facilitative effect on the apparent contrast of the centrally embedded texture patch. In the presence of a low contrast annular grating, the perceived contrast of the centrally embedded texture was markedly higher than the contrast matched reference patch without a surround. In further investigation of this effect, Xing and Heeger (2001) observed that surround-masking psychophysical performance also was influenced by the width and orientation of the surround annulus - a high contrast surround (80%) with a diameter of $12^{o}$ produced the greatest level of suppression and reduced psychophysical performance for all observers. The suppressive effects were reversed however, when the surround annulus diameter was narrowed to $7^{o}$ – even though the annulus contrast was high (80%).

Xing and Heeger (2001) noted that the psychophysical properties of receptive field (RF) excitation (facilitation) and RF inhibition (suppression) depend upon the contrast of central and surround stimuli and moreover, the diameter of the surround annulus. Excitatory RF processes were postulated to be dominant under low contrast /

narrow surround diameter stimulus conditions – occurring mainly within the foveal field of vision. Inhibitory RF processes, on the other hand, were argued to be dominant under high contrast / extended surround stimulus configurations – occurring chiefly in the peripheral field of vision. In line with these findings, Tadin et al. (2003) observed that the inspection time for discrimination of the motion direction of drifting Gabor patches, showed a strong interaction between stimulus contrast and stimulus size. While for small patches, duration thresholds were smallest for high contrast gratings, the opposite was true for large patches - optimal motion discrimination occurred under low contrast conditions.

The functional role of RF inhibition in V1 includes the attenuation of afferent input with high contrast gain (Webb, Dhruv, Solomon, Tailby, & Lennie, 2005) ; the gating of statistically redundant afferent information – sensory filtering (Schwartz & Simoncelli, 2001) and feature segmentation modulated by orientation selectivity (Shapley et al., 2003). Single-unit recordings of anesthetised cats (Freeman, Durand, Kiper, & Carandini, 2002) suggest RF inhibition in V1 is likely to be relayed from lateral geniculate nucleus (LGN), through mechanisms involving thalamo-cortical synaptic depression (Carandini, et al., 2002).

From computational modelling, primate neurophysiology and psychophysical literature on visual suppressive phenomena, it has been suggested that the RF suppression of cells in LGN and V1 through surround-masking is likely to suppress sensory gain control resources, thereby reducing the signal to noise ratio (SNR) of sensory/afferent information. This, in turn, would generate perceptual ambiguity and representational noisiness (Carandini, et al., 2002; Dakin et al., 2005; Dosher & Lu, 1998; 2000; Freeman, et al., 2002; Lu & Dosher, 1998; 1999; 2008; Schwartz & Simoncelli, 2001; Webb, et al., 2005). Preliminary electrophysiological evidence from nonlinear visual evoked potential (VEP) recordings suggests that those with sub-optimal arithmetical ability of developmental origin show disinhibited sensory gain control mechanisms as well as impoverished change detection performance under high contrast conditions (Jastrzebski, Crewther & Crewther, 2015).

An earlier psychophysical study demonstrated that children with low mathematical skills show higher motion coherence discrimination thresholds than age-matched controls (Sigmundsson, Anholt, & Talcott, 2010), suggesting that developmental dyscalculia (DD) – poor arithmetical ability despite normal intelligence, may be associated with a visual perceptual disorder in contrast gain control or external noise exclusion (Carandini, 2004; Sperling, Zhong-Lin, Manis, & Seidenberg, 2005). Curiously, many developmental disorders such as autism spectrum disorder (ASD), attention deficit hyperactivity disorder (ADHD), Williams syndrome (WS), and developmental dyslexia share a common perceptual deficit in motion coherence discrimination – particularly for global motion coherence stimulus configurations (Braddick & Atkinson, 2011; Cornelissen et al., 1998; Laycock, Crewther, & Crewther, 2007; Stein, Talcott, & Walsh, 2000). It has been well established that poor motion coherence sensitivity may be attributed to atypical development of the dorsal visual stream (Braddick & Atkinson, 2011; Laycock, et al., 2007).

The acquisition of visual number estimation skills for individuals with WS – a neurodevelopmental disorder strongly associated with DD – has been shown to be more variable and delayed over the course of developmental time compared to neurotypical age-matched controls (Ansari, Donlan, & Karmiloff-Smith, 2007). Over the course of development for the typically developing group, there was a graded increase in the mean proportion of correct responses and concomitant decrease in the coefficient of variation (COV), while the WS group only showed a marginal performance increase and very little decrease in the COV.

Similar to the individuals with WS (Ansari, et al., 2007), Piazza, et al., (2010) also noted an absence of improved of visual estimation (number acuity) from early to late childhood of those diagnosed with DD. By contrast, the age-matched control group demonstrated decreased number acuity thresholds (Weber fractions) across developmental time. The Weber fractions of 10-year-old DD observers were not unlike those of the 5 year old typically developing children. A longitudinal study (Halberda, Mazzocco, & Feigenson, 2008) noted that early childhood proficiency with visual estimation ability was the best predictor of later symbolic math achievement during early adolescence (14 years) – even when other factors contributing to math achievement such as general intelligence were controlled for.

Thus, there is evidence to suggest that visual estimation ability in early childhood predicts later mathematical achievement during the course of cognitive development (Halberda, et al., 2008). But what are the visuo-perceptual and developmental factors that predict this sense of number acuity? According to Gallistel and Gelman (2000), the perceptual noisiness during visual estimation follows Weber's law, where the discriminability between two numerosities become more impoverished as the magnitude difference (ratio) between them decreases, and the number of elements within the distribution increases. In other words, more numerous set sizes with smaller differences between them will result in overlap of the signal distributions that represent the numeric perceptual sets – the scalar variability. Could the scalar variability (noisiness) of numerosity comparison be influenced by the functional quality of inhibitory gain control mechanisms discussed earlier? If high contrast surround-masking causes impairment of numerosity comparison accuracy of neurotypical observers, it shows cause to infer that poor number acuity previously observed in DD (c.f. Piazza, et al., 2010) may stem from developmentally anomalous inhibitory gain control mechanisms that play a role in the elimination of redundant visual information, i.e., perceptual noise exclusion (Carandini, et al., 2002; Dakin, et al., 2005; Lu & Dosher, 2008; Schwartz & Simoncelli, 2001).

## 3.1. Materials and methods

### 3.1.1. Participants

18 young adults with normal/corrected to normal vision (mean age: 23.8, SD = 6.06 years, 13 females) participated in this experiment. This sample mostly comprised undergraduate psychology students who were awarded course credit for their participation, and post-graduate students who participated voluntarily without compensation. The study was carried out in accordance with the Helsinki declaration and approved by the Swinburne University of Technology ethics committee (see appendix A for confirmation of ethics approval). Upon inspection of the raw data, it was apparent that there were two individuals with psychophysical responses that were markedly deviant from the remaining 16 participants, and hence were excluded from the analysis.

**Experiment 1a**

### 3.1.2. Stimuli

The stimuli were generated using VPixx software (version 2.79 - www.vpixx.com), presented on a 1680 x 1050 pixel Mac Pro cinema display with a frame rate of 60Hz, and viewed at a distance of 50cm. The 3 main parametric variations of these experiments were background luminance of the central stimulus region (uniform/grey and zero/black); numerosity comparison of number without an annular surround (uniform/grey background luminance and zero/black background luminance); and surround contrast (low 25% and high 95%). The central stimulus region (CSR) was a $6.5^{o}x6.5^{o}$ aperture containing white (168.38 cd/$m^2$) 10 x 10 pixel dots, drifting randomly inside the CSR at 2.14deg/s. Interleaved with the frames of the CSR and dots, was additive random dynamic binary noise (RDBN) of .2° granularity, giving the appearance of transparent noise. Additive noise was interleaved with the CSR stimuli in order to achieve the effect of perceptual ambiguity and statistically redundant input. For the zero luminance CSR, the additive RDBN was at 90% contrast, and at 20% for uniform (grey). The mean luminance for black, grey, and white was 0.30 cd/$m^2$, 40.07 cd/$m^2$, and 168.33 cd/$m^2$ respectively.

When observers made their visual estimation judgements, the CSR was enveloped by either a high or low contrast annulus having an outer radius of 17.5° and inner radius of 3.4° and filled with RDBN – also of 0.2° granularity. There was no overlap between the CSR and surround. Because additive RDBN was interleaved with the dots, the mean luminance for CSR and surround were no longer equivalent. Therefore, separate mean luminance measurements were taken for the CSR and surround. This revealed that the mean luminance for the uniform/grey CSR was 43.95 cd/$m^2$, and 24.3 cd/$m^2$ for the zero/black CSR. The mean luminance of the high contrast surround was 89.69 cd/$m^2$, and 40.39 cd/$m^2$ for the low contrast surround. The range of dot numerosities was 8 - 104, where the minimum value of dots that could be displayed within the initial (reference) CSR was 8 and the maximum for estimating more dots was104.

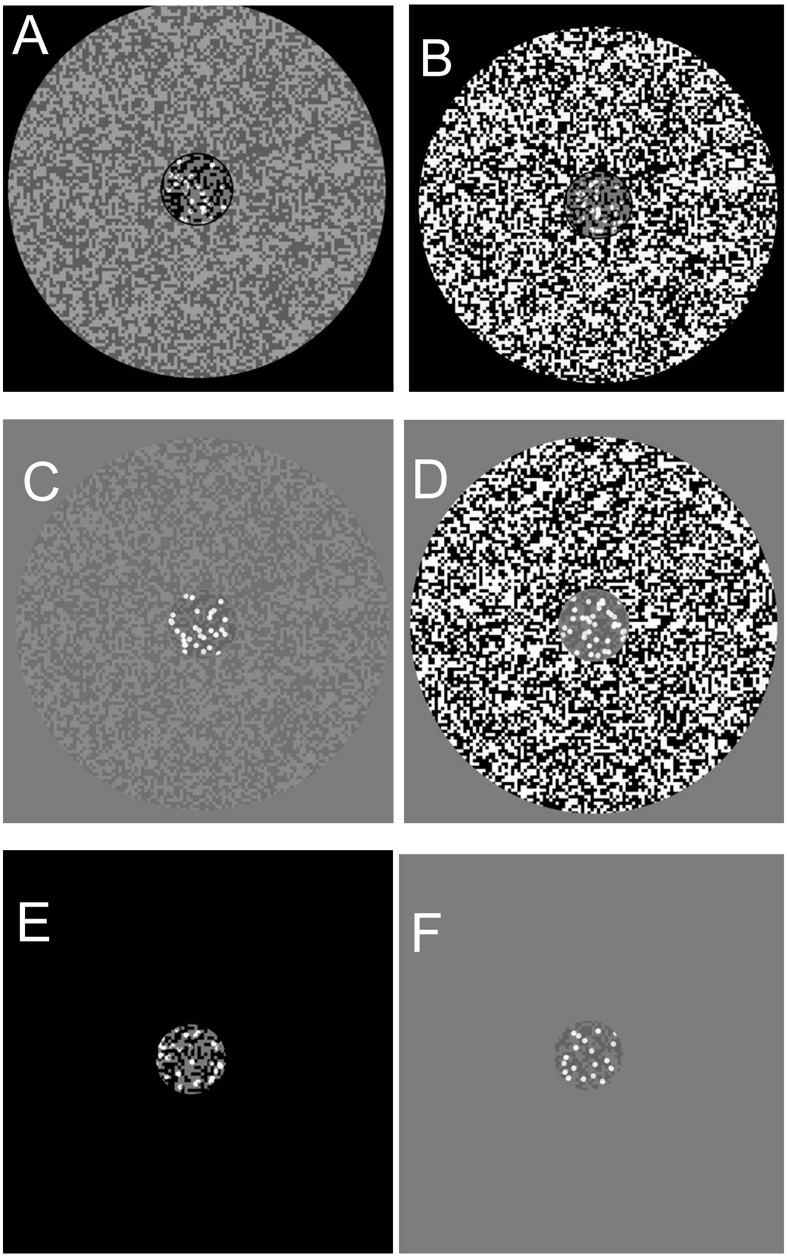


Figure 3.1. Centre and surround contrast stimulus configurations. (A) Black central stimulus region(CSR)/low contrast surround (B) black CSR/high contrast surround (C) grey CSR/low contrast surround (D) CSR/high contrast surround (E) black CSR/zero luminance background (F) grey CSR/uniform luminance background.

As seen from figure 3.1, there were 6 centre/surround configurations. For each experimental run, there were 50 trials per condition (i.e. 50 trials with fewer dots than the reference, and 50 trials with more dots respectively). Therefore, participants undertook a total of 6 experimental runs featuring the psychophysical method of constant stimuli, which was parametrically varied by CSR background luminance (uniform/zero); numerosity comparison with no surround, where the background luminance matched the CSR; surround contrast (high/low). Participants took brief rests between experimental runs in order to minimise fatigue.

As can be seen in figure 3.2, the stimulus sequence within an experimental trial contained 3 CSR stimuli at different times. The first CSR to appear within the trial sequence contained the reference set of dots, which remained on the screen for 1000ms (CSR1). The second CSR (CSR2) was replaced with RDBN that was matched to the contrast of the annular-surround that served as an inter-stimulus interval (ISI) of 750ms. The final CSR to appear in a trial – like CSR1, also contained a set of dots, however this time, the CSR was embedded in a high or low contrast annulus (CSR3). The difference ratio of dots between CSR1 and CSR3 was held constant at 1:0.5 throughout all experimental conditions.

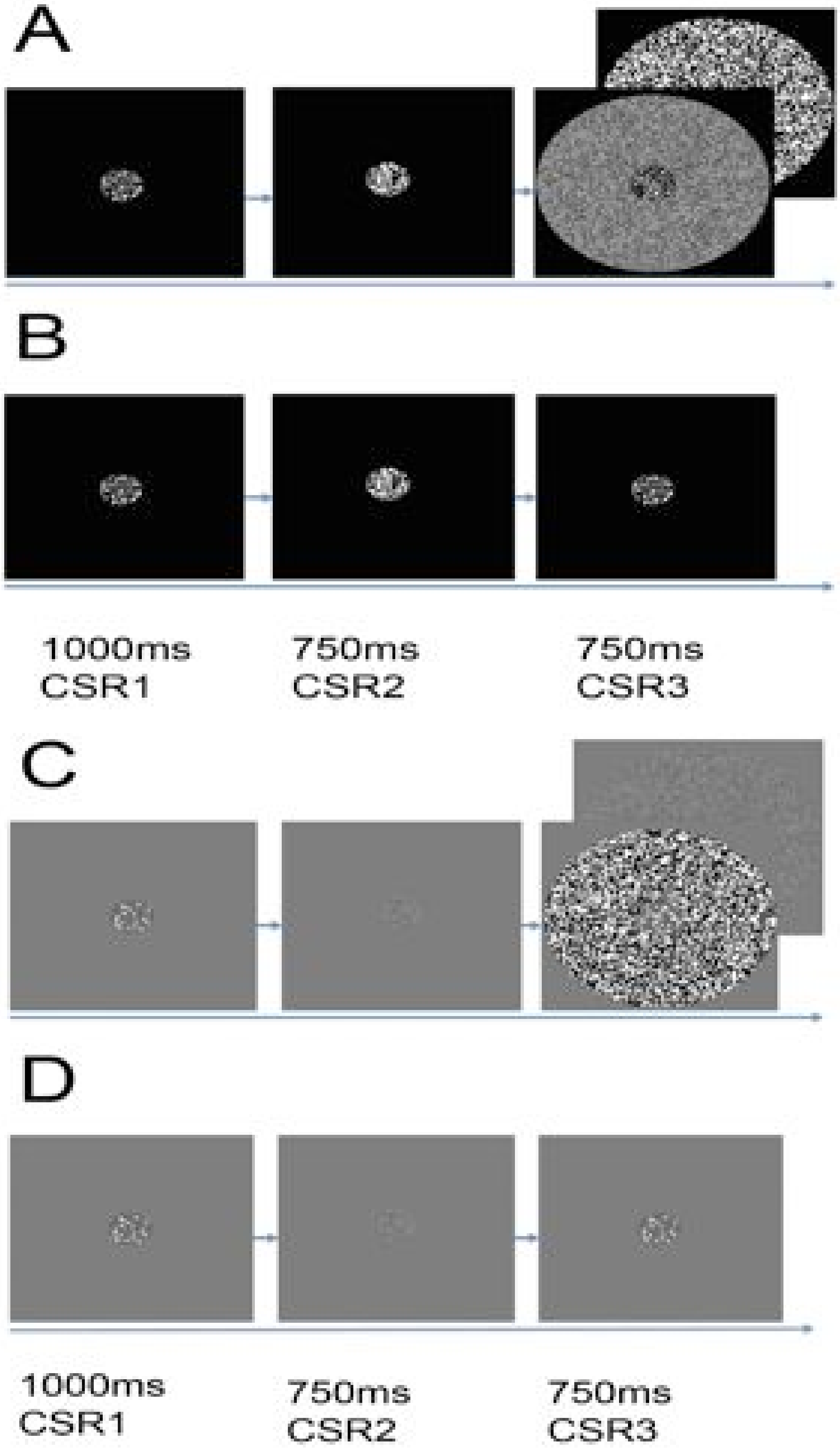


Figure 3.2. Trial sequence of (A) black centre high/low contrast surround (B) black centre zero luminance background (no surround) (C) grey centre high/low contrast surround (D) grey centre uniform luminance background (no surround). Each trial would begin with a CSR that contained a reference set of dots (CSR1) that appeared on the screen for 1s. The CSR1 was then replaced by random dynamic binary noise (CSR2) that served as an inter-stimulus interval (ISI) of 750ms. The final stimulus presentation within a trial was CSR3, which contained a second set of dots either enveloped by a high or low contrast surround (see A and C), or no surround (see B and D). Observers made speeded responses as to whether there were more or less dots in CSR3 as compared to CSR1.

### 3.1.3. Procedure

Numerosity estimation is affected by many variables. Here, the effect contrast gain saturation on the accuracy of numerosity comparison judgements was examined by a series of 2 X 2 factorial designs that varied in central contrast, surround contrast, no surround, and numerosity. The objective of these experiments was to indicate by 2 alternate forced choice (2AFC) method whether CSR3 contained a fewer or more dots than CSR1. Observers indicated their responses from the onset of CSR3. Participants were instructed to respond as quickly and as accurately as possible. Each experimental run was counterbalanced for condition across subjects in order to control for the effects of fatigue.

## 3.2. Results (Experiment 1a)

For simplicity, only the mean proportions of correct responses (PCR) for numerosity comparison of more and less dots across experimental conditions were examined. Differences in PCR were compared through a two-way, within subjects analysis of variance (ANOVA), with focus on the effect that surround contrast (high/low/none) had upon the PCR for numerosity comparison of more and fewer dots. Subsequent ANOVAs explored the combination of other factors thought to affect numerosity comparison ability, such as centre contrast (grey centre / black centre), as a more detailed exploration into how various combinations in centre-surround contrast influence the PCR, and to note any variables other than surround contrast which may have confounded the effects of reduced PCRs observed in this study.

Table 3.1. Mean and standard deviation (*SD*) for proportion of correct responses

| | Centre | | | |
|---|---|---|---|---|
| | Grey centre (grc) | | Black centre (blc) | |
| Surround | Mean | *SD* | Mean | *SD* |
| Low contrast | | | | |
| Fewer dots | .45 | *(.14)* | .41 | *(.13)* |
| More dots | .51 | *(.13)* | .58 | *(.09)* |
| High contrast | | | | |
| Fewer dots | .35 | *(.12)* | .51 | *(.10)* |
| More dots | .50 | *(.16)* | .40 | *(.10)* |
| No surround | | | | |
| Fewer dots | .39 | *(.11)* | .44 | *(.13)* |
| More dots | .54 | *(.14)* | .50 | *(.11)* |

N=16

**3.2.1. Effect of surround contrast and set size**

Table 3.1 shows the mean and standard deviation (SD) of the PCR across each condition and experimental run. There was a significant main effect for surround contrast *($F(1, 15) = 5.75$, $p = .03$, partial $\eta^2 = .28$),* and no significant effect for set size of dots under black centre conditions (blc) (see figure 3.3A). The surround contrast by dot set interaction was nonetheless highly significant *($F(1, 15) = 37.33$, $p = <.000$, partial $\eta^2 = .71$).* Post-hoc comparisons (paired t-tests) for this interaction revealed that the mean PCR for estimating less dots in the presence of the low contrast surround, was significantly lower than estimating more dots under the same surround contrast conditions *($t(15)=2.38$, $p = .002$)*. Under the high contrast surround condition the mean PCR for estimation of more dots was significantly lower than estimation of less dots *($t(15)=3.68$, $p = .031$)*.

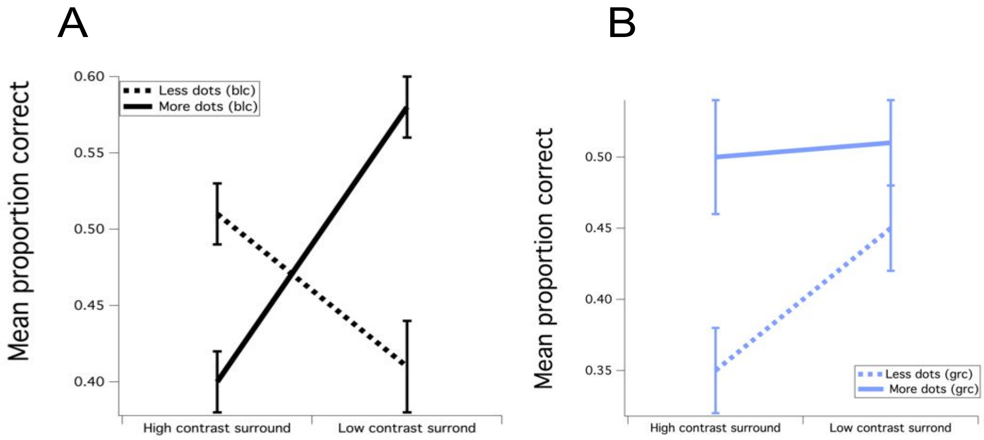


Figure 3.3. Main effects of surround contrast and set of dots (A) there was a highly significant surround contrast by dot set/number interaction for black centre and 1:.5 difference ratio, where under high contrast surround conditions, observers had much more difficulty in accurate discrimination of more dots in CSR3 (B) the grey centre and 1:.5 difference ratio made it significantly more difficult for observers to accurately discriminate less dots in CSR3 under high contrast surround conditions.

There was a marginally significant main effect for surround contrast with grey centre (grc) during numerosity comparison of dots (figure 3.3B), where under high contrast surround conditions, the PCR for more and less dots were at or below chance level *($F(1, 15) = 4.94$, $p = .042$, partial $\eta^2 = .25$)*. There was no significant effect for number, or significant surround contrast by dot set interaction *($F<1$)*. Considered as a whole, these results suggest that for the zero luminance centre condition, the high contrast surround had the most adverse impact upon the ability to discriminate whether there were more or fewer dots in CSR3 compared to CSR1.

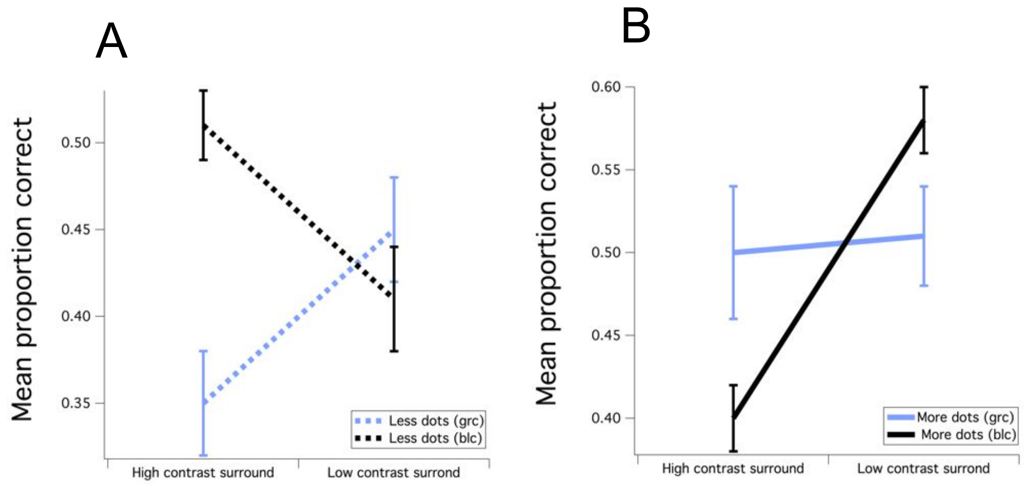


Figure 3.4. Main effects of surround contrast by centre contrast (A) The main effect for surround contrast during estimation of fewer dots with a 1:0.5 difference ratio was not significant, where it was much more difficult for observers to accurately estimate fewer dots under high contrast surround conditions with grey centre than what it was for the black centre (B) the significant centre contrast by surround contrast for estimation of more dots with 1:0.5 difference ratio suggested that the black centre/high contrast surround configuration may have made observers perceive fewer dots in CSR3 than its veridical representation.

### 3.2.2. Effect of surround contrast and centre contrast

A series of 2 (surround contrast) by 2 (centre contrast) within subjects ANOVAs were performed to examine whether the effects of numerosity comparison ability observed in figure 3.3A and 3.3B were influenced by the contrast of the CSR. A surround contrast (high/low) by centre contrast (grc/blc) ANOVA for the PCR of less dots revealed a significant main effect for centre contrast *(F (1, 15) = 5.83, p = .029, partial* $\eta^2$ *= .28)* but not surround contrast (figure 3.4A). Moreover, the surround contrast by centre contrast interaction observed in figure 3.4A was highly significant *(F (1, 15) = 21.76, p = <.000, partial* $\eta^2$ *= .59)*, implying that the mean PCR for estimation of less under the grey centre and high contrast surround condition, was substantially lower than the black centre (blc) and high contrast surround condition. A paired t-test confirmed that these mean PCR differences were highly significant *(t(15)=4.48, p = <.000)*.

The surround contrast (high/low) by centre contrast (grc/blc) ANOVA for the PCR of more dots (figure 3.4B) revealed a significant main effect for surround contrast *(F (1, 15) = 11.81, p = .004, partial* $\eta^2$ *= .44)* but not centre contrast *(F<1)*, where numerosity comparison of more dots was impaired by the high contrast but not low contrast surround. This surround contrast by centre contrast interaction was significant *(F (1, 15) = 10.69, p = .005, partial* $\eta^2$ *= .41),* implying that the mean PCR for estimation of more dots under zero luminance centre and high contrast surround conditions for more dots, was significantly lower than that of the PCR with a grey centre and high contrast surround *(t(15)=2.78, p = .014)*. It is also worth noting that the mean PCR for estimation of more dots under grey centre and low contrast surround condition was significantly lower than the PCR with black centre and low contrast surround *(t(15)=2.40, p = .03)*.

The effects observed in figure 3.4A and 3.4B suggest that the contrast of the central stimulus region has an influential role in the perceived numerosity of dots, where it was markedly difficult for observers to discriminate fewer dots under high contrast surround conditions when the central stimulus region was grey, and conversely, the ability to discriminate more dots under high contrast surround conditions was difficult for observers when the central stimulus region was black.

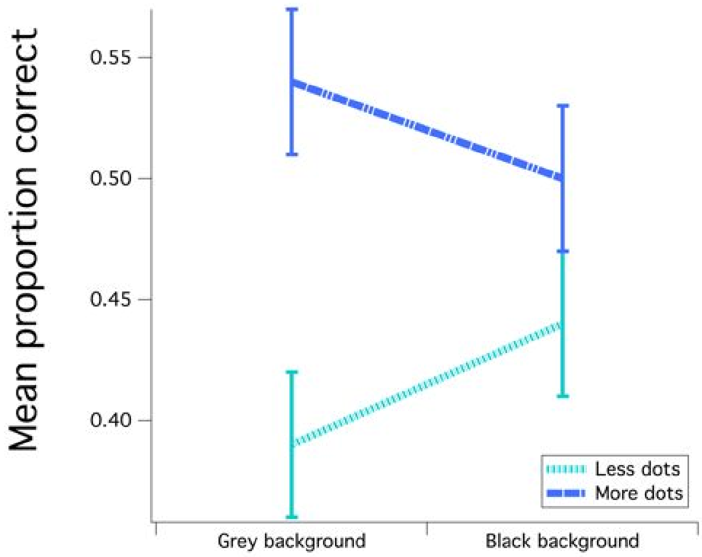


Figure 3.5. Main effects of background luminance by dot set . A significant main effect emerged for dot set but not for background luminance, indicative that the uniform/grey luminance background made it slightly easier for observers to accurately estimate that there were more dots in CSR3.

### 3.2.3. Effect of background contrast and dot set size

A 2 (grey/black background) by 2 (less/more dots) within subjects ANOVA was run to examine the differences in mean PCR when a surround did not envelop the central stimulus region. There was a significant main effect for set size of dots *(F (1, 15) = 6.21, p = .025, partial* $\eta^2$ *= .29)* but not for background region *(F<1)*, where it was easier for observers to accurately discriminate more dots under grey centre/grey background stimulus configuration (see figure 3.5). The background by dot set size interaction was also not significant *(F<1)*.

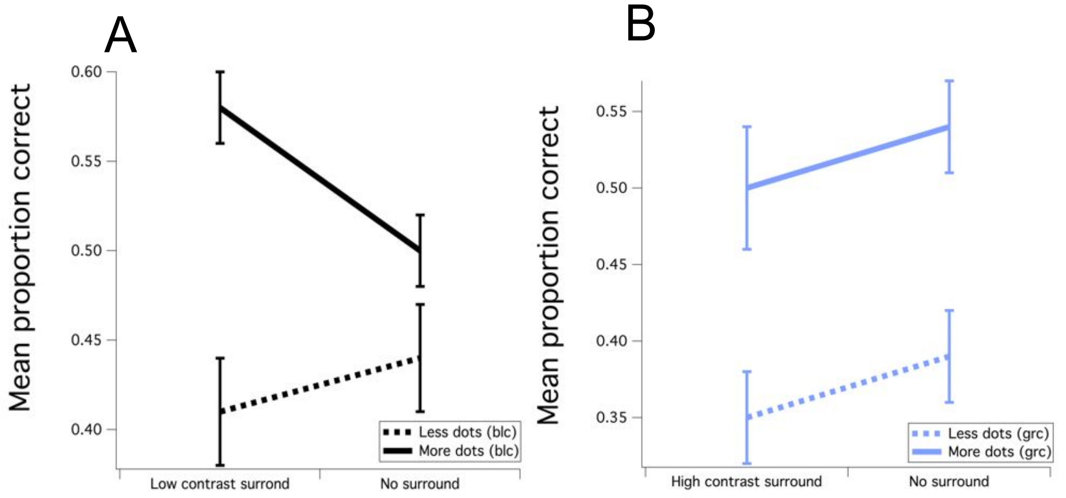


Figure 3.6. Main effects of surround/No surround by dot set (A) it was apparent by the higher mean proportion of correct responses (PCR) for estimation of more dots within the low contrast surround, that observers were able to accurately estimate when there were more dots in CSR3 (B) a significant main effect for dot set but not surround contrast for grey central stimulus region.

### 3.2.4. Effects of surround/black background and dot set size

In order to examine in more detail whether the effects of surround contrast on numerosity comparison were distinguishable from those of background luminance (no surround), a 2 (high contrast surround/zero luminance background) by 2 (less dots/more dots) ANOVA for black centre revealed that there were no significant main effects for neither surround *(F<1)* or set of dots *(F<1)*. If no significant differences exist between the mean PCR for high contrast surround and black background it suggests that indeed, the black background luminance had the same effect as the high contrast surround. In order to confirm the inhibitory effects of the black background upon estimation judgements of dots within a black central stimulus region, a surround (low contrast surround/black background) by dot set (less dots/more dots) within subjects ANOVA was run. There was a significant main effect for dot set $(F\ (1,\ 15) = 7.07,\ p = .018,\ partial\ \eta^2 = .32)$ but not for surround *(F<1)*, meaning that comparison judgements of more dots were easier for observers under black centre/low contrast surround conditions (see figure 3.6A). The surround by dot set size interaction was not significant *(F<1)*.

### 3.2.5. Effects of surround/grey background and dot set size

The next set of within subjects ANOVAs tested differences in mean PCR for surround (high and low contrast) and no surround of the grey centre/grey background stimulus configuration. A 2 (low contrast surround/uniform luminance background) by 2 (less dots/more dots) ANOVA for grey centre revealed that there were no significant main effects for surround *($F<1$)* or set of dots *($F<1$)*. These findings suggest that the low contrast surround that enveloped the CSR3 with a grey centre had the same effect as the grey background with no surround.

The last ANOVA (high contrast surround/no surround) by (less dots/more dots) for grey centre revealed a highly significant main effect for dot set *($F(1, 15) = 9.25$, $p = .008$, partial $\eta^2 = .38$)* but not for surround *($F<1$)*, meaning that irrespective of surround conditions (high contrast surround/grey background), it was once again easier for observers to make discrimination judgements of more dots (see figure 1.6B). In particular, it was apparent that the mean PCR of fewer dots for high contrast surround and no surround was markedly lower than the PCR for more dots.

## 3.3. Experiment 1b

The previous experiments examined differences in accuracy for numerosity comparisons using the method of constant stimuli, where the mean proportion of correct button responses for fewer and more (left and right arrow) were examined separately. Because of this, it was not possible to control for the possibility that the higher proportion of correct responses for low contrast and no surround conditions was attributed to response bias, the tendency to respond toward one particular stimulus with higher frequency owing to extraneous factors such as useless guessing, or preferred hand.

Therefore, the aim of this experiment was to further explore the effects of surround-masking on numerosity judgements by means of the parameter estimation by sequential testing (PEST) method, a bias-free measure of perceptual threshold estimation. If difference thresholds for numerosity judgements are greater with high contrast surround compared with low and no surround contrast conditions, this would provide further evidence for a functional relationship between sensory gating mechanisms and number acuity.

If contrast-gain saturation induced by surround-masking has a disruptive effect upon visual estimation, then the ANS is indeed likely to be influenced by perceptual properties, given its susceptibility toward the overloading of RF inhibitory resources.

### 3.3.1. Stimuli

The stimulus set up and temporal sequence of each trial was identical to experiment 1a (section 3.1.2). The difference in the number of dots between the test and reference was varied using VPEST (VPixx software's Parameter Estimation by Sequential Testing) in order to obtain psychophysical thresholds numerosity judgements. VPEST implements a maximum-likelihood technique to set the difference in dot numbers for the current trial based on performance in all trials up to that point. This method is robust against observer expectation effects (response bias), and requires relatively few trials to systematically convergence on a threshold (Leek, 2001; Pentland, 1980; Taylor, Forbes, & Creelman, 1983).

### 3.3.2. Procedure

The experiments were performed in a darkened room. Participants completed a block of trials for each of the six centre-surround configurations. The order of blocks was counterbalanced across participants. Within each block, 2 separate thresholds were obtained, operationalized as the number of dots required to accurately discriminate fewer from more with the maximum limit of dots at 50 and 75 respectively. PESTs were terminated either after 50 trials, or at the 95% confidence level (parameter estimate within ± 0.1 log units of the true threshold). Each block took less than 5 minutes to complete, and participants were given brief breaks in between blocks.

Participants made two alternate forced choice (2AFC) key-presses to indicate whether the test region contained more (right keyboard arrow) or fewer (left keyboard arrow) dots than the reference. The numerosity judgements were made following the onset of the test stimulus, with the trial terminating trial after the participant's response. Participants were instructed to fixate upon the CSR, and to respond as quickly and as accurately as possible.

### 3.3.3. Results

Each of the six experimental blocks performed resulted in two PEST thresholds, one for 50 max and 75 max dot limits. As earlier noted, this psychophysical threshold (independent variable) was operationalized as the number of dots required in order to accurately discriminate more from fewer. This resulted in 12 different threshold estimates across all experimental runs that were compared through a series of within-subjects ANOVAs (analysis of variance). There were six 2 by 2 ANOVAs performed, which individually examined: 1) effect of surround contrast and maximum dot limit, holding constant CSR3 contrast; 2) effect of CSR3 contrast and surround contrast, holding constant the maximum dot limit

### 3.3.4. Effect of surround contrast and maximum dot limit

The means and *SD*s of the thresholds are shown in Table 3.2. For the grey (low contrast) CSR, a 2 (high and low surround contrast) by 2 (50 and 75 max dot limit) within subjects ANOVA revealed a significant main effect of surround contrast ($F$ (1,15)=15.00, $p$=. 006, *partial* $\eta^2$=. 41), where thresholds under high contrast surround conditions were substantially greater than low contrast conditions (figure 3.7a). There was no significant effect of maximum dot limit, nor was there a surround contrast by maximum dot limit interaction. These findings suggested that for a grey test region, observers required substantially more dots to make accurate judgements with a high contrast surround.

For the black (high contrast) CSR, a 2 (high and low surround contrast) by 2 (50 and 75 max dot limit) within-subjects ANOVA revealed no significant effect for surround contrast or maximum dot limit (figure 3.7b). These findings suggest that under high contrast centre conditions, the surround contrast had no influence upon judgment thresholds.

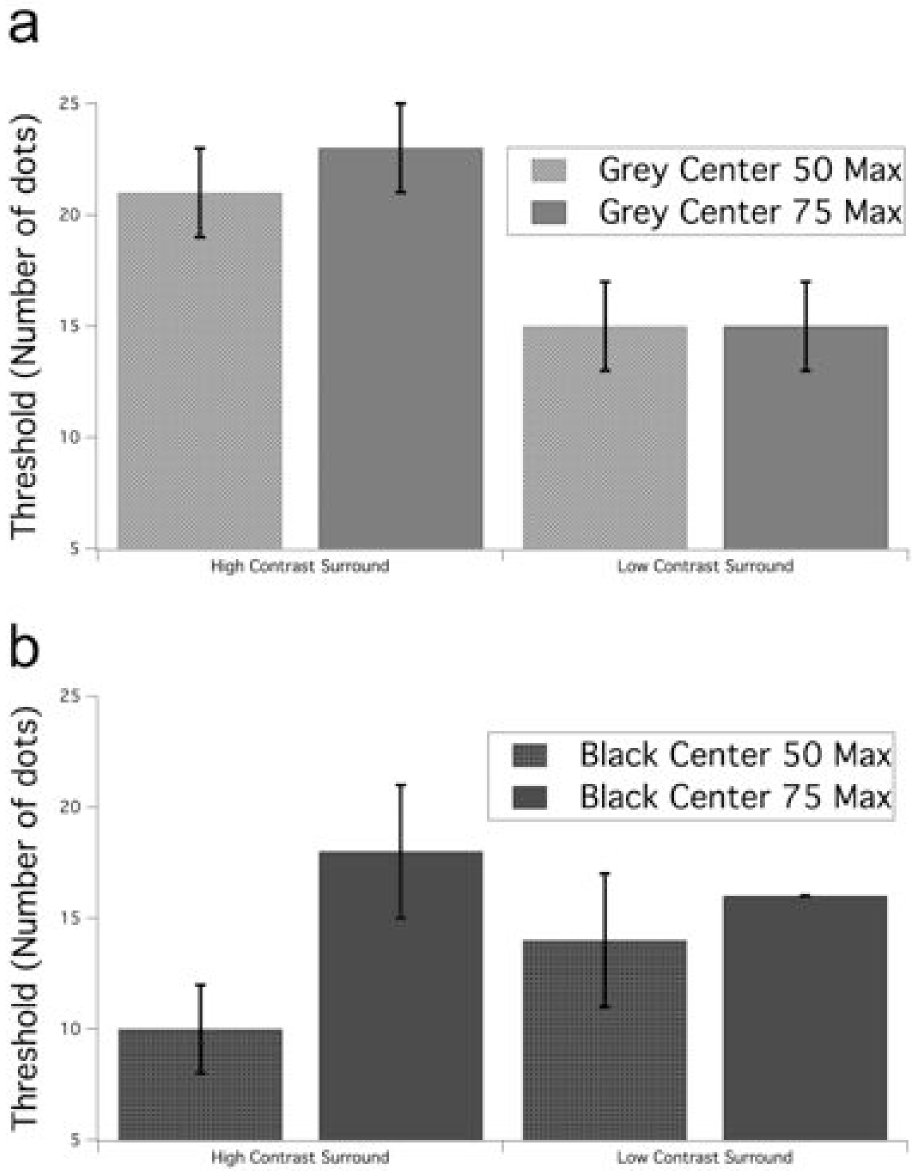


Figure 3.7. Effects of surround contrast and maximum dot limit (3.7a) two (surround contrast) by two (maximum dot limit) ANOVA, holding grey centre constant (3.7b) two (surround contrast) by two (maximum dot limit) ANOVA, holding black centre constant. It can be seen from figure 3.7a that observers required significantly more dots to make accurate estimation judgements under high contrast compared to low contrast conditions, with no significant effect for maximum dot limit. Figure 3.7b however, shows that there was no significant effect for surround contrast or maximum dot limit. The vertical lines on top of each graph represent the standard error (SE) of the mean threshold.

Table 3.2. Mean and Standard Deviation (SD) for Visual Estimation Thresholds

| | Centre | | | |
|---|---|---|---|---|
| | **Grey** | | **Black** | |
| **Surround** | Mean | *SD* | Mean | *SD* |
| **Low Contrast** | | | | |
| **75 Max Dots** | 15 | *(10)* | 16 | *(4)* |
| **50 Max Dots** | 15 | *(7)* | 14 | *(12)* |
| **High Contrast** | | | | |
| **75 Max Dots** | 22 | *(9)* | 18 | *(11)* |
| **50 Max Dots** | 21 | *(8)* | 10 | *(9)* |
| **No Surround** | | | | |
| **75 Max Dots** | 14 | *(9)* | 15 | *(6)* |
| **50 Max Dots** | 14 | *(9)* | 7 | *(9)* |

N=18

### 3.3.5. Effect of CSR contrast and surround contrast

The next set of ANOVAs was performed to examine the influence of centre and surround contrast, under conditions where the max dot limit was set to 50 or 75. For the 50 max dot limit condition (figure 3.8a), a 2 (high or low contrast surround) by 2 (grey or black test stimulus) repeated measures ANOVA revealed no significant effects of surround or centre contrast on numerosity judgement thresholds. For the 75 max dot limit condition (figure 3.8b), there was a marginally significant main effect of surround contrast on numerosity thresholds *($F$ (1,15)=4.66, $p$=. 05, partial $\eta^2$=. 24)*, thresholds under high contrast surround conditions were substantially greater than low contrast conditions. There was no significant main effect of centre contrast, and there was no significant interaction between centre and surround contrasts. Paired t-tests were performed to separately examine the main effects of surround contrast, which revealed significantly greater dot thresholds for high contrast than low contrast surround conditions when the test stimulus was grey *($t$ (15)=3.08, $p$=. 008, 2-tailed)*.

When the test stimulus was high contrast however, there were no significant differences between dot thresholds under high or low contrast surround conditions.

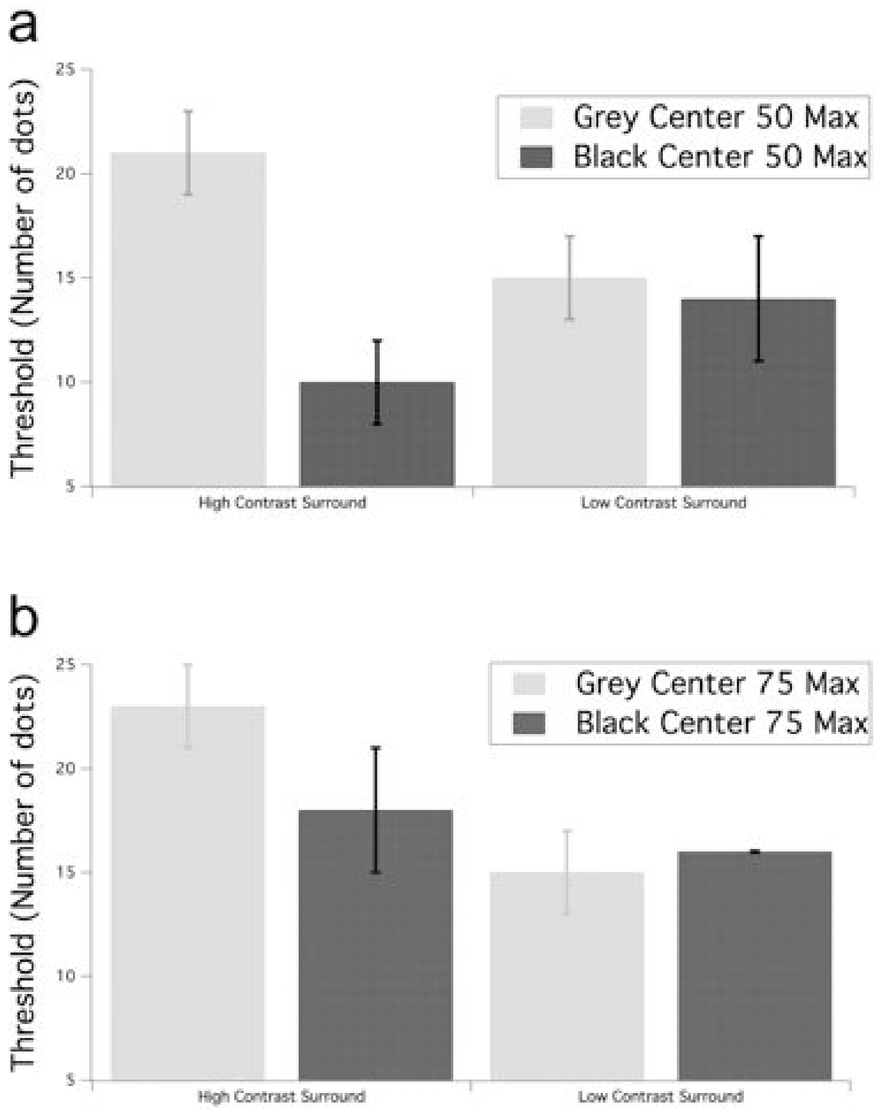


Figure 3.8. Effect of CSR contrast and surround contrast (3.8a) two (centre contrast) by two (surround contrast) ANOVA, holding 50 maximum dot limit constant (3.8b) two (centre contrast) by two (surround contrast) ANOVA, holding 75 maximum dot limit constant. Figure 3.8a shows there was no significant effect for centre or surround contrast when 50 max dots was held constant. It can be seen from figure 3.8b that observers once again required significantly more dots to make accurate estimation judgements under high contrast compared to low contrast conditions, with no significant effect for centre contrast when 75 max dots was held constant. The vertical lines on top of each graph represent the standard error (SE) of the mean threshold.

## 3.4. Discussion

Here the effects of high sensory load on the ability to make numerosity comparison judgements were examined. The form of peripheral visual stimulation implemented here – surround-masking, has been consistently demonstrated to impair the contrast discrimination of centrally embedded texture regions, making them appear dimmer to the observer than veridically so (Chubb, et al., 1989; Dakin, et al., 2005; Xing & Heeger, 2000; 2001). The perceptual inefficiency induced by surround-masking has been postulated to arise from contrast gain saturation, that is, a swamping of available sensory filtering or RF inhibitory resources that serve to attenuate contextually uninformative or noisy input (Carandini, 2004; Dakin, et al., 2005; Webb, et al., 2005). In view of this, it was expected that high contrast gain of the surrounding stimulus, would by these RF suppressive mechanisms, deleteriously affect numerosity comparison of neurotypical observers. Indeed as expected, the mean proportion of correct responses across observers was significantly lower during numerosity comparison judgements of centrally presented elements embedded in a high contrast surround annulus, compared to low contrast and no surround configurations.

Investigation into the relationship between RF inhibitory resource limits and the perception of non-symbolic number representation is novel. However, this investigation was spurred not only by the earlier psychophysical studies on surround-masking, but also from preliminary electrophysiological and psychophysical evidence, which indicated that young adults with self reported difficulty in mathematics displayed greater contrast saturation levels of their visually evoked potentials (VEPs) during high contrast gain, compared to an age matched control group who reported no difficulty with mathematics (Jastrzebski, et al., 2015). Also, the math-impaired individuals in this study displayed significantly delayed visual inspection times (stimulus duration thresholds) in the accurate change detection of high Michelson contrast multi-digit numbers, compared to the control group who did not report being impaired with math. In combination with one another, the absences in VEP response saturation during high contrast gain, and the impairment in change detection of numerals under high but not low contrast conditions, were indicative of a relationship between poorer RF inhibitory mechanisms or reduced sensory gating resources, and mathematical impairment.

Relating the findings of the Jastrzebski, et al., (2015) study back to the current investigation, it may be well to speculate here about the individual differences in numerosity comparison ability, its relationship to the functional quality of RF suppressive mechanisms, and their influence upon the cognitive development of higher-order mathematical computations such as arithmetical or multiplicative operations. In relation to the observations of Halberda, et al., (2008) that numerosity comparison proficiency of pre-school aged children predicts competency with high-order mathematics later in development, it could be inferred that the high contrast surround had psychophysically induced one of the behavioural characteristics of DD by limiting the available RF inhibitory (noise exclusion) resources of neurotypical observers. By this reasoning, it is therefore conceivable that the origins of DD may stem from peri-natal derived offset in the neurodevelopment of noise exclusion mechanisms (Johnson, 2011).

It was found that centre/surround contrast influenced numerosity comparison judgements of more and fewer dots differently – with more dots being easier to discriminate within a black centre/low contrast surround, and less dots being more difficult to discriminate within a grey centre/high contrast surround. For the estimation of more dots under black centre/low contrast surround condition (see figure 1.3A), it is conceivable that this centre/surround configuration created the illusion that dots within CSR3 were more 'numerous' than dots in CSR1, where an earlier psychophysical investigation into visual estimation revealed that the perceived numerosity was affected by luminance of dots (Ross & Burr, 2010). Such effects of luminance were found to increase the perceived numerosity of dots with decreasing luminance. Alternatively, it was likely that the effects of centre and surround contrast had increased the signal to noise ratio (SNR) of afferent input, thereby lowering the perceptual ambiguity in the difference between CSR1 and CSR3. The opposite centre-surround effects on numerosity comparison observed in figures 3.4A and 3.3B, where the estimation of fewer dots was most impoverished under high contrast surround/grey centre conditions, indicated either that the high contrast surround also created the illusion of more dots than veridically so, or that it lowered the SNR of afferent input by swamping the available inhibitory RF resources, hence creating noisiness or scalar variability in the discriminability between CSR1 and CSR3 (Gallistel & Gelman (2000).

However, it was uncertain as to whether these effects of surround-masking on numerosity comparison were contaminated by button response bias, where the mean proportion of correct responses for estimation judgements of 'fewer' and 'more' dots were analysed separately, meaning that extraneous factors such as useless guessing and observer expectations were not corrected for. To ensure that responses were unbiased, the PEST methodology was implemented in order to estimate the number of dots required for observers to judge whether a test stimulus had fewer or more dots than a reference stimulus. In agreement with the main findings of experiment 1a (using the method of constant stimuli), it was found that numerosity judgement thresholds were significantly higher with high contrast surround, compared with low contrast surround conditions. The main findings from experiment 1b (that significantly more dots were required to accurately discriminate fewer from more dots under high contrast surround conditions) suggests that the decisional process involved in numerosity estimation judgements were uncontaminated by observer response bias.

### 3.4.1 Conclusion

These experiments had temporarily induced an impoverished ability to make numerosity comparison judgements in neurotypical observers through high contrast surround-masking. The main findings of this study have yielded evidence for a functional link between inhibitory mechanisms within in LGN/V1, and numerosity comparison ability. The findings further suggest that weak numerosity comparison skills observed in DD children (Piazza, et al., 2010) is unlikely to derive from an innate defect in the cognitive representation of 'more or less' in itself, but rather, a visuo-perceptual disorder commonly observed in those with developmental disorders such as WS (Braddick & Atkinson, 2011), and autism-spectrum disorder (Sutherland & Crewther, 2010).

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# The Effects of Surround-masking on Numerosity Comparison: A Magnetoencephalographic and Behavioural Investigation

# 4.1.Overview

While the psychophysical experiments on inhibitory processes discussed in the previous chapter have revealed insight into the information processing limits on visual perception, they were not informative about underlying brain processes that occur as a result of surround-masking. There are nonetheless many neuroimaging investigations that have examined the electrophysiological and metabolic response characteristics of inhibition and surround masking, and the inhibitory/excitatory responses that accompany psychophysical performance.

The best-described suppressive phenomenon in fMRI literature over the last decade is the negative BOLD response (Shmuel, Augath, Oeltermann, & Logothetis, 2006; Wade & Rowland, 2010; Zenger-Landolt & Heeger, 2003). The negative BOLD response (NBR) has been characterized as a regional decrease in cerebral blood flow (CBF) and concomitant rise in deoxy-haemoglobin – seen as a high amplitude negative haemodynamic response well below baseline (Shmuel et al., 2006). The NBR moreover, has been evidenced to correlate strongly with decreased neural activity (electrophysiological response), and not reduced CBF of vascular origin or blood stealing (Shmuel et al., 2006). The NBR has been generated most optimally in para-foveal and more eccentric retinotopic regions of striate cortex via high contrast visual stimulation (Muthukumaraswamy, Edden, Jones, Swettenham, & Singh, 2009; Wade & Rowland, 2010), and saturation of the magnocellular channel at high contrast gain (Wade & Rowland, 2010).

These neuroimaging investigations into the suppressive mechanisms of visual perception have revealed much insight into the mechanisms of sensory filtering in humans. For example, through magnetic resonance spectroscopy (MRS), the concentration of the inhibitory neurotransmitter gamma amino butyric acid (GABA) has been found to negatively correlate with the NBR (Muthukumaraswamy et al., 2009) and surround suppression (Edden, Muthukumaraswamy, Freeman, & Singh, 2009). The NBR, most importantly, occurs during surround-masking, where V1 suppression in response to high contrast annular gratings correlated with elevated contrast discrimination psychophysical thresholds (Zenger-Landolt & Heeger, 2003). A final word about the NBR is that it is likely to be of a low-order origin within the visual hierarchy such as LGN or V1 (Wade & Rowland, 2010; Zenger-Landolt & Heeger, 2003). Hence the NBR is likely to be a functional reflection of visual suppression associated with the saturation of sensory gating resources as discussed in Part 3.

There has been no systematic investigation into the effects of surround masking on the ability to make more/less comparison judgements of non-symbolic number sets beyond counting range. There has nonetheless been one recent fMRI investigation into the effects of attentional load over the ability to count and subitize peripherally presented number sets under dual task conditions (Vetter, Butterworth, & Bahrami, 2010). The task required observers to subitize (rapidly count elements 1 to 4) or enumerate (count elements 5 to 7) high contrast peripherally presented elements amid low contrast distracters whilst simultaneously performing a central colour detection task. The behavioural responses revealed that under dual task conditions, reaction times (RTs) and response accuracy (RA) for subitizing and enumeration of peripheral elements were markedly impaired as compared to the single task condition (not performing the central colour detection task). A comparison of RA and RTs for subitization and enumeration of peripheral elements moreover revealed that observers were more impaired at enumerating (counting elements that ranged from 5 to 7) than subitizing (counting elements that ranged from 1 to 3). fMRI analysis revealed an effect in right temporo-parietal junction (rTPJ) for subitizing peripheral elements – with an increase in BOLD of this visual association area. There was a concomitant decrease in BOLD signal of rTPJ during the enumeration of peripheral elements.

Vetter et al., (2011) postulated that the stimuli used in their estimation/subitization experiment were operationalized so as to modulate rTPJ as a function of attentional load in accordance with Lavie's theory of attentional load (Lavie, 2005). However, the estimation/subitization task the investigators used to test attentional load, had not been partialed out for the effects of sensory load – as according to Lavie (2005), the neural mechanisms of sensory and attentional load are functionally separate. Given that the enumeration/subitization target stimuli were high contrast sinusoidal discs amid low contrast ones, it is likely that the effects observed following attentional load modulations on rTPJ were attributed to RF surround-suppression via feedback from V1 or LGN (Zenger-Landolt & Heeger, 2003). This was because the high attentional load stimuli (high contrast elements that range from 5 to 7) induce similar effects to that of surround masking (Zenger-Landolt & Heeger, 2003). Essentially, the investigators notion of high attentional load was confounded with high sensory load. Vetter et al., (2011) used suppressive stimuli for their enumeration stimuli, and did not implement a ‘resting baseline’ state in their general linear model (GLM) during the analysis of load dependent modulations within rTPJ – in fact, it was intentionally omitted. It was concluded that the BOLD modulations of rTPJ for subitizing and enumerating conditions were influenced by the number of elements, and was not an effect of “un-specific processes of…load related task demands” (pg. 733).

Vetter et al., (2011) did not distinguish attentional load from sensory load in the parameterization of their experimental design. Therefore, it was inconclusive as to whether load dependent modulations of rTPJ were attributed to sensory or attentional load. If however, the investigators had controlled for the effect of load on rTPJ via the manipulation of element contrast (i.e. enumeration vs. subitization of high vs. low contrast elements), it may have been possible to ascertain whether rTPJ suppression during enumeration was due to the effect of increased attentional load or sensory load.

A number of fMRI investigations have reported rTPJ suppression (or BOLD deactivations) in response to increased sensory and attentional load (Ansari, Lyons, van Eimeren, & Fei, 2007; Corbetta & Shulman, 2002; Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007; Todd, Fougnie, & Marois, 2005). From this, it has been postulated that rTPJ BOLD suppression is a result of the neural mechanisms of filtering out irrelevant sensory information (Shulman et al., 2007). Conversely, rTPJ suppression has also been reported to occur when sensory gating resources become saturated or capacity limited by high attentional and sensory demands imposed upon the visual system – this type of rTPJ suppression has been argued as inattentional blindness (Todd et al., 2005).

Finally, rTPJ BOLD suppression has been implicated with a functional role in numerosity comparison judgements of non-symbolic number sets well beyond the enumeration range (Ansari et al., 2007). That is, increased BOLD of rTPJ occurred when observers were required to make more/less judgements of non-symbolic sets within the subitizing range (1 to 4). A respective decrease on BOLD below baseline levels in rTPJ was noted when observers made comparison judgements of perceptual sets that were too great to subitize or count (Ansari et al., 2007). If rTPJ BOLD suppression is a neural marker for sensory filtering processes, and estimation of non-symbolic perceptual sets, then it begs the question as to what effects surround masking might have upon the perception of, and ability to make comparison judgements of large non-symbolic number sets?

There has been much fMRI literature which has examined the effects of suppression in V1 via high sensory load, and its influence upon visual perception (Muthukumaraswamy et al., 2009; Schwartz et al., 2005; Shulman et al., 2007; Todd et al., 2005; Wade & Rowland, 2010; Zenger-Landolt & Heeger, 2003), however, there has so far been no investigation into the effects of surround masking upon the perception of non-symbolic numerical sets, and the ability to make more/less judgements. Moreover, there has been little inquiry into the impact of weakened sensory gating resources on the developmental course of learning, attention and cognitive development.

# Part 4:
# Mathematical Cognition Profiles of Autistic and Schizotypal Tendency

Abstract

A number of studies into the neuropsychological assessment of schizotypal personality disorder have revealed an associated impairment of arithmetical ability and spatial working-memory. From these observations, the aim of the following study were to further explore the relationship between schizotypal/autistic traits and cognitive performance on arithmetic, spatial working-memory, and verbal comprehension via the WAIS-IV arithmetic, digit-span, vocabulary sub-tests, and computerised tasks that also tested arithmetic and numerical/spatial associations. Bivariate correlations revealed no significant relationships between any of the schizotypal traits and cognitive assessment measures. There was nonetheless, a significant correlation between autistic traits 'attention to detail', 'imagination', 'attentional shifting', and cognitive performance scores for WAIS-IV digit-span sub-tests, and Ravens advanced progressive matrices. Moreover, there were no significant correlations between autistic traits and arithmetical performance. It may be concluded from these observations that autistic traits such as 'attentional shifting' and 'attention to detail' have an influential effect upon spatial working-memory skills, but not arithmetical ability.

## 4.2. Introduction

As noted earlier (Part 1), adolescents with schizotypal personality disorder at risk of developing psychotic illness, have been shown to under perform significantly in spatial reasoning and arithmetical ability assessment batteries than demographically matched controls (Mitropoulou et al., 2005; Trotman et al., 2006; Weiser et al., 2003). In order to further explore whether there was a relationship between each of the schizotypal traits and cognitive performance, the Schizotypal Personality Questionnaire (Raine, 1991), Autistic Spectrum Quotient (AQ) questionnaire (Baron-Cohen, et al., 2001), and series of cognitive tests were administered to a sample of individuals with no known psychiatric or neurological conditions.

It was of special interest to determine which of the nine SPQ traits out of (1) ideas of reference, (2) magical thinking, (3) excessive social anxiety, (4) unusual perceptual experiences, (5) odd or eccentric behaviour, (6) no close friends, (7) odd speech, (8) constricted affect, and (9) suspiciousness were associated with arithmetical skills, mathematical problem solving, numerical comparison, vocabulary, and abstract reasoning. Given that the arithmetical cognitive deficits found in schizotypal personality disorder have been linked with greater severity of negative symptoms (Trotman et al., 2006), it was expected that participants with higher scores for SPQ negative symptoms (constricted affect, excessive social anxiety, and no close friends) would perform significantly worse in mathematical problem solving, numerical comparison, and arithmetic. Individuals with high AQ trait scores however, were expected to perform well on the cognitive assessment tasks, given that high functioning autism has been well associated with mathematical achievement (Baron-Cohen, et al., 2001).

The neuropsychological profile of individuals with sub-clinical levels of schizotypal traits has not been systematically explored to the same level as for instance, diagnosed schizophrenia, high functioning autism, Aspergers syndrome, or ADHD. Hence, the aim of the following experiments were to establish whether the neuropsychological profile previously observed in schizotypal personality disorder (Mitropoulou et al., 2005; Trotman et al., 2006; Weiser et al., 2003) is generalizable toward the non-psychiatric population and the variation in schizotypal traits within it.

## 4.3. Method

Following online consent for participation in this study, volunteers completed an online demographics questionnaire followed by a combined version of the AQ and Schizotypal personality questionnaire (SPQ). The AQ questionnaire was combined with the SPQ in order to control for cognitive bias in the respondents attitude toward schizotypal traits, and to moreover ensure a uniform response distribution across participants. Following completion of the online SPQ/AQ questionnaire, the student investigator contacted participants in order to schedule a time to undergo cognitive assessment. Cognitive assessment included administration of the Wechsler Adult Intelligence Scale (WAIS-IV), and Ravens Advanced Progressive Matrices in order to assess non-verbal intelligence. After the completion of WAIS-IV sub-tests and Ravens matrices, participants completed a series of computerised psychometric tasks that tested response times to a magnitude comparison task and arithmetical ability.

### 4.3.1. Participants

There were 46 people who participated in this study (34 females) with normal/corrected to normal vision, and a mean age of 25 years (SD=7 years). The education level of this sample was such that 25 (54.3%) completed secondary education, 9 (19.6%) completed technical and further education (TAFE), 10 (21.7%) completed tertiary education, and 2 (4.3%) participants attained post-graduate education. This sample mostly comprised of 1$^{st}$ year undergraduate psychology students who were awarded course credit for their participation – the remaining participants volunteered without compensation. The study was carried out in accordance with the Helsinki declaration and approved by the Swinburne University of Technology ethics committee (see appendix B).

### 4.3.2. Materials

**Online questionnaire (component 1)**

As earlier noted, volunteers undertook a combined version of the SPQ and AQ questionnaire following consent of participation in order to quantify the extent of schizotypal and autistic traits of each participant. The items of the SPQ and AQ scales were combined randomly (to control for social bias that participants may have held toward their own held perceptions of schizotypal and autistic traits). The SPQ (Raine,

1991) is a self-report questionnaire that measures the extent of schizotypal traits. The SPQ is made up of 74 items that are divided into 9 separate sub-scales (see appendix C for each item in questionnaire). The AQ (Baron-Cohen, et al., 2001) is a 50-item questionnaire that measures the extent of autistic traits within non-clinical populations. The AQ is made up of 5 sub-scales, each featuring facets of the autistic phenotype, having 10 items per sub-scale (see appendix D for each item in questionnaire).

#### 4.3.3. Procedure

***SPQ***. This online version of the SPQ was made up of a 4 element response format, where 1 point was scored if respondents clicked on 'yes' or 'maybe', and 0 points for 'no' or 'unsure'. A total SPQ score for each participant was determined by summing responses to all 74 items. A total score for each sub-scale was constructed in the same manner.

***AQ***. The original response format of the AQ is a Likert type scale where respondents report whether they 'definitely agree', 'slightly agree', 'slightly disagree', 'definitely disagree'. However, for the purposes of combining the AQ with SPQ into one questionnaire, the response format was modified to be the same as the SPQ, which was 'yes', 'maybe', 'no', or 'unsure' in order to eliminate response bias. Half of the items in the AQ (25) are reverse scored, where one point is scored for items that respondents 'definitely disagree' or 'slightly disagree' with, and 0 points for 'definitely agree' or 'slightly agree'. One example of a reverse scored item was: "When I'm reading a story, I find it difficult to work out the characters intentions". In terms of the current study, respondents scored 1 point if they indicated 'yes' or 'maybe' and 0 points for 'no' or 'unsure' for this example of a reverse scored item.

**Cognitive testing (component 2)**

Following completion of the combined AQ and SPQ questionnaire, participants were administered various cognitive assessment instruments that were in pen/paper, verbal, and computerised form. All cognitive evaluation tests were administered in one session, which took approximately 90 minutes to complete. After signing the informed consent statement, participants were firstly administered the Ravens advanced progressive matrices. Following was the administration of WAIS-

IV and arithmetic sub-tests. Participants then undertook a set of computerised tasks that were rapid response judgments of numeric magnitude and true/false judgements of multi-operation arithmetical problems.

### 4.3.4. Materials

The Ravens advanced progressive matrices is a pen and paper based assessment of non-verbal intelligence and abstract reasoning. An item is comprised of a panel with a missing segment of a pattern, with an option of 8 possible segments that complete the design (see figure 4.1). Participants were required to select one of the 8 possible segments they believed to complete the top panel matrix/design. Participants were administered a total of 48 items that were divided into 2 sets. Set 1 was a booklet of 12 items/matrices, and set 2 was made up of another 36. Each design became increasingly more complex as progress was made through item 1 to 12 and 1 to 36 respectively.

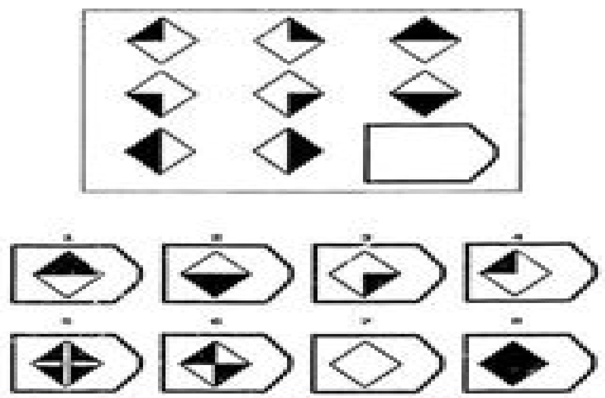


Figure 4.1. Ravens advanced progressive matrices example problem. Participants are required to indicate which of the 8 lower patterns fit with the main pattern above.

The WAIS-IV (fourth edition) is a well-validated instrument in the standardised measure of global IQ. It comprises 15 sub-tests that measure various facets of intelligence such as verbal comprehension (similarities, vocabulary, information, comprehension sub-tests); perceptual reasoning (block design, matrix reasoning, visual puzzles, figure weights, picture completion sub-tests); working memory (digit span, arithmetic, letter-number sequencing sub-tests); and processing speed (symbol search, coding, cancellation sub-tests).

For the purposes of the current investigation, only the vocabulary, digit span, and arithmetic sub-tests were administered. The working memory sub-tests were administered because these cognitive domains have been thought to be functional constituents of mathematical reasoning. The vocabulary sub-test was administered to control for the likelihood that poor mathematical ability was attributed to poor verbal comprehension.

The vocabulary sub-test comprised a booklet of 30 words (one per page) that were nouns (e.g. glove), adjectives (e.g. tranquil) or verbs (e.g. plagiarise), where the task objective was to define each word presented. The digit-span sub-test comprised a list of digit strings from 0 to 9 that increased in numerosity (length) per trial. It was broken down into 3 further sub-tests that were forward, backward and sequencing. The objective of forward digit span was for the examinee to recall a list of digits read out by the examiner verbatim. For backward digit span, the examinee was required to recall the list of digits in the reverse order they were read out. Finally, for sequencing, examinees were required to recall the list of digits read out in sequential order. All 3 sub-categories of digit-span were made up of 8 trials, having 2 string sets of the same length per trial. The arithmetic sub-scale was made up of 22 arithmetical problems read out by the examiner that increased in complexity as the test progressed. The more complex problems for example, included multiple operators and more than one step in order to obtain a solution.

The magnitude comparison task was generated via VPixx version 2.9 software (VPixx.com) and displayed on a 1680 x 1050 LCD Mac Pro Cinema monitor that refreshed at 60 Hz. The stimuli consisted of a centrally presented grey circle (4.5 x 4.5 deg) with the number 55 within it, which was flanked by numbers that ranged from 11 to 99. A trial consisted a single presentation of the stimulus

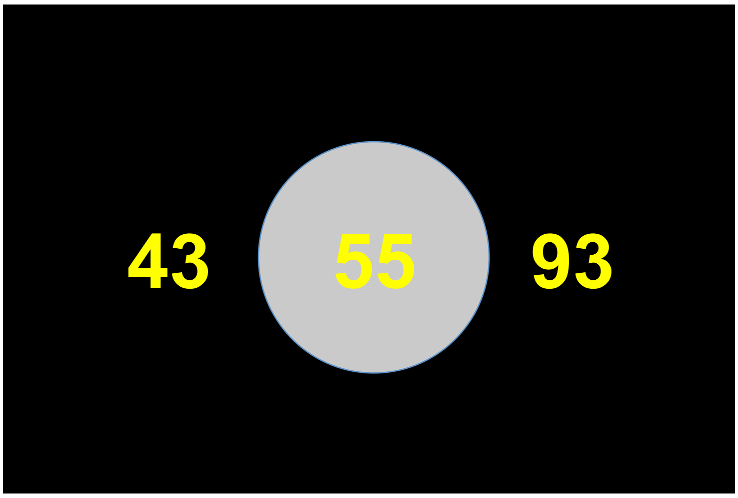



Figure 4.2.Example stimuli of magnitude comparison task. In congruent trials, participants indicated by the left arrow key when numbers less than that 55 appeared on the left side of the display, and respectively, the right arrow key when numbers greater than 55 appeared on the right side of the display. On incongruent trials, numbers greater than 55 appeared on the left hand side of the display, and numbers less than 55 appeared on the right hand side of the display.

shown in figure 4.2. The main experimental design was made up of 2 blocks, where participants attended to the number flanker less than 55 in one block, and more than 55 in the other. The task objective was to indicate by keyboard press (left or right arrow) whether the attended to numeric representation (less or more than 55) was the left or right number flanker. Each experimental block was made up of 30 trials that were semantically congruent (e.g. number 33 as left flanker during the attend to less than 55 block) and semantically incongruent (e.g. number 13 as the right flanker during the attend to more than 55 block). If participants did not respond within the 2-second time frame, the trial would lapse and proceed to a new one.

The true/false judgement tasks were also generated via VPixx version 2.9 and presented on the same Mac Pro Cinema display as the magnitude comparison tasks. The stimuli for this experiment comprised of a centrally presented multi-operation math problem, which included a solution that was true or false (see figure 4.3 for example stimuli). The variables that made up the multi-operation problems were organised such that the resultant (for true or false problems) did not exceed 10. For each trial, the multi-operation stimulus was displayed for 4 seconds to allow the participant ample time to solve the problem. The task objective was to indicate by keyboard press whether the answer to the multi-operation problem was true (1 key) or false (0 key). The experimental design was made up of 2 blocks having 15 trials of true and false problems (total 30 trials), with additive and subtractive operands (+, -) in one block, and divisive and multiplicative operands (÷, x) in the other block.

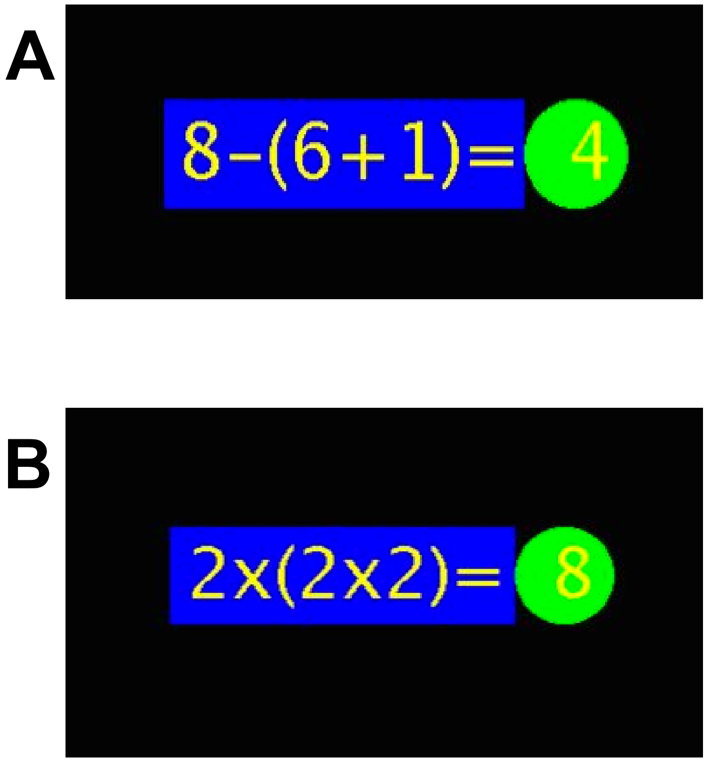



Figure 4.3.Example stimuli of true/false judgement task. These experiments were made up of two blocks, where block 1 contained trials with problems that contained additive and subtractive operands (A), and block 2 contained divisive and multiplicative operands (B). Stimulus A was an example with a false answer, and stimulus B was an example with a true answer. Each block contained an equal number of true and false problems.

### 4.3.5. Procedure

**The Ravens advanced progressive matrices**

Participants were firstly administered set 1 progressive matrices, which was a booklet of 12 matrices with one problem per page. Participants indicated on a separate answer sheet which of the sub-patterns numbered 1 to 8 completed the matrix design. There was no set time limit for the completion of set 1, as the matrices were not difficult. Once the participant completed set 1, which took no longer than 5 minutes across all 46 participants, set 2 was administered (a book of 36 matrices) with a 20-minute time limit. A score for Ravens matrices was obtained by summing the number of correct answers for set 1 and 2, then divided by 48 to obtain the percentage of correctly completed matrices.

***WAIS-IV***. The vocabulary sub-test was administered verbally to the participant, where the examiner pointed to each word to be defined. Each elucidation could score a maximum point of 2, or a minimum point of 1, depending upon how concise the participant's definition was. The examiners decision as to what score a participant should receive was obtained by looking up what score (1, 2, or 0) was assigned for that word in the administration and scoring manual. The test was discontinued after 3 consecutive scores of 0, that is, for incorrect definitions.

The digit span sub-test (forward, backward, sequencing) was also verbally administered, where the examiner read out the string of digits from the administration and scoring manual, then the examinee repeated them back to the examiner verbatim (forward), in reverse order (backward), or in ascending order (sequencing). Each trial (a string pair) could score a maximum of 2 points, where maximum points were awarded for correct recall of both digit string items in a trial. The sub-test was discontinued following a score of 0 for 1 trial (i.e. incorrect recall of both items).

Problems from the arithmetical ability sub-test were read out to the examinee from the WAIS-IV administration and scoring manual, starting at problem number 6, given that all examinees were over the age of 16. Correct answers to problems were awarded 1 point, and the examiner then proceeded to the next question. The test was discontinued after 3 consecutive incorrect responses (a score of 0).

The scoring process for each sub-test entailed the summing of points to obtain a total raw score, which was a maximum of 57 for vocabulary, 16 for forward, backward, and sequencing (48 total digit span), and 22 for arithmetic ability. The raw scores for each sub-test were then converted to scaled scores via a look up table in the administration and scoring manual. The scaled score for each sub-test was determined by an index of the participants' age group, where a raw score was converted to a scaled score (standardized) score from the respective age group.

**4.3.6. Magnitude comparison and true/false judgement task**

Given that the magnitude comparison and true/false judgement tasks were both computerised tests, participants received verbal instructions from the investigator on how to undertake them. In order to control for the effects of task fatigue, experimental blocks were counterbalanced across subjects.

# 4.4. Results

## 4.4.1 Mean SPQ and AQ scores

The mean score for each sub-scale of the SPQ and AQ can be found in table 4.1, and table 4.2 respectively. For this sample, it was worth noting that on average, excessive social anxiety was the highest scoring sub-scale of the SPQ, and magical thinking the lowest. The mean SPQ score for this sample (25.72) was considered to be within non-clinical and low range of the schizotypal spectrum (Raine, 1991). As for the AQ, attention to detail was the highest scoring sub-sale, and communication skills the lowest. The total AQ score for this sample (13.83) was once again within the low range of the autistic trait continuum (Baron-Cohen, et al., 2001).

Table 4.1.Mean and standard deviation of AQ scores

| **AQ Sub-Scale** | **Mean** | ***(SD)*** |
|---|---|---|
| Communication skills | 1.83 | *(1.66)* |
| Imagination | 2.20 | *(1.67)* |
| Social skills | 2.74 | *(2.0)* |
| Attentional shifting | 3.22 | *(2.0)* |
| Attention to detail | 3.78 | *(2.0)* |
| Total AQ score | 13.83 | *(6.68)* |

N=46

Table 4.2. Mean and standard deviation of SPQ scores

| **SPQ Sub-scale** | **Mean** | ***(SD)*** |
|---|---|---|
| Ideas of reference | 3 | *(2.46)* |
| Excessive social anxiety | 4 | *(2.48)* |
| Magical thinking | 1.43 | *(1.77)* |
| Unusual perceptual experience | 2.25 | *(1.94)* |
| Odd and eccentric behaviour | 3.1 | *(2.48)* |
| No close friends | 3.22 | *(2.70)* |
| Odd speech | 3.76 | *(2.58)* |
| Constricted affect | 2.52 | *(2.20)* |
| Suspiciousness | 2.52 | *(2.32)* |
| Total SPQ | 25.72 | *(14.55)* |

N = 46

### 4.4.2. Cognitive assessment and performance

Please refer to table 4.3 for the mean score of each WAIS sub-test including Ravens matrices, table 4.4 for mean magnitude comparison RTs, and table 4.5 for the mean percentage accuracy of the true/false judgement task. From here, it was worth noting that the scaled WAIS scores from this sample were representative of the

Table 4.3.Mean and standard deviation of WAIS sub-test and Ravens matrices scores

| **WAIS Sub-test scaled score** | | |
|---|---|---|
| | **Mean** | ***(SD)*** |
| Digit-span forward | 10.91 | *(2.83)* |
| Digit-span backward | 10.10 | *(3.32)* |
| Digit-span sequencing | 11.10 | *(2.61)* |
| Digit-span total | 10.63 | *(3.0)* |
| Arithmetic | 11.13 | *(3.0)* |
| Vocabulary | 12.19 | *(2.17)* |
| Ravens (% correct) | .61 | *(.13)* |

N=46

Table 4.4. Mean and standard deviation of magnitude comparison response times

| **Numeric comparison** | | |
|---|---|---|
| | **Mean** | **(SD)** |
| Less than 55 right arrow | 1.12ms | *(.115ms)* |
| More than 55 right arrow | 1.06ms | *(.103ms)* |
| Less than 55 left arrow | 1.10ms | *(.107ms)* |
| More than 55 left arrow | 1.10ms | *(.124ms)* |

N=46

Table 4.5. Mean and standard deviation of true/false judgement scores (correct)

| **Mathematical operation (Correct out of 30)** | | |
|---|---|---|
| | **Mean** | **(SD)** |
| Arithmetic (Add/Subtract) | 21 | *(5.67)* |
| Multiplication (Divide/Multiply) | 20 | *(5.48)* |

N=46

normal population (WAIS-IV administration and scoring manual). The computerised magnitude comparison and true/false arithmetical judgement task were developed by the investigator as part of this dissertation, and hence, was not a standardized or established measure of mathematical proficiency. Therefore, Pearson's ***r*** correlations were performed between the mean response times (RTs) for the 4 magnitude comparison conditions (see table 4.6), mean number of correct responses for the true/false judgement task (see table 4.7), and mean scaled scores for each WAIS sub-test. A significant correlation between the validated WAIS scores and computerized task variables would indicate that the magnitude comparison and true/false judgement tasks are related measures of mathematical proficiency.

Table 4.6.Table of correlations between WAIS sub-test scores and magnitude comparison RTs

| | **Correlation Coefficients** | | | | | | |
|---|---|---|---|---|---|---|---|
| | **DS Total** | **DS Fwd** | **DS Bkwd** | **DS Seq** | **Arith** | **Voc** | **Rav** |
| Less 55 right arrow | -.29* | -.01 | -.23 | -.36** | -.37** | -.18 | -.13 |
| More 55 right arrow | -.21 | .12 | -.17 | -.37** | -.40** | -.29* | -.17 |
| Less 55 left arrow | -.21 | .13 | -.18 | -.30* | -.39** | -.10 | -.13 |
| More 55 left arrow | -.16 | .06 | -.11 | -.33* | -.50** | -.26* | -.07 |

Note: N=46, **p <.05, **p <.001*

Table 4.7.Table of correlations between WAIS sub-test scores and true/false judgement scores

| | Correlation Coefficients | | | | | | |
|---|---|---|---|---|---|---|---|
| **True/False** | **DS Total** | **DS Fwd** | **DS Bkwd** | **DS Seq** | **Arith** | **Voc** | **Rav** |
| Arithmetic | .41** | .11 | .35** | .45** | .35** | .14 | .08 |
| Multiplication | .53** | .22 | .49** | .45** | .58** | .20 | .29* |

Note: N=46, **p <.05, **p <.001, 1 tailed*

It can be seen from table 4.6 (previous page) that there was a significantly negative correlation between the arithmetic WAIS sub-test and all 4 magnitude comparison conditions, meaning that participants with greater arithmetic WAIS scores had significantly shorter RTs for magnitude comparison judgements with numbers less than 55 on the right side of the display *(r(45)=-.37, p=.006)*; numbers more than 55 on the right side of the display *(r(45)=-.40, p=.002)*; numbers less than 55 on the left side of the display *(r(45)=-.39, p=.004)*; and numbers more than 55 on the left side of the display *(r(45)=-.50, p=<.000)*. The scatterplots in figure 4.6 show the strength of these correlations. There was a significant negative correlation between the WAIS sequencing sub-test and all 4 magnitude comparison conditions, where participants with greater ability to recall digit strings in sequential order had significantly faster RTs for less than 55 right arrow *(r(45)=-.36, p=.007)*; more than 55 right arrow *(r(45)=-.37, p=.005)*; less than 55 left arrow *(r(45)=-.30, p=.02)*; and more than 55 left arrow *(r(45)=-.33, p=.01)*. The scatterplots in figure 4.7 and figure 4.8 show the strength of these correlations.

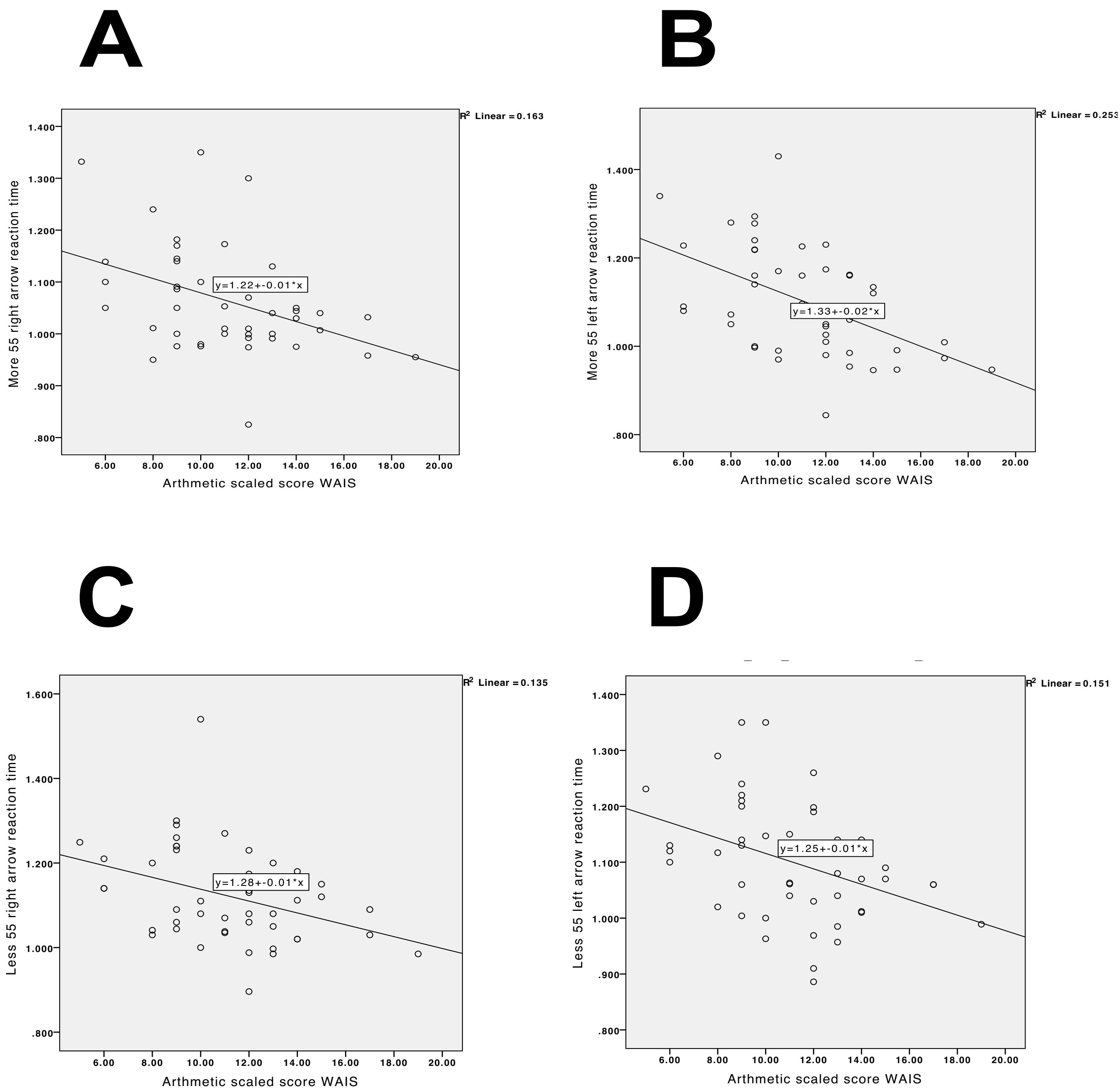



Figure 4.4. Scatter plots of correlations between WAIS-arithmetic scaled score and magnitude comparison response times (RTs). Dependent variables: A – Number greater than 55, right arrow key press (congruent); B – Number greater than 55, left arrow key press (incongruent); C – Number less than 55, right arrow key press (incongruent); D – Number less than 55, left arrow key press (congruent).

Finally, there was a positive correlation between the WAIS arithmetic sub-test and true/false multiplication judgements *(r(45)=.58, p=<.0005)*, also true/false arithmetic judgements *(r(45)=.43, p=.001)*, meaning that a higher WAIS arithmetic sub-test scores were associated with a greater number of correct true/false judgement responses. Also, there were significant correlations between both true/false judgement conditions (arithmetic/multiplication) and 3 out of 4 of the WAIS digit span sub-tests, where only the forward digit span sub-test showed non-significant correlations.

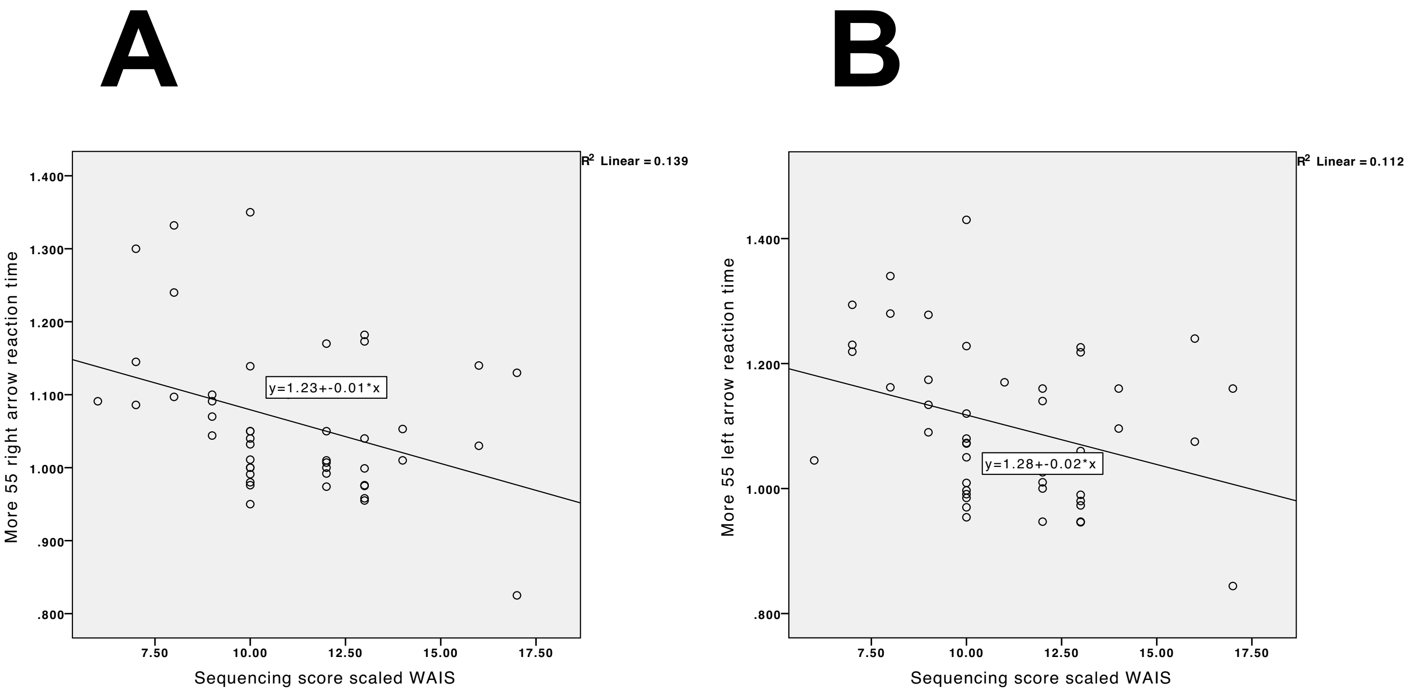



Figure 4.5. Scatter plots of correlations between WAIS-sequencing scaled score and magnitude comparison RTs. Dependent variables: A – Number greater than 55, right arrow key press (congruent); B – Number greater than 55, left arrow key press (incongruent).

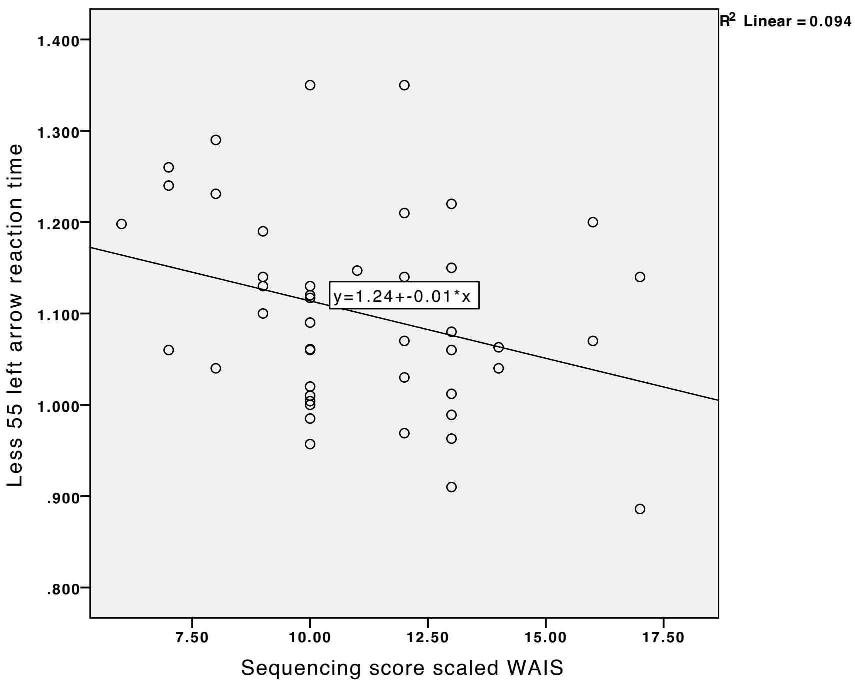



Figure 4.6. Scatter plot of correlations between WAIS-sequencing scaled score and magnitude comparison RTs. Dependent variable: Number less than 55, left arrow key press (congruent).

Overall, the negative correlations between all 4 magnitude comparison conditions, WAIS arithmetical and digit span sub-tests (table 4.6) suggest not only that the computerized tasks developed by the investigator were soundly related to a cognitive assessment battery with established face and construct validity, but more compellingly, that number sequencing and arithmetic are the most prominent cognitive processes among these variables when making magnitude comparison judgements. In terms of the cognitive processes involved with making accurate true/false judgements of multi-operation problems, the significant correlations with WAIS arithmetic, backward and sequencing digit span sub-tests (not forward) suggests evidence for a functional role in number sequencing, and recall of numeric information that is spatially incongruent – especially for making true/false judgements of multiplication problems.

### 4.4.3. Between groups analysis of SPQ/AQ and cognitive assessment variables

A two way median split procedure was performed on the total SPQ, AQ and WAIS arithmetical sub-test scores in order to ascertain whether there were significantly different sub-populations within the main sample. Each data point from these variables were then categorised into either low or normal AQ, SPQ and WAIS arithmetic scores. An independent t-test was then performed on each of these categorised variables, which revealed a highly significant difference between low and normal WAIS arithmetic sub-test scores *(t(44)=8.93, p=<.0005)* – but not for the low/normal SPQ or AQ groups. There were also no significant WAIS arithmetical ability group differences in total AQ or SPQ scores. Thereafter, all further between group analyses were performed with low/normal WAIS arithmetic sub-test scores (WAIS-arith group) as grouping variable.

Table 4.8. Mean and standard deviation of between group differences in WAIS sub-test scores

| | **Group** | | | |
|---|---|---|---|---|
| | **Low arithmetic** | | **Normal arithmetic** | |
| **WAIS Sub-test scaled** | **Mean** | ***(SD)*** | **Mean** | ***(SD)*** |
| Digit-span forward | 10.10 | *(3.11)* | 11.54 | *(2.48)* |
| Digit-span backward | 9.10 | *(3.1)* | 10.84 | *(3.33)* |
| Digit-span sequencing | 10.35 | *(2.21)* | 11.65 | *(2.80)* |
| Digit-span total | 9.35 | *(2.81)* | 11.61 | *(2.86)* |
| Arithmetic | 8.40 | *(1.5)* | 13.23 | *(2.02)* |
| Vocabulary | 11.30 | *(1.75)* | 12.88 | *(2.25)* |
| Ravens (% correct) | .55 | *(.12)* | .65 | *(.12)* |
| | N=20 | | N=26 | |

Table 4.8 shows the mean group differences (low and normal WAIS-arith) in each of the WAIS sub-tests performed, including Raven's matrices scores. An independent t-test revealed that there were significant group differences (1 tailed) between WAIS forward digit span *(t(44)=1.74, p=.04)*; backward digit span *(t(44)=1.81, p=.03)*; sequencing digit span *(t(44)=1.71, p=.04)*; digit span total *(t(44)=2.68, p=.005)* WAIS-arith *(t(44)=8.93, p=<.000);* WAIS vocabulary *(t(44)=2.60, p=.005)*; and Raven's percentage correct *(t(44)=2.52, p=.005)*.

Table 4.9. Mean and standard deviation of between group differences in magnitude comparison Response Times (RTs)

| | Group | | | |
|---|---|---|---|---|
| | Low arithmetic | | Normal arithmetic | |
| | Seconds | | Seconds | |
| **Numeric comparison** | **Mean** | **(SD)** | **Mean** | **(SD)** |
| Less than 55 right arrow | 1.17 | *(.128)* | 1.08 | *(.086)* |
| More than 55 right arrow | 1.10 | *(.113)* | 1.03 | *(.085)* |
| Less than 55 left arrow | 1.15 | *(.111)* | 1.06 | *(.087)* |
| More than 55 left arrow | 1.16 | *(.129)* | 1.05 | *(.097)* |
| | N=20 | | N=26 | |

There were also significant WAIS-arith group differences between mean magnitude comparison RTs (see table 4.9), where the low WAIS-arith group showed markedly delayed RTs for numbers less than 55 with right arrow key press *(t(44)=2.94, p=.002)*; numbers more than 55 with right arrow key press *(t(44)=2.43, p=.005)*; less than 55 with left arrow key press *(t(44)=3.08, p=.002)*; and more than 55 with left arrow key press *(t(44)=3.27, p=.001)*. Finally, it can be seen from table 4.10 that there were significant WAIS-arith group differences between the number of correct responses for true/false judgements of arithmetic *(t(44)=2.78, p=.004)*; and multiplication *(t(44)=6.25, p=<.0005).*

Table 4.10. Mean and standard deviation of between group differences in true/false judgement scores (number correct)

| | Group | | | |
|---|---|---|---|---|
| **Mathematical operation** | **Low arithmetic** | | **Normal arithmetic** | |
| | **Mean** | **(SD)** | **Mean** | **(SD)** |
| Arithmetic (Add/Subtract) | 18.5 | *(5.95)* | 22.88 | *(4.72)* |
| Multiplication (Divide/Multiply) | 15.8 | *(4.56)* | 23.30 | *(3.58)* |
| | N=20 | | N=26 | |

### 4.4.4. Analysis of co-variance (ANCOVA) of cognitive assessment variables

An unexpected finding from the between groups analysis (independent t-tests) were significantly lower WAIS-vocabulary and Ravens matrices scores of the low WAIS-arith group. It was likely that extraneous factors contributed to these differences, which could not be explained by poor abstract (Ravens) or semantic (WAIS-vocabulary) reasoning alone. Hence, a one-way ANCOVA was implemented with WAIS-arithmetic scaled score as the dependent variable, WAIS-arith group as the independent variable, and WAIS vocabulary as the co-variate. This revealed a highly significant main effect for WAIS-arith group *(F (1,43)=61.98, p=<.0005)*, but not for the WAIS-vocabulary covariate, meaning for this population, vocabulary (comprehension) had no influence upon the cognitive processes involved with arithmetical manipulations required to solve problems for the WAIS-arithmetic sub-test.

Given that there was no significant correlation between WAIS-arithmetic scaled score and Ravens per-cent correct, it was not possible to perform an ANCOVA on these variables. From table 4.7 however, it can be seen that there was a significant correlation between number of correct true/false judgements for the multiplication condition and Ravens percentage correct *(r(45)=.29, p=.02)*. Therefore, a second one-way ANCOVA was implemented with true/false judgements (multiplication) as the dependent variable, WAIS-arith group as the independent variable, and Ravens score (percentage correct) as the co-variate. A significant main effect was once again found for WAIS-arith group *(F (1,43)=31.67, p=<.0005)*, but not for the Ravens score covariate, meaning that even when non-verbal IQ was controlled for, arithmetical ability had the biggest influence on making accurate true/false judgements of multi-operation problems. Overall, these findings suggest that a lower level in accuracy of making true/false judgements, or solving the WAIS-arithmetic sub-test problems was not attributed to poor comprehension or low IQ.

### 4.4.5. Which SPQ and AQ traits correlate with what cognitive functions?

As earlier discussed, individuals with a high level of schizotypal traits have been noted to be markedly impaired in arithmetical ability compared to neurotypical controls (Mitropoulou et al. 2005; Trotman et al., 2006; Weiser et al., 2003). However, there have been few if any investigations into which SPQ or AQ traits correlate with WAIS-IV subtests that evaluate digit-span and arithmetical ability. Hence, zero-order correlations (Pearson's R) were performed between all 9 SPQ sub-scale scores, all 5 AQ sub-scale scores, all of the WAIS sub-tests, all 4 magnitude comparison conditions, and true/false judgement scores.

Table 4.11. Table of correlations between WAIS sub-test scores and AQ traits

| | Correlation Coefficients | | | | | | |
|---|---|---|---|---|---|---|---|
| | DS Total | DS Fwd | DS Bkwd | DS Seq | Arith | Voc | Rav |
| Communication skills | .08 | .03 | .15 | -.06 | -.19 | -.07 | -.05 |
| Imagination | .28* | .19 | .20 | .21 | -.05 | -.20 | -.26* |
| Social skills | .11 | .18 | .04 | .00 | .09 | -.02 | .18 |
| Attentional shifting | -.18 | -.02 | -.03 | -.27* | -.23 | -.07 | -.09 |
| Attention to detail | .46** | .40** | .41** | .17 | .10 | .02 | .05 |
| Total AQ | .21 | .23 | .23 | .02 | -.09 | -.10 | -.02 |

Note: N=46, **p <.05, **p <.001*

For all 9 SPQ sub-scale scores, there were no significant correlations between any of the WAIS sub-tests or computerised task scores (magnitude comparison or true/false judgements). Nonetheless, it can be seen from table 4.11 that there was a significant correlation between the AQ imagination sub-scale score, WAIS digit span total scaled score *(r (45)=.28 p=.03)*, and the Ravens percentage correct score *(r*

*(45)=-.26 p=.04)*, meaning that participants in this sample with poor imagination were able to recall more digit strings, but had a lower non-verbal IQ or pattern matching ability.

There was also a significant correlation between AQ attentional shifting sub-scale and WAIS digit span sequencing score *(r (45)=-.27 p=.03)* – indicative that participants with poor attentional shifting mechanisms had a lower capacity for number sequencing of longer digit strings. Finally, there was a significant moderate correlation between the AQ attention to detail sub-scale, WAIS digit span total scaled score *(r (45)=.46 p=.001)*; WAIS digit span forward score *(r (45)=.40 p=.003)*; and WAIS digit span backward score *(r (45)=.41 p=.002)*, meaning that participants with higher attention to detail scores were able to retain and recall more lengthily digit strings for forward and backward digit span tasks.

Table 4.12.Table of correlations between magnitude comparison RTs and AQ traits

| | **Correlation Coefficients** | | | |
|---|---|---|---|---|
| | **Less 55 Right** | **More 55 Right** | **Less 55 Left** | **More 55 Right** |
| Communication skills | .20 | .17 | .19 | .22 |
| Imagination | .12 | .14 | .10 | .06 |
| Social skills | -.01 | .04 | .06 | .08 |
| Attentional shifting | .29* | .23 | .24 | .20 |
| Attention to detail | .02 | .06 | -.04 | .15 |
| Total AQ | .17 | .17 | .15 | .19 |

Note: N=46, **p <.05, **p <.001*

There were no significant correlations between all 5 AQ sub-scores and true/false judgement scores of arithmetic and multiplication conditions. However, table 4.12 shows that when all 5 AQ sub-scale scores were correlated with all 4 magnitude comparison conditions, the only significant correlation was between attentional shifting and less than 55 with right arrow key press RT *(r (45)=.29 p=.02)*.

# 4.5. Discussion

In this part of the study, a series of analyses were performed including correlations between the WAIS-IV subtest scores and computerised tasks (magnitude comparison and true/false judgement); a between groups analysis (independent t-tests) of SPQ/AQ, WAIS-IV and computerised task scores via a 2 way median split procedure; ANCOVAs between non-verbal IQ and arithmetical cognition variables; and a correlation analysis between SPQ/AQ scores and WAIS-IV/computerised task variables. Each of these analyses revealed novel insights into the interplay between autistic personality traits, WAIS-IV sub-test performance and differences in arithmetical ability.

### 4.5.1 Correlation analysis between WAIS-IV and computerised tasks

The purpose of these analyses was two-fold. Firstly, to determine whether the computerised tasks developed by the PhD candidate were of sound construct validity in relation to the WAIS-IV sub-tests, which are well validated measures of arithmetical ability. Secondly, to examine if and how WAIS-IV sub-test scores related with magnitude comparison RTs and true/false judgement scores. In summary, the WAIS-arithmetic and WAIS-sequencing sub-tests correlated negatively with all four-magnitude comparison RTs that were left arrow/less than 55 (congruent); right arrow/more than 55 (congruent); left arrow/more than 55 (incongruent); right arrow/less than 55 (incongruent). Significant positive correlations were also found between the true/false judgement scores (multiplication and arithmetic), WAIS-arithmetic sub-test, WAIS-digit span total, WAIS-backward digit span, and WAIS-sequencing scores.

It may be inferred from these correlations that the computerised tasks developed by the investigator were of sound construct validity relative to the WAIS standardised and validated measures of mathematical cognition and working memory. Moreover, the negative correlation between WAIS-arithmetic sub-test scores and magnitude comparison RTs would suggest not only that Higher WAIS-arithmetic scores were associated with faster magnitude comparison RTs, but also that a sound internal spatial representation of the number line is required to accurately solve multi-operational problems of increasing complexity (Dehaene, Bossini & Giraux, 1991). Likewise, the negative correlation between WAIS-sequencing and all four magnitude comparison RTs would support the notion of a functional link between a left to right spatial representation of increasing magnitude, and the semantic congruency of number sequencing along a continuum, for at least western based culture (Dehaene et al., 1993).

The positive (and significant) correlations between the true/false judgement scores of arithmetic, multiplication conditions, WAIS-digit span total, WAIS-digit span backwards and WAIS-digit span sequencing, but not WAIS-digit span forward warrants further investigation. A likely explanation for the non-significant correlation between true/false judgement scores and WAIS-forward digit span scores could have signified the redundancy of cognitive functions involved with recall of digit strings in a forward direction for divisive/multiplicative and additive/subtractive operands in arrival of accurate true/false mathematical judgements (working memory/short term memory). The significant correlations between true/false judgment scores, WAIS-sequencing and WAIS-backward digit span scores conversely suggests that cognitive processes related to semantic sequencing of numbers and recall of digits in reverse order play a functional role in the short term memory retention of operands during true/false judgements of multi-operational problems.

The most compelling findings from this set of analyses were the negative correlations between the WAIS-arithmetic, WAIS-sequencing sub-tests, and all four magnitude comparison RTs. These correlations were predictable given the established functional role of visuo-spatial working memory in the recruitment of spatial imagery, where for instance, representational space spatially corresponds with the mental number line (Bachtold, Baumuler & Brugger, 1998; Szucs, Devine, Soltesz, Nobes & Gabriel, 2013; Walsh, 2003). It may be well to speculate from these observations – that higher WAIS-arithmetic scores and WAIS-sequencing scores were correlated with faster magnitude comparison RTs because of the recently proposed notion that visuo-spatial working memory is coordinated by inhibition or attentional suppression (James, 1890/1950; Szucs, et al., 2013).

This postulation was warranted from a number of previous behavioural investigations into the link between inhibitory processes associated with executive functioning, visuo-spatial working memory capacity, and mathematical ability in children (Bull & Lee, 2014; Bull & Scerif, 2001; Marzocchi, Lucangeli, De Meo, Fini & Cornoldi, 2002; Szucs, et al., 2013). Most recently for example, Szucs, et al., (2013) found a significant correlation between maths performance, magnitude comparison Stroop task RTs, and distance effect RTs from a physical size magnitude comparison Stroop task. The RTs from these two variables were averaged together to form an “inhibition score” given the previous link between number-Stroop interference, facilitation /inhibition, and attentional switching (Bull and Scerif, 2001). Essential findings relevant to this thesis were that math performances of 9-10 year old children were positively correlated with inhibition scores and visuo-spatial working memory. A multiple regression analysis revealed that visuo-spatial working memory and inhibition scores were significant predictors of maths performance.

In light of the correlations observed within this thesis, it is conceivable that WAIS-sequencing sub-test scores (elements of visuo-spatial working memory) correlated negatively with all the magnitude comparison RTs because of interference suppression (inhibitory) and facilitation (congruent) processes occurring in the course of making magnitude comparison judgements. It was possible that the congruent magnitude comparison conditions (more than 55/right arrow and less than 55/left arrow) generated Stroop like facilitation (faster RTs) and incongruent conditions (more than 55/left arrow and less than 55/right arrow) generated Stroop interference (slower RTs). These associations are, however, only speculative as few conclusions can be drawn from zero-order correlations about attentional suppression and facilitatory mechanisms during magnitude comparison judgements. The only suggestion that could be made with certainty was that there were moderate associations between standardised measures of arithmetical ability (WAIS-IV working memory sub-tests) and the measures of numerical cognition developed by the investigator.

#### 4.5.2. Between groups analysis of SPQ/AQ and WAIS-IV variables

This section comprised a set of independent t-tests of SPQ/AQ sub-scales and WAIS-IV sub-tests, where a 2 way median split into low and middle scores was performed. This was done in order to examine whether there were significant differences between AQ and SPQ scores within the sample. Secondly, behavioural literary evidence has indicated individuals with schizotypal personality disorder (Mitropoulou, et al., 2005; Trotman, McMillan & Walker, 2006; Weiser, et al., 2003) and autism (Aagten-Murphy, et al., 2015; Meaux, Taylor, Pang, Vara, & Batty, 2014) were characterised by poor mathematical and visual estimation abilities. Hence, the essential aim of this investigation was to examine if participants in the above average

SPQ and AQ group had significantly lower WAIS-IV sub-test scores than the low SPQ/AQ group.

Contrary to expectations, there were no significant differences between normal and low SPQ group scores or normal and low AQ group scores given that the participant scores in this study were not in the clinically significant range - 30+ for the AQ questionnaire (Baron-Cohen et al., 2001), and 50+ for the SPQ (Raine, 1991). To recapitulate, there were significant arithmetical ability (WAIS-arithmetic sub-test score) group differences between all WAIS digit span sub-test scores; WAIS-vocabulary sub-test scores and Ravens percentage correct scores, where the low WAIS-arithmetic group scored lower on all these assessments than the normal WAIS-arithmetic group. The low WAIS-arithmetic group also scored significantly lower in both true/false judgement conditions; also, the low WAIS-arithmetic group had significantly delayed magnitude comparison RTs than the normal WAIS-arithmetic group. In relation to these findings, it has been postulated that the functional quality of visuo-spatial working memory depends on the proficiency of attentional suppressive mechanisms as measured by number Stroop interference (Bull & Scerif, 2001; Szucs, et al., 2013). If this were the case for the observed magnitude comparison RTs of the low WAIS-arithmetic score group, then the slower RTs for semantically incongruent stimuli would have been attributed to poor interference suppressive mechanisms.

The essential findings from the between groups analysis of WAIS-IV subtests and computerised tasks was that participants in the low WAIS-arithmetic group had significantly poorer performance in all the WAIS-spatial working memory sub-tests including forward, backward, and sequencing digit span sub-tests as compared to the normal WAIS-arithmetic group. These findings were in accord with those of the Szucs, et al., (2013) study, where dyscalculic children were observed to be significantly impaired in a battery of spatial working memory assessments that evaluated the counting of dot matrices, and short term recall indexes compared to age matched controls after correcting for verbal IQ and non-verbal IQ. The dyscalculic participants in the Szucs et al., investigation however, had a formal diagnosis of developmental dyscalculia in its pure form, where participants whom presented with co-morbidities such as dyslexia were screened out of the sample.

Noteworthy in the Szucs, et al., (2013) study was the evidence for dissociation between verbal and spatial working memory, where there were no significant differences in performance of word recall, list recall storage, list recall processing or digit recall between dyscalculics and controls. It was not possible to distinguish spatial and verbal working memory of the sample tested in this thesis, given that vocabulary but not verbal working memory was assessed. Low WAIS-arithmetic participants did, however, have significantly lower WAIS-vocabulary scores than normal WAIS-arithmetic participants. Despite this, an ANCOVA with WAIS-arithmetic score as the dependent variable later revealed that low and normal WAIS-arithmetic groups did not differ significantly in WAIS-vocabulary scores when included as a co-variate, meaning that once verbal comprehension of participants was controlled for, participants in the low WAIS-arithmetic group still had significantly lower WAIS-arithmetic scores than the normal WAIS-arithmetic group. It may be concluded from these findings that low arithmetical ability was not attributed to poor verbal comprehension.

The non-significant group differences between low and normal AQ/SPQ scores were likely to have occurred because they were drawn from a normal sub-population comprised mainly of undergraduate psychology students with no known psychiatric or developmental disorders. If for instance, AQ and SPQ scores from a larger sample size were grouped by a 3-way median split (i.e. low, medium, high SPQ/AQ scores) with an excluded middle, then the mean group differences between low and high SPQ/AQ groups would more likely be statistically significant. Hence, future investigations into arithmetical ability of individuals with schizotypal and autistic tendency will involve the administration of the SPQ and AQ to a larger sample (100+ participants), then contacting participants for further testing following group classification of scores within the sample.

The literature that found evidence for impaired mathematical ability in autism and schizotypal personality disorder comprised a population of participants who were formally diagnosed with these disorders, and a control group that was matched for age, gender and socio-economic background. As a matter of course, the mean differences in mathematical ability between experimental and control groups were found to be highly significant (Aagten-Murphy, et al., 2015; Mitropoulou, et al., 2005; Trotman, et al., 2006; Weiser, et al., 2003). In view of this, if future investigations into mathematical ability using the same cognitive assessment battery and computerised tasks here – only with clinical and age matched control groups – it is feasible that significant group differences would be observed in WAIS-arithmetic and WAIS-digit span scores.

#### 4.5.3. Correlations between SPQ/AQ scores and WAIS-IV/computerised task performance

In this component of the analysis, zero-order correlations were performed between all 9 SPQ sub-scale scores; all 5 AQ sub-scale scores; all of the WAIS-IV sub-tests; all 4 magnitude comparison RTs; and all two true/false judgement scores. Contrary to expectations, there were no significant correlations between any of the 9 SPQ sub-scale scores; WAIS-IV sub-tests; or computerised task scores (magnitude comparison or true/false judgements). Nonetheless, the AQ imagination sub-scale score positively correlated with WAIS-digit span total score, and negatively correlated with the Raven's percentage correct score. There was also a negative correlation between the AQ-attentional shifting sub-scale and WAIS-digit span sequencing score. The AQ-attention to detail sub-scale was positively correlated with the WAIS-digit span total score, WAIS-forward and WAIS-backward digit span scores. Finally, there was a positive correlation between AQ-attentional shifting and the less than 55/right arrow key-press RTs of the magnitude comparison task.

Firstly, in terms of the correlations between AQ-imagination; Raven's percentage correct scores; and WAIS-digit span total scores, these findings indicate that participants with low imaginative skills (as indicated by higher AQ-imagination scores) had lower Raven's percentage correct scores. In a broader context, these findings signify that neurotypical individuals with low imaginative skills have more difficulty with problem solving strategies required for complex pattern matching (i.e. using Boolean logic to solve abstract problems). It could be that less imaginative participants were more advantaged in their ability to accurately recall longer digit-strings by their higher AQ-attention to detail scores, given that this sub-scale positively correlated with total WAIS-digit span sub-scores.

The correlation between the AQ-attentional shifting; WAIS-digit span sequencing; and RTs for numbers less than 55 with right arrow key-press, were indicative that participants with poorer attentional shifting ability were impaired in the ability to recall longer digit strings in their sequential order, and secondly required more time to make accurate magnitude comparison judgements of semantically incongruent numerical information.

The positive correlations between AQ-attention to detail sub-test scores; total WAIS-digit span; WAIS-digit span forward; and WAIS-digit span backward scores suggested that participants with higher recall of forward and backward digit strings, were advantaged by their strong attentional focus to the read out of individual digits that made up strings. These observations were in accord with previous literature positing a local over global processing advantage in neurotypical populations with autistic tendency (Sutherland & Crewther, 2010). Noteworthy was the non-significant correlation between AQ-attention to detail and WAIS-digit span sequencing scores. It may be inferred from this finding (or lack of finding) that the cognitive processes involved with attentional focus to parts over wholes was functionally unnecessary in the recall of digit strings in sequential order.

Also noteworthy was the absence of significant correlation between measures of arithmetical ability (true/false judgements and WAIS-arithmetic scores) and the 5 AQ sub-scales (attention to detail, attentional shifting, imagination, communication skills, and social skills). The question begs as to whether this was an indication that high AQ scoring participants with sound numeric and arithmetic skills – as the prevailing theory posits (Baron-Cohen, Ashwin, Aswin, Tavassoli & Chakrabarti, 2009; Baron-Cohen, Wheelwright, Skinner, Martin & Clubley,2001) – did not need to engage local processing mechanisms (attention to detail) or cognitive resources for solving arithmetical problems.

Contrary to this, a recent behavioural investigation into numerical/arithmetical ability of ‘high functioning autism’ revealed that compared to control participants matched for age, sex, IQ and socio-economic status, the autistic group showed significantly impaired performance in an arithmetical and mathematical achievement test (Aagten-Murphy, et al., 2015). However, limited conclusions can be drawn about the relationship between AQ scores of participants in this thesis, and their arithmetical ability given that a) there were no significant correlations and b) that there were no significant WAIS-arithmetic group differences between AQ scores.

Perhaps the most pertinent findings observed for this component of the analysis were the correlations between AQ-attentional shifting scores, WAIS-digit span sequencing scores, and RTs for numbers less than 55 with right arrow key-press. The positive correlations between AQ attentional shifting scores and semantically incongruent magnitude comparison RTs found here were not unlike those observed in a behavioural investigation into the relationship between attentional switching (shifting), attentional inhibition, mathematical ability and spatial working memory, where perseverative errors on the Wisconsin card sorting test (a validated measure of attentional shifting) correlated positively with increased interference effects of a number Stroop-task after controlling for intelligence and reading ability (Bull & Scerif, 2001).

A final comment, the conclusions drawn from this analysis about the relationship between executive functions such as attentional shifting; attention to detail (global vs. local attention); and imagination (mental imagery and abstraction) were limited by a number of factors including the absence in standardised testing of executive functioning (e.g. WAIS-IV-block design, matrix reasoning or visual pictures), and the raw correlation approach in the first pass exploration of relationships between variables. Future analyses thus should involve partial and part correlations in order to firstly determine the unique contribution of variables within a given model, and the percentage of variance explained by its effect upon a given dependent variable.

# Part 5:
# Magnetoencephalography of Surround-Masking

Abstract

For Part 5 (magnetoencephalography of surround masking), MEG recordings were then taken whilst participants underwent a surround-masking of numerosity task in order to examine spatial and temporal characteristics associated with the saturation of sensory gating resources during numerosity comparisons. The main findings for Part 5 revealed a positive relationship between arithmetical ability and response times (RTs) of numerosity comparison judgements under high contrast centre/high contrast surround conditions. These correlations indicated that high contrast visual stimulation via surround-masking, had a disruptive effect on numerosity judgements of participants with normal arithmetical ability, whereas judgements of participants with low arithmetical ability appeared to be impervious to such conditions. A within-groups spatio-temporal cluster analysis of these MEG responses indicated an increased load on attentional resources when observers made numerosity comparison judgements under high contrast centre/high contrast surround conditions. An increased load on attentional resources was evidenced by the spatial localisation of significant clusters within left frontal and parietal regions of the sensor array. The peak event related field (ERF) responses under these conditions were not unlike the correct related negativity (Luu & Tucker 2003) – a negative peak response within pre-frontal regions ~130ms to 150ms post stimulus onset. The main findings suggest that numerosity comparison judgements were influenced by inhibitory gain control and noise exclusion mechanisms within the geniculo-striate relay.

# 5.0 Introduction

There are a growing number of MEG investigations into the electromagnetic response profile associated with inhibitory and gain control mechanisms such as surround suppression, and the stimulus/psychophysical properties that drive them. For example, one of the first MEG studies to examine the visually evoked response pattern of surround suppression, demonstrated that the initial peak amplitude (~90ms) to a low/medium contrast sinusoidal grating (40%) flanked by a high contrast surround grating, was of lower amplitude as compared to when the central grating was presented without the high contrast surround (Ohtani, Okamura, Yoshida, Toyama, & Ejima, 2002). The authors suggested that the smaller peak amplitude for when the test stimulus (low contrast central grating) was flanked by the surround stimulus (high contrast grating) was indicative of reduced neuronal activity through inhibitory interactions in V1 and or V2.

More recent MEG investigations into inhibitory interactions in V1 have revealed that luminance and Michelson contrast variations have a modulatory effect upon suppressive mechanisms in LGN and V1, characterized by narrow band gamma oscillations (Adjamian, Hadjipapas, Barnes, Hillebrand, & Holliday, 2008; Hall et al., 2005; Muthukumaraswamy et al., 2009; Sedley & Cunningham, 2013). That is, high contrast visual stimulation has been consistently demonstrated across MEG and electroencephalographic (EEG) studies to produce evoked gamma oscillations possessing a centre frequency of ~40Hz-70Hz with a narrow bandwidth of ~10Hz-20Hz in V1 (Sedley & Cunningham, 2013). This ‘visual gamma’ is unique to occipital regions of the cortex and has been proposed to be a neural marker for filtering out of redundant visual information (Sedley & Cunningham, 2013).

Taking all these observations into consideration, it is worth noting that visual gamma oscillations have been observed as anomalous in schizophrenia, such that induced responses to Mooney faces are characterized by lower gamma spectral power in occipito-parietal MEG sensors (gradiometers) compared to neurotypical observers (Grützner et al., 2013; Uhlhaas & Singer, 2010). Visual gamma power anomalies in schizophrenia have been evidenced toward a deficiency in the GABA synthesizing enzyme glutamic acid decarboxylase (GAD-67), which has also been linked with functionally aberrant suppressive and inhibitory mechanisms in V1 (Behrendt & Young, 2004; Uhlhaas & Singer, 2010; Yoon et al., 2010).

### 5.1.Dorsal stream functioning and its relation to numerical ability and gating

A recent psychophysical study demonstrated that children with low mathematical skills showed higher motion coherence discrimination thresholds than age-matched controls (Sigmundsson, Anholt, & Talcott, 2010). These findings suggested there was evidence that developmental dyscalculia (DD) may be associated with a perceptual disorder in surround-suppression or external noise exclusion (Carandini, 2004; Sperling, Zhong-Lin, Manis, & Seidenberg, 2005). This conclusion was warranted by the psychophysical literature that suggested developmental disorders such as autism spectrum disorder (ASD), attention deficit hyperactivity disorder (ADHD) and developmental dyslexia all share a common perceptual deficit in motion coherence discrimination – particularly for global motion coherence (Braddick & Atkinson, 2011; Cornelissen et al., 1998; Laycock, Crewther, & Crewther, 2007; Stein, Talcott, & Walsh, 2000).

There are a number of other characteristics of dorsal-stream related perceptual deficits. Among them are poor spatial reasoning (Milner & Goodale, 2006) – a cognitive function essential in the addition and subtraction of numeric information a long a magnitude continuum (Ansari, 2008; Walsh, 2003). Atypical dorsal-stream development has also been associated with abnormal magnocellular responses, where visually evoked potentials (VEPs) of magnocellular responses for those of high autistic tendency, show markedly greater VEP amplitudes to high contrast flicker compared to those with low autistic tendency (Sutherland & Crewther, 2010). The absence of VEP response saturation during high contrast flicker of high autistic tendency participants was likely to reflect a defect of sensory gating mechanisms within the magnocellular channel. It is currently uncertain however, whether this aspect of anomalous visual development is from a defect of the magnocellular channel its self, or whether it is related to a pervasive disturbance of inhibitory RF segments within the geniculate-striate relay.

### 5.2 Can surround masking temporarily induce DD in neurotypical observers?

To pose a question such as the one above is to infer that disorders such as DD are of perceptual and low-level origin (Ansari & Karmiloff-Smith, 2002), not exclusively a high-order deficit – as argued by some of the early investigators of DD (Ardila & Rosselli, 2002; Butterworth, 2005; S. Dehaene, Molko, Cohen, & Wilson, 2004; Geary, 2004; Isaacs, Edmonds, Lucas, & Gadian, 2001; Kaufmann, Lochy, Drexler, & Semenza, 2004; Kucian et al., 2006; Molko et al., 2003; Rotzer et al., 2008; Rotzer et al., 2009; Sandrini & Rusconi, 2009; Stanescu-Cosson et al., 2000; Von Aster & Shalev, 2007; Wilson & Dehaene, 2007). There is also an implicit assumption that poor estimation ability – one of the behavioural markers of DD (Halberda, Mazzocco, & Feigenson, 2008; Piazza et al., 2010), is attributed to a developmentally disturbance of sensory gating mechanisms, which is likely to offset the progression of attentional and perceptual development involved with learning arithmetical and numerical concepts (Ansari & Karmiloff-Smith, 2002; Gilger & Kaplan, 2001). Such psychophysical evidence has let to the hypothesis that developmental dyslexia (poor reading) may be related to an inability to filter out external noise (Sperling, Lu, & Manis, 2004; Sperling et al., 2005). These ideas fall in line with the theoretical framework of the perceptual template model (PTM) discussed in chapter 1, where such deficits in noise exclusion have been conceived as lower signal to noise ratio (SNR) of visual input (Dosher & Lu, 2000; Dosher & Lu 1998; Lu & Dosher 2008; Lu & Dosher 1998; Lu & Dosher, 1999).

**5.3. How is surround masking likely to temporarily induce dyscalculia in neurotypical observers?**

If high contrast surround masking has an illusory effect upon the perceived contrast of a central texture region (Dakin, Carlin & Hemsley, 2005), then what effect should it have upon perceived numerosity, or the ability to make non-symbolic comparison judgements? If the illusory effects of surround masking are a consequence of swamped or saturated sensory filtering resources in LGN and V1, then input signal noisiness is likely to be a low-order contributor towards impoverished representations of number in neurotypical observers. But, what of observers with visuo-perceptual disorders or dorsal-stream functional anomalies?

Dakin et al., (2005) psychophysically demonstrated that observers with schizophrenia were relatively “immune” to the effects of surround masking. The high contrast surround markedly impaired Neurotypical observers’ contrast matching judgements, while at ceiling performance when no surround enveloped the texture region. Schizophrenic observers on the other hand, showed a more striking difference – the high contrast surround had no effect on their contrast matching judgements. Dakin et al., (2005) concluded this immunity was likely to originate from a functional anomaly of surround suppression and sensory gain control.

Dakin et al., (2005) also concluded that impoverishment of visual context by the high contrast surround, was likely to have disrupted mechanisms at a low-order/sensory level (i.e. RF suppression) rather than the attentional/high-order level of neural organization. Hence, if surround masking has a deleterious effect upon the ability to make numerosity comparison judgements in neurotypical observers, it may be well to infer that the poor numerosity comparison abilities in DD (i.e. Piazza et al., 2010) stems from anomalous sensory gain control development rather than a high-order cognitive deficit of numeric representation.

There may be new theoretical implications about the physiological locus of developmental dyscalculia should high contrast surround masking impair the ability to make more/less comparison judgements in neurotypical observers. Namely, it would suggest that poor numerosity comparison ability – a characteristic of dyscalculia – is attributed towards poor sensory gain control, where swamped gating resources in eliminating noisiness is likely to induce the illusion of 'more' elements than its veridical representation. The notion dyscalculia being induced by surround-masking would be problematic toward the widely held postulation that poor numerosity comparison mechanisms are the result of a discrete functional defect within a set of temporal and parietal cortical regions that subserve 'numerical processing' (Butterworth, Varma, & Laurillard, 2011; Landerl, Göbel, & Moll, 2013; Piazza et al., 2010; Pinel & Dehaene, 2013; Rubinsten, 2009; Wilson & Dehaene, 2007).

Instead, a surround masking induced inefficiency in making numerosity comparison judgements would not only indicate that developmentally anomalous estimation mechanisms are functionally pervasive, but also that the developmental course of numeric representation may be viewed as a ubiquitous and dynamic interaction between cortical systems, rather than discrete cortical structures working in isolation from one another (Johnson & Munakata, 2005; Johnson, 2001; Annette Karmiloff-Smith, 2009). Poor sensory gating mechanisms therefore, shape the learning of more complex mathematical operations from early childhood and onwards into adulthood (Ansari & Karmiloff-Smith, 2002; Johnson & Munakata, 2005). This theory does not fit well with the notion of developmental dyscalculia being the result of a congenital defect within temporo-parietal cortices (Butterworth et al., 2011; Landerl et al., 2013; Wilson & Dehaene, 2007).

## 5.4. A MEG investigation into surround masking of non-symbolic number

As demonstrated from the findings of Part 4, participants in the low arithmetic group performed significantly poorer than the normal arithmetic group in all tasks that evaluated performance in symbolic math such as the WAIS-arithmetic sub-test, true/false judgements for arithmetical and multiplicative operations, and symbolic number magnitude comparisons. By these observations, it has been well established that the neuropsychological profile of developmental dyscalculia comprises of such domain specific cognitive deficits in symbolic mathematics, which has moreover been correlated with poorer non-symbolic number acuity than individuals with normal arithmetical skills (Halberda, Mazzocco & Feigenson, 2008; Mazzocco, Feigenson & Halberda, 2011).

One of the most controversial issues of numerical cognition research relates to questions of the symbol-grounding problem: how can the relationship between symbolic and non-symbolic representation be explained, and whether symbolic representations of number acquire their semantic meaning via mapping onto the non-symbolic approximate number system (ANS) from earlier in development? (Liebovich & Ansari, 2016). In the context of numerical cognition development, it has been contended that low symbolic mathematical achievement is attributed to a weakened ANS from early in development, and that the ANS serves as a foundation for the acquisition of higher order arithmetical computations (Halberda et al., 2008; Mazzocco et al., 2011; Piazza, 2010).

In contrast to this notion however, it was recently proposed that the symbol-grounding problem cannot be explained by the assumption that the foundation of symbolic number meaning stems solely from the ANS, where non-symbolic number is unlikely to be number specific or purely numerical, given that there is no way to measure pure association between symbolic and non-symbolic numerosity, and that instead, high order cognitive control resources are likely to be recruited in order to disambiguate numerical from non-numerical dimensions of magnitude (continuous variables) as part of non-symbolic number processing (Liebovich & Ansari, 2016).

In view of these postulations, a series of bi-variate correlations between MEG surround-masking RTs (non-symbolic number), symbolic number comparison RTs, and WAIS-arithmetic sub-test scores were performed in order to explore the relationship between symbolic and non-symbolic numerosity, and to ascertain whether non-numerical parameters of magnitude such as contrast gain through surround-masking was related to individual differences in arithmetical ability.

The chief aims of the following experiments were to examine the neuromagnetic responses associated with surround-masking of numerosity, and to explore whether variations in arithmetical ability were related to behavioural performance of the surround-masking experiments. Further aims were to examine whether variations in SPQ and AQ traits were related to behavioural performance of the surround-masking experiments, and arithmetical ability. Analyses of the MEG responses were exploratory. Hence, the predictions on spatial and temporal response characteristics of this data were tentative. Some of the main questions of interest were:

- In what way do the cortical activation profiles for centre contrast (mid/high), surround contrast (high/low) and numeric representation (more/less) differ from one another?
- What differences are there in the time series and peak amplitudes of significant clusters across all conditions?
- In what way does surround contrast and centre contrast modulate the peak amplitude of significant spatio-temporal clusters?

## 5.5. Method

### 5.5.1. MEG response properties of surround-masking

Once component 2 of the study (cognitive testing) was completed, participants were scheduled a MEG and MRI scan at a time which suited them most conveniently. Of the 46 participants who completed component 1 and 2, 12 participants did not undergo a MEG/MRI scan for various reasons including unsuitability (i.e. noisy signal trace), unavailability, and failure to show up for the scheduled booking.

### 5.2.2. Materials

**MEG surround-masking stimuli**

The parameters of the MEG surround-masking stimuli – that is, diameter of the central stimulus region; diameter of surround annulus; contrast of surround annulus (high/low); luminance of the central stimulus region (zero/uniform); and brightness of dots (white), were identical to those described in the methods section of experiment 1 (see section 3.1.2 for details). There was, however, a minor modification to the trial sequence (figure 5.1), where onset of the central stimulus region occurred 500ms after onset of the surround (see figure 3.4 for trial sequence). This was to distinguish responses evoked by the surround annulus from high-order responses induced by the central stimuli.

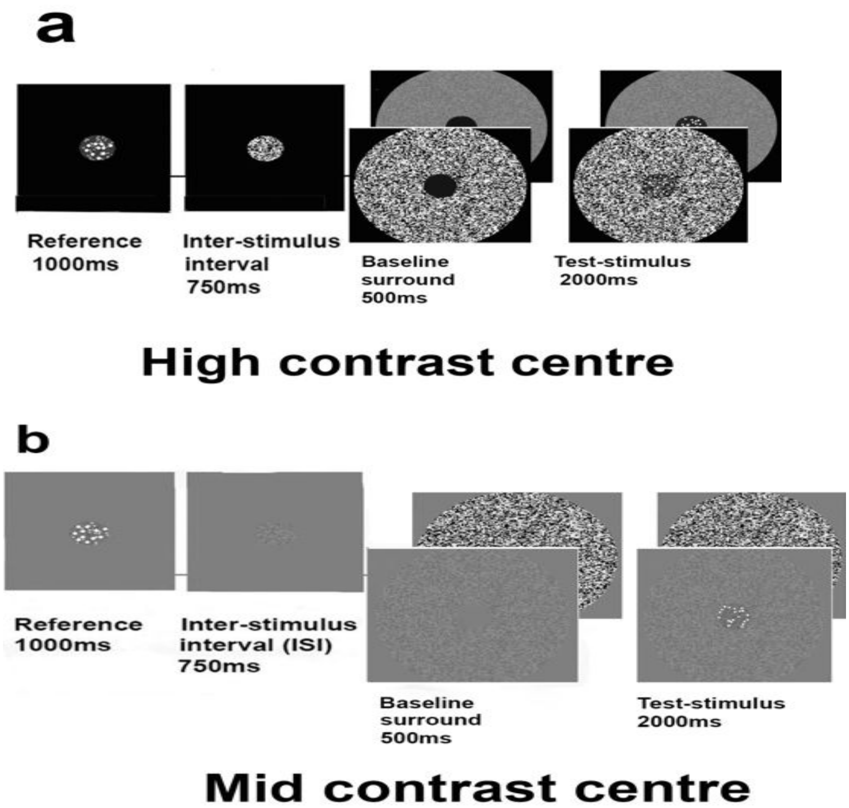



Figure 5.1.Trial sequence of MEG modified surround-masking experiments. The surround-masking of numerosity stimuli from experiment one were modified slightly for the purposes of undertaking the tasks in the MEG scanner. Instead of the simultaneous onset of centre and surround stimuli (as in experiment 1), the surround annulus was presented 500ms before the central stimulus, with a 2000ms presentation time of the centre and surround stimuli. Trial sequence for high contrast centre block (a), trial sequence for mid contrast centre block (b).

One other modification to the experimental design was the amalgamation of high contrast and low contrast surround conditions into one experimental run, where block 1 contained trials that only had the zero luminance (black) central stimulus region, and the other block contained trials with only uniform luminance (grey) central region stimuli. This modification of the experimental design was to minimise jitter in head position coordinates across conditions.

Each block (black centre/grey centre) contained 4 conditions: less dots/high contrast surround; more dots/high contrast surround; less dots/low contrast surround; more dots/low contrast surround, with 30 trials per condition. Both blocks took approximately 12 minutes to run through, and participants took brief rests to stretch and move around between blocks. Participants indicated whether there were more or fewer dots via RESPONSEixx, a handheld button box device (figure 5.2). Participants pressed the left button (green) if they saw fewer dots and the right button (red) if they saw more dots. The centre/surround stimulus remained on the display until there was a button pressed, and would then proceed to another trial. All conditions within an experimental block were fully randomised.


Figure 5.2.RESPONSEixx button box. Pressing the green button indicated numerosity estimation judgements of ‘more dots’, and pressing the red button indicated numerosity estimation judgements of ‘fewer dots’. The button responses and response times per trial were recorded onto an excel spreadsheet.

### 5.5.3. MEG data acquisition

MEG data was recorded from the Elekta Neuromag306 (Vectorview) system comprised of a triplet sensor array with 204 paired planar gradiometers, and 102 magnetometers within a magnetically shielded room. Prior to commencement of the MEG experiments, five head position indicator (HPI) coils were attached to the participant, with 3 of them situated across the forehead, and the last 2 on left/right mastoids. In order to control for electrocardiographic (ECG) artefacts, there was one bipolar electrode placed on each wrist, and two more bipolar electrodes placed above and below the right eye to record and control for vertical electro-oculographic (EOG) artefacts. The ground electrode was placed just below the right elbow.

The digitization of each HPI coil, and the delineation of fiducial landmarks (left/right pre-auricular points and nasion) were executed via the Fastrack Polhemus device, a 3D digitiser pen. Following the digitization of fiducials and HPI coils, the digitizer pen traced the head shape of the participant.

The surround-masking experiments that were customised for participants to perform inside the MEG scanner were displayed on a 1920 X 1080 pixel rear projector screen (width 45.4cm) at a viewing distance of 117cm. While participants were undertaking the tasks, trigger pulses that marked onset of stimuli within the MEG trace, were sent via the Datapixx response delivery hardware. During the experiments, the head position relative to the sensor array was monitored continuously via the HPI coils.

### 5.5.4. MEG data pre-processing

The MEG recordings were band-pass filtered at 0.01-333Hz at a sampling rate of 1kHz. The first step in off-line pre-processing entailed the removal of external noise from the raw recordings via MaxFilter software version 2.2 (Elekta Neuromag). This was achieved by implementation of the temporal extension of signal space separation (tSSS) see Taulu and Simola, (2006) for a detailed description of its theoretical framework and functionality. Each participant's raw data (fiff file) was corrected with head movement compensation, and then normalized to a common head coordinate system via MaxFilter software.

The MaxFiltered raw data was then subjected to further pre-processing via MNE-Python (version 0.9.0) MEG/electroencephalographic (MEEG) software (Gramfort, et al., 2013). Here, the raw data was band-passed filtered at 1-40Hz using the infinite impulse response (IIR) method. Bad channels were noted by the raw data log and by visual inspection, and were excluded from analysis. Events of interest were then partitioned into epochs by the respective event ID along the stimulus trigger line. Epochs were rejected if the peak-to-peak amplitude of gradiometers exceeded 4000e-13 (40nAm) and magnetometers 4e-12 (4pAm) respectively. The epoch length was a total of 500ms, where tmin was -200ms, and tmax was 300ms. Independent components analysis (ICA) was then performed on acceptable epochs in order to remove ECG and EOG artefacts from the data. The epochs for each event were then averaged into evoked responses per condition across all 34 subjects. Finally, the evoked responses for each condition were baseline corrected, where evoked fields were standardized relative to the zeroed out baseline period of
-200-0ms.

### 5.5.5. Procedure

After being greeted by the investigator at MEG laboratory reception, participants completed a MEG screening questionnaire to determine whether there were metallic implants that would make them unsuitable for scanning. After the removal of metallic items or piercings from their person, participants underwent a brief MEG scan in order to check for noise or small metallic objects the participant may have been unaware of. Following this, the HPI coils were attached, and the participant's head shape was digitized. The ECG/EOG electrodes were then attached. The investigator then read out instructions to the participant on how to perform the MEG tasks, and then was given practice trials of each experiment to perform until they were familiarised with the tasks.

# 5.6. Results

### 5.6.1. Surround-masking MEG analysis (behavioural responses)

**Mean MEG surround-masking RTs**

The mean and standard error for each of the MEG surround-masking RTs can be found within table 5.1. A graphic representation of these mean differences can be seen from the bar graphs within figure 5.1. It should be noted that a technical problem with the button response box occurred for 20 out of 34 of the participants behavioural response data and therefore, an analysis on the effects of surround masking upon numerosity comparison accuracy could only be performed on 14 out of 34 of the participants.

A series of paired t-tests (repeated measures) were performed in order to independently explore mean response times per condition with concern to differences in background luminance, centre contrast, surround contrast, and numerosity. The t-tests performed here were not post-hoc or family-wise comparisons, each hypothesis being tested is independent from all others. Independence was determined by Pearson's *r* correlations, which revealed non-significant relationships between variables for each t-test performed. Paired t-tests instead of ANOVAs were performed on the RT data in order to ensure consistency between within groups comparisons performed here and in section 5.7.7, the MEG surround-masking event-related field analysis.

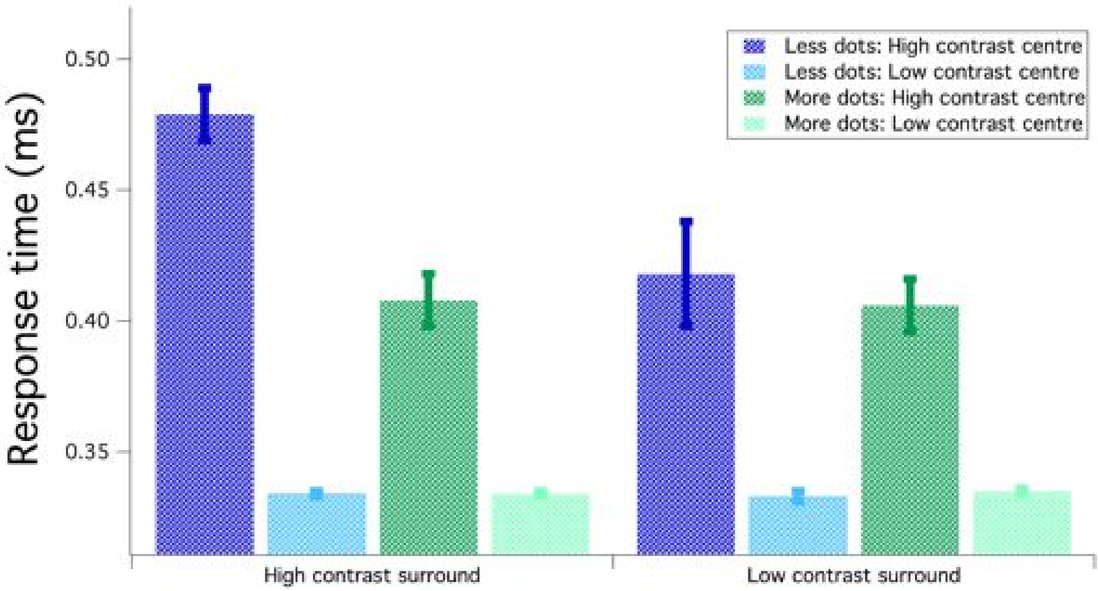



Figure 5.1.Bar graph of mean response times (RTs) and standard error for MEG surround-masking stimuli. Note that the central stimulus contrast had a greater effect on numerosity estimation judgements than surround stimulus contrast. That is, irrespective of surround stimulus contrast, it was apparent that numerosity estimation RTs were substantially faster when the central stimulus was mid contrast (grey). In contrast to this, the high contrast centre appeared to have the most disruptive effect on numerosity estimation, with prominently more delayed RTs, even in the presence of a low contrast surround. The mean standard error for each RT is located in the centre of each bar.

Table 5.1.Mean and standard deviation of MEG surround-masking RTs

| | Centre | | | |
|---|---|---|---|---|
| | **Grey centre (grc)** | | **Black centre (blc)** | |
| | Mean | *SD* | Mean | *SD* |
| **Surround** | | | | |
| **Low contrast** | | | | |
| Less dots | .333 | *(.007)* | .418 | *(.098)* |
| More dots | .335 | *(.008)* | .406 | *(.087)* |
| **High contrast** | | | | |
| Less dots | .335 | *(.007)* | . 479 | *(.065)* |
| More dots | .333 | *(.008)* | .408 | *(.072)* |

N=34

A paired t-test revealed no significant effect on response accuracy for any high contrast/low contrast surround conditions. These observations for high and low contrast surround conditions may be explained by the prolonged duration of the surround stimuli as compared to the psychophysical experiments discussed in experiment one – the psychophysics of surround-masking.

### 5.6.2. Uniform (grey) centre/surround contrasts

The first two t-tests compared the mean differences between RTs for high contrast centre/high contrast surround and low contrast centre/low contrast surround stimuli. There was a highly significant difference between RTs for fewer dots with high contrast centre/high contrast surround (LHccHcs) and fewer dots with low contrast centre/low contrast surround (LLccLcs), where on average, observers took

~140ms longer to make comparison judgements of fewer dots during LHccHcs conditions *(t(33)=12.75, p=<.000)*. Likewise, there were also significant differences between RTs for more dots with high contrast centre/high contrast surround (MHccHcs) and more dots with low contrast centre/low contrast surround (MLccLcs) stimuli, where it took ~70ms longer for observers to accurately discriminate more dots during MHccHcs conditions *(t(33)=5.78, p=<.000)*. These differences were striking, however, it was not certain whether the delayed RTs for the high contrast stimulus configuration was attributed to the centre or the surround. The next sets of paired t-tests were therefore implemented to disambiguate the effects of centre contrast from surround contrast.

**5.6.3. Centre contrast effects**

The following set of paired t-tests compared RT differences between centre contrasts holding constant surround contrast. There was a significant difference between RTs for LHccHcs and fewer dots with high contrast centre/low contrast surround (LHccLcs), where observers required ~60ms more time to make an accurate comparison judgement under LHccHcs conditions *(t(33)=3.17, p=<.001, 1 tailed)*. However, there were no significant differences between RT comparisons of MHccHcs and more dots with high contrast centre/low contrast surround (MHccLcs); fewer dots with low contrast centre/high contrast surround (LLccHcs) and LLccLcs, or more dots with low contrast centre/high contrast surround (MLccHcs) and MLccLcs stimulus conditions. It can be inferred from these findings that it was most difficult for observers to make numerosity comparison judgements during the LHccHcs condition, and that under high contrast centre and high contrast surround conditions, it was markedly more difficult for observers to accurately discriminate fewer dots than what it was to discriminate more dots. These findings however, only partly examined the effects of centre contrast from surround contrast – the next set of t-tests performed held constant the centre contrast in order to further examine these effects.

**5.6.4. Surround contrast effects**

The next 4 paired t-tests ascertained whether it was centre contrast or surround contrast that had the most deleterious effect upon numerosity comparison judgements. For the first comparison – LHccHcs and LLccHcs – there was a highly significant difference between these two RTs, where observers required ~140ms longer to make accurate numerosity comparison judgements of the LHccHcs stimulus *(t(33)=12.42, p=<.0005)*. There was also a significant difference between RTs of MHccHcs and MLccHcs, where the RTs for making numerosity comparison judgements during the MHccHcs condition were delayed by ~70ms *(t(33)=5.91, p=<.0005)*. The paired t-tests for comparisons of LHccLcs and LLccLcs conditions revealed a significant difference between these RTs where there was a ~80ms delay for observers when they made numerosity comparison judgements during the LHccLcs condition *(t(33)=5.09, p=<.0005)*. Finally, the paired t-tests for comparisons of MHccLcs and MLccLcs conditions were also significant, where a ~70ms delay was observed for comparison judgements of the MHccLcs stimulus condition *(t(33)=4.68, p=<.0005)*. Overall, these findings indicate that irrespective of surround contrast, the high contrast centre had the most adverse impact upon numerosity comparison judgements of more and fewer dots.

### 5.6.5. Numerosity (fewer dots/more dots)

The next set of paired t-tests examined mean RT differences between numerosity (fewer dots/more dots). The first comparison – LHccHcs and MHccHcs – revealed a significant difference between this RT contrast, where observers required ~70ms longer to make accurate comparison judgements during the LHccLHcs condition *(t(33)=4.27, p=<.005)*. As expected, there were no significant differences between RTs for LLccLcs and MLccLcs conditions. Curiously, there were no significant differences between RT comparisons of LHccLcs and MHccLcs, or RT comparisons of LLccHcs and MLccHcs stimulus conditions.

In order to affirm that these RT differences were attributed to the centre but not surround contrast, two final paired t-tests were implemented that contrasted the RTs of LLccHcs with MHccLcs, which revealed a significant difference between these variables *(t(33)=4.75, p=<.0005)*, and LHccLcs with MLccHcs RTs – also significant *(t(33)=4.98, p=<.0005)*. For the LLccHcs and MHccLcs contrast, observers RTs were delayed by ~70ms during the MHccLcs condition. Conversely, for the LHccLcs and MLccHcs contrast observer RTs were delayed by ~80ms during numerosity comparison judgements of LHccLcs stimuli. Overall, it was apparent from these observations that the high contrast centre had most adversely impacted the ability to make accurate estimation judgements, which was contrary to the findings observed in experiment one. It appeared to be central and not surround contrast that had an effect on perceived number of dots.

### 5.6.6. Correlations with surround-masking RTs and cognitive variables

Spearman's rho rank order correlations were performed between the RTs for all 8 MEG surround-masking conditions, each WAIS sub-test (table 5.2), and the RTs for all 4 magnitude comparison conditions (table 5.3) as part of an exploratory analysis into an existing relationship between these variables. The correlations performed were bivariate, hence, it was unnecessary to correct for multiple comparisons. From examination of table 5.2, it can be seen that the only MEG surround-masking RTs that correlated with WAIS-arith sub-test scores was LHccHcs *($r(33)=.38$, $p=.01$)*, which suggested that observers with good arithmetical skills had the most delayed RTs when required to make numerosity comparison judgements of fewer dots under high contrast centre/high contrast surround conditions – the strength of this correlation can be observed from figure 5.2. Just as compelling was the MHccHcs correlation with the WAIS digit span backwards score *($r(33)=.41$, $p=.008$)*, and the WAIS total digit span score *($r(33)=.40$, $p=.01$)*. These correlations suggested that higher backward digit-span and total digit-span scores were moderately associated with prolonged RTs during the comparison of more dots under high contrast centre/high contrast surround conditions. Please refer to figure 5.3 for the scatterplots of these correlations.

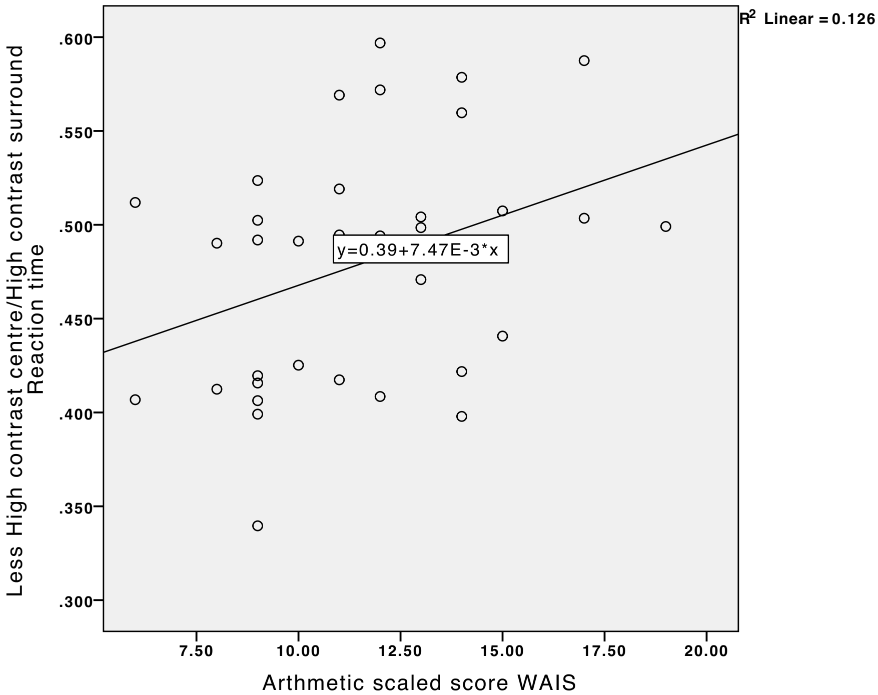



Figure 5.2.Scatter plot of correlation between WAIS-arithmetic scaled score and MEG surround-masking stimuli. Dependent variable: Comparison judgment RT of fewer dots under high contrast centre/high contrast surround conditions. Note by the positive correlation that higher WAIS-arithmetic scores were associated with more delayed numerosity comparison RTs.

Table 5.2. Table of correlations between MEG surround-masking RTs and WAIS sub-test scores

| | Correlation coefficients | | | | |
|---|---|---|---|---|---|
| | **DS Total** | **DS Fwd** | **DS Bkwd** | **DS Seq** | **Arith** |
| **Black centre** | | | | | |
| Less dots high contrast surround | .28 | .11 | .28 | .13 | .38* |
| More dots high contrast surround | .40* | .28 | .41** | .26 | .15 |
| Less dots low contrast surround | .15 | -.02 | .27 | .11 | .01 |
| More dots low contrast surround | -.08 | -.06 | -.01 | -.19 | -.18 |
| **Grey centre** | | | | | |
| Less dots high contrast surround | -.05 | -.11 | .03 | .03 | -.25 |
| More dots high contrast surround | .01 | .09 | -.01 | .11 | .08 |
| Less dots low contrast surround | .24 | .12 | .22 | .20 | -.07 |
| More dots low contrast surround | -.19 | -.09 | -.16 | -.13 | .02 |

Note: N=34, **p <.05, **p <.001, 1 tailed*

Table 5.3. Table of correlations between MEG surround-masking RTs and Magnitude comparison RTs

| | Correlation coefficients | | | |
|---|---|---|---|---|
| | **More than 55 right arrow** | **Less than 55 right arrow** | **More than 55 left arrow** | **Less than 55 left arrow** |
| **Black centre** | | | | |
| Less dots high contrast surround | -.39* | -.35* | -.35* | -.32* |
| More dots high contrast surround | -.13 | -.34* | .04 | -.30* |
| Less dots low contrast surround | -.13 | .06 | .01 | .14 |
| More dots low contrast surround | .15 | .24 | .03 | .11 |
| **Grey centre** | | | | |
| Less dots high contrast surround | .12 | -.07 | .13 | .00 |
| More dots high contrast surround | .19 | .21 | .06 | .26 |
| Less dots low contrast surround | .28 | .24 | .34* | .32* |
| More dots low contrast surround | .21 | .15 | .11 | .00 |

Note: N=34, **p <.05, **p <.001, 1 tailed*

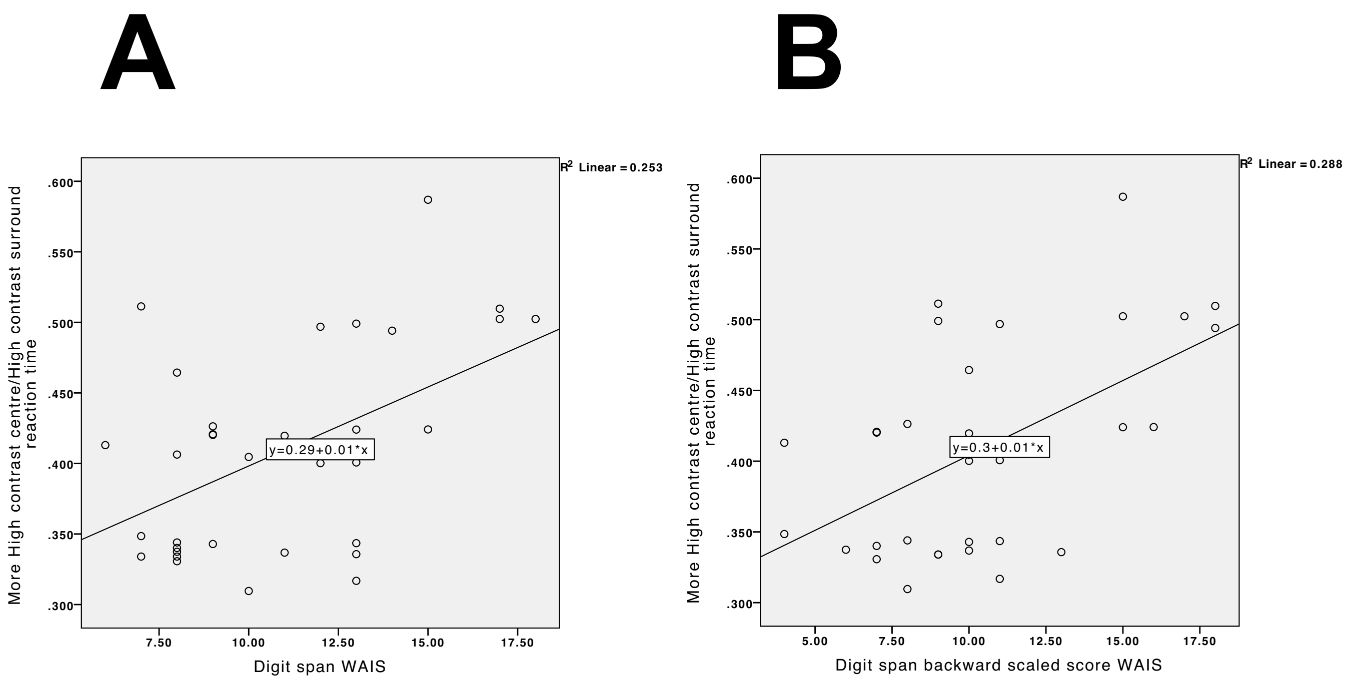



Figure 5.3.Scatter plots of correlations between WAIS-digit span and MEG surround-masking RTs. Correlations: A – Comparison judgment RT of more dots under high contrast centre/high contrast surround conditions and WAIS digit span total scaled score; B – Comparison judgment RT of more dots under high contrast centre/high contrast surround conditions and WAIS digit span backward scaled score. Note by the positive correlation that higher WAIS scores were associated with more delayed numerosity comparison RTs.

A more striking pattern emerged for the correlations between MEG surround-masking RTs and magnitude comparison RTs, where LLccLcs RTs was characterised by a significantly positive correlation between the magnitude comparison RTs of more than 55 with left arrow key press *(r(33)=.34, p=.02)*, and less than 55 with left arrow key press *(r(33)=.32, p=.03)*, meaning that observers with more delayed RTs during the comparison of fewer dots under low contrast centre/low contrast surround conditions, also had prolonged RTs for the magnitude comparison judgements of numbers more than 55 with left arrow (incongruent), and less than 55 with left arrow (congruent).

An opposite pattern emerged for the RTs of LHccHcs, characterised by a significantly negative correlation with all 4 magnitude comparison conditions including RTs for numbers more than 55 with right arrow key press *(r(33)=-.39, p=.01)*; numbers less than 55 with right arrow key press *(r(33)=-.35, p=.02)*; numbers more than 55 with left arrow key press *(r(33)=-.35, p=.02)*; and numbers less than 55 with left arrow key press *(r(33)=-.32, p=.03)*. It can be inferred from these significant correlations that observers with more delayed RTs during the comparison of fewer dots under high contrast centre/high contrast surround conditions had much faster RTs for all 4 magnitude comparison conditions. Please see figure 5.4 showing the strength of these correlations.

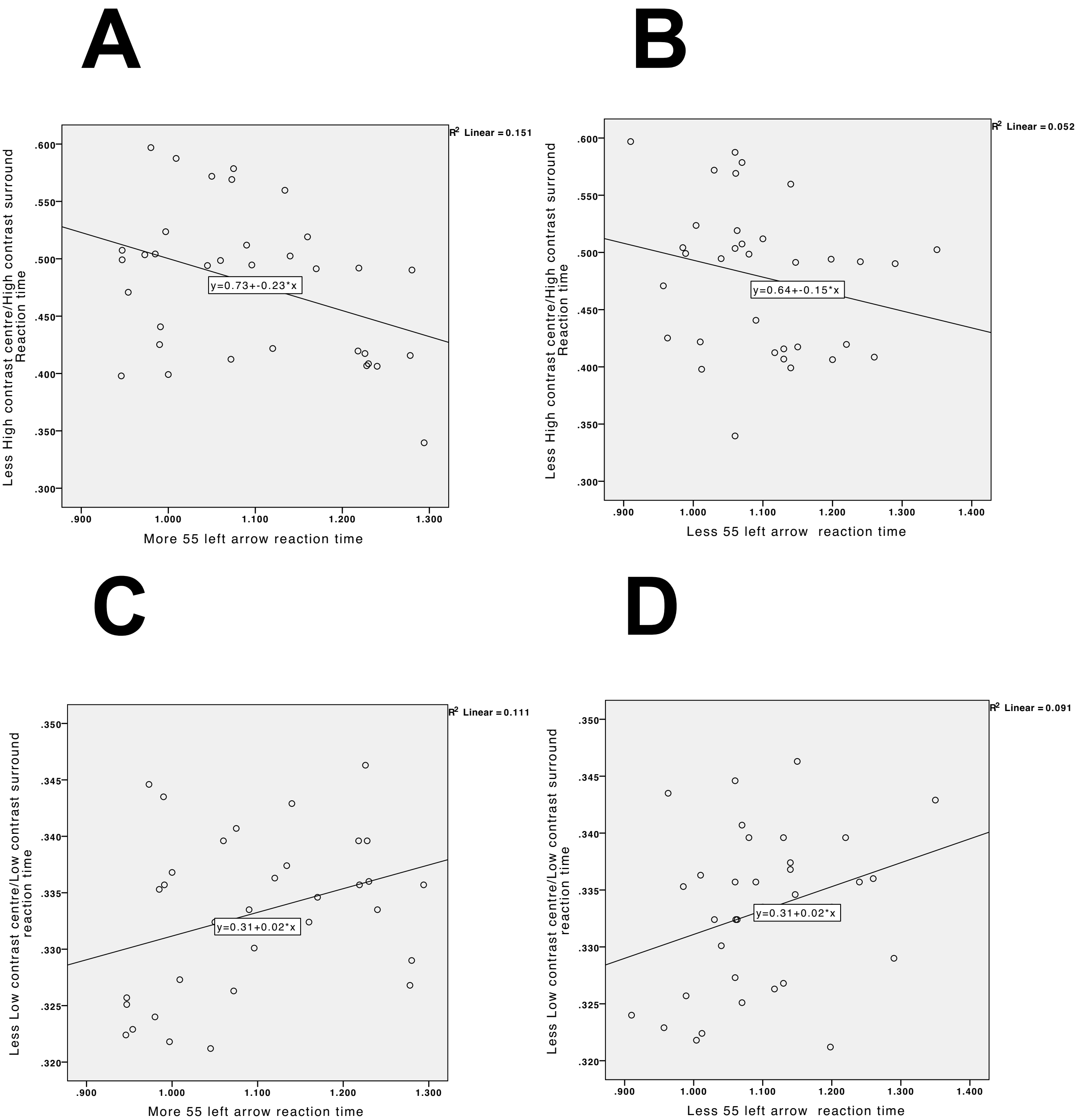



Figure 5.4. Scatter plots of correlations between magnitude comparison RTs and MEG surround-masking RTs. Note from panel A and panel B that the correlations between RTs for numerosity comparison judgements of fewer dots under high contrast centre/high contrast surround conditions (dependent variable) and magnitude comparison RTs (independent variable) were negative, which suggested that participants with faster magnitude comparison RTs were most adversely affected by the high contrast centre and surround conditions in the numerosity comparison of fewer dots. Panel C and panel D show a strikingly opposite effect, where the correlations between RTs for numerosity comparison judgements of fewer dots under low contrast centre/low contrast surround conditions (dependent variable) and magnitude comparison RTs (independent variable) were positive, which suggested that participants with slower magnitude comparison RTs were most adversely affected by the low contrast centre and surround conditions during the comparison of fewer dots.

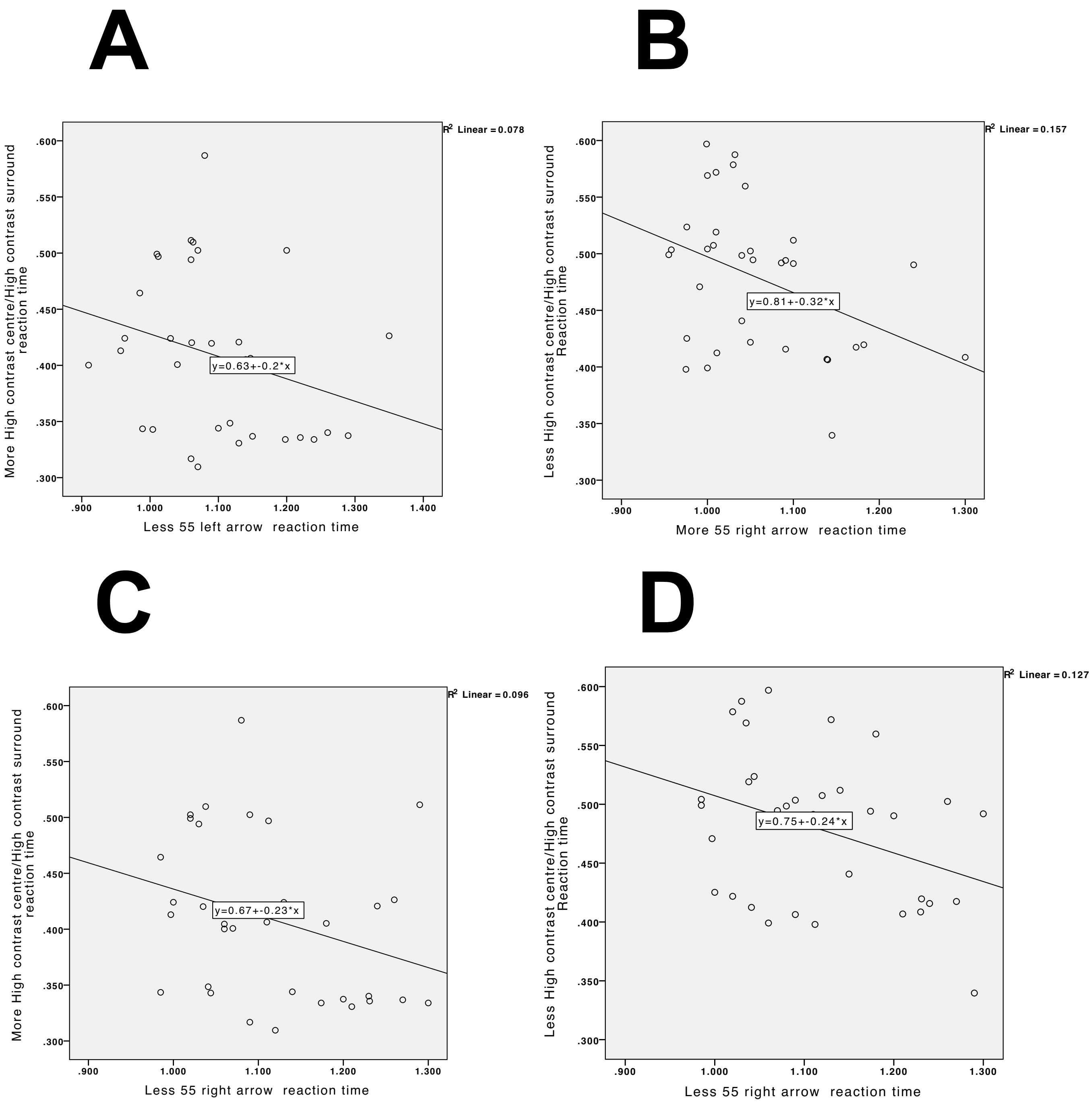



Figure 5.5. Scatter plots of correlations between magnitude comparison RTs and MEG surround-masking RTs. Dependent variables: Panel A – Comparison judgement RTs for more dots under high contrast centre/high contrast surround conditions; Panel B – Comparison judgement RTs for fewer dots under high contrast centre/high contrast surround conditions; Panel C – Comparison judgement RTs for more dots under high contrast centre/high contrast surround conditions; Panel D – Comparison judgement RTs for fewer dots under high contrast centre/high contrast surround conditions. It was apparent from all four panels that there was a negative correlation between numerosity comparison RTs under high contrast centre/high contrast surround conditions and magnitude comparison RTs. This suggested that participants with slower magnitude comparison RTs were faster when making numerosity comparison judgements under high contrast centre/high contrast surround conditions, meaning that participants with slower magnitude comparison RTs were uninfluenced by saturating effects of the high contrast stimuli.

The MHccHcs RTs were characterised by a significantly negative correlation between magnitude comparison RTs of numbers less than 55 with right arrow key press *(r(33)=-.34, p=.02)*; and numbers less than 55 with left arrow key press *(r(33)=-.30, p=.04)*, meaning that observers with more delayed RTs during the comparison of more dots under high contrast centre/high contrast surround conditions , had much quicker RTs for magnitude comparison judgements which required a left arrow key press. The scatterplots for these significant correlations can be seen within figure 5.5.

Finally, as seen from table 5.5, there were only 3 significant correlations between all 8 MEG surround-masking conditions, and both the true/false mathematical judgement task conditions. To elaborate, the LHccHcs RTs were characterised by a significantly positive correlation between accuracy scores for true/false judgements of addition/subtraction condition *(r(33)=.33, p=.02)* and multiplication/division condition *(r(33)=.39, p=.01)*, indicative that observers with higher accuracies for true/false judgements of addition/subtraction and multiplication/division conditions, had delayed RTs for comparison judgements of fewer dots during high contrast centre/high contrast surround conditions – please see figure 5.6 for scatterplots of these correlations. There was last of all a significantly positive correlation between MHccHcs RTs and true/false judgement scores of the multiplication/division condition *(r(33)=.32, p=.03)*, where higher accuracy scores for true/false judgements of multiplication/division mathematical problems were associated with delayed RTs during the comparison of more dots under high contrast centre/high contrast surround conditions.

Table 5.4. Table of correlations between MEG surround-masking RTs and True/false judgment scores

| | Correlation coefficients | |
|---|---|---|
| | **True/False: Addition/Subtraction** | **True/False: Multiplication/Division** |
| **Black centre** | | |
| Less dots high contrast surround | .33* | .39* |
| More dots high contrast surround | .19 | .32* |
| Less dots low contrast surround | -.07 | .07 |
| More dots low contrast surround | -.17 | -.18 |
| **Grey centre** | | |
| Less dots high contrast surround | -.01 | -.17 |
| More dots high contrast surround | -.14 | .03 |
| Less dots low contrast surround | -.10 | -.16 |
| More dots low contrast surround | .15 | -.01 |

Note: N=34, **p <.05, **p <.001, 1 tailed*

Overall, a consistent pattern emerged when MEG surround-masking RTs were correlated with WAIS sub-test scores, magnitude comparison RTs, and true/false judgement accuracy scores. In particular, MEG surround-masking RTs of high contrast centre/high contrast surround conditions appeared to most deleteriously impact the discrimination judgements of observers with good mathematical skills (e.g. negatively correlated with magnitude comparison RTs). Most curiously however, MEG surround-masking RTs for low contrast centre/low contrast surround conditions, appeared to have had the most adverse effect upon the numerosity comparison judgements from observers with delayed magnitude comparison RTs. It may be inferred that those with delayed RTs for magnitude comparison judgements also had lower mathematical skills.

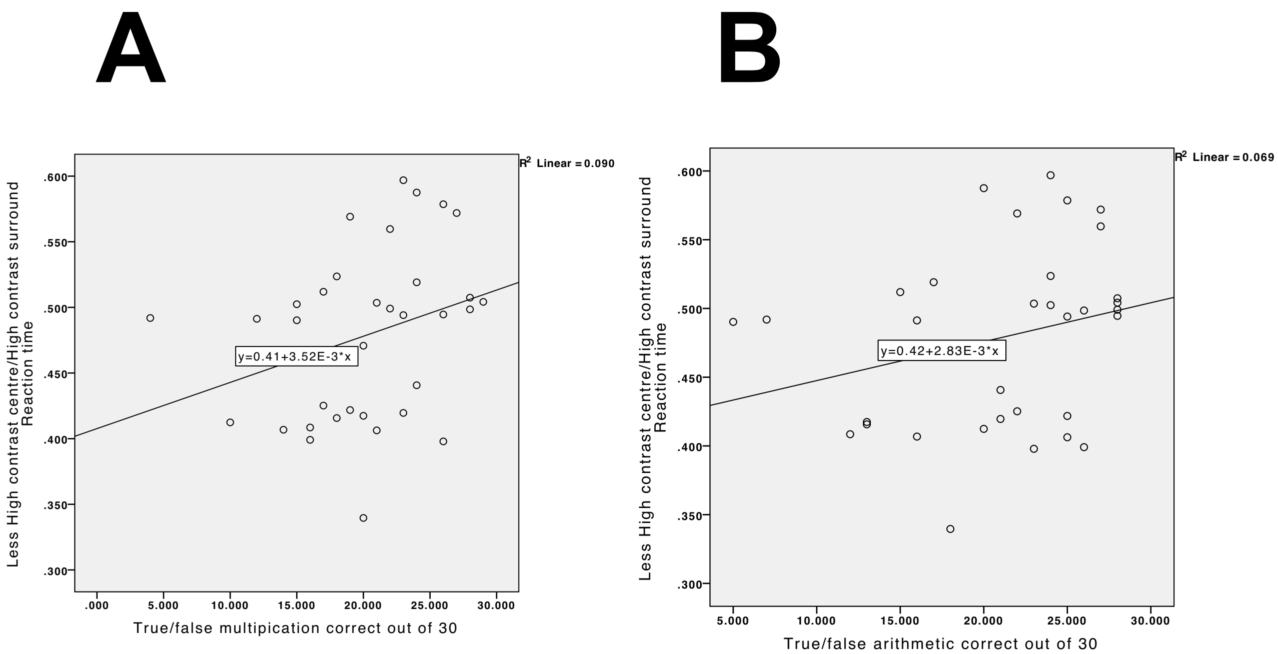



Figure 5.6.Scatter plots of correlations between true/false judgement scores and MEG surround-masking RTs. Panel A and panel B shows that the correlation between numerosity comparison RTs for fewer dots under high contrast centre/high contrast surround conditions (dependent variable), true/false multiplication (A), and true/false arithmetic (B) correct scores were positively correlated. This suggested that the higher true/false judgement scores were, the more disruptive the high contrast stimulus was in the comparison of fewer dots.

### 5.6.7. MEG surround-masking event related field (ERF) analysis

Analysis of the MEG evoked fields were performed by means of a within-groups (repeated measures) spatio-temporal permutation F-test in sensor space with magnetometers using MNE-Python version 0.9.0 software (Gramfort, et al., 2013). The analysis comprised of two main parts, where the first set of contrasts compared responses between ERFs for the onset of surround-annular stimuli (surround-mask only), and onset of the respective central stimulus. The second set of contrasts were a further investigation into the ERF response properties of the statistically significant differences between MEG surround-masking RTs as described by the paired t-tests in section 5.7.1.

The spatio-temporal permutation tests implemented here were corrected for multiple comparisons, and used the F-ratio as the statistical threshold by which compared conditions differed significantly in sensor space spatially and temporally. Spatio-temporal signatures above the F-threshold were formed into a cluster of sensors based on mean differences across conditions (Maris & Oostenveld, 2007). The non-parametric design of this spatio-temporal cluster test is ideal for MEG data –

with its high dimensionality and quite often non-gaussian distribution. Permutation tests as such are statistically robust to such violations (Maris & Oostenveld, 2007).

### 5.6.8. Surround mask and centre ERF contrasts

The surround-mask and central stimulus contrasts were performed in order to examine the likelihood of separate spatio-temporal clusters between sensory driven responses evoked by empty annular stimuli (surround-mask), and top-down responses induced by high-order processes involved with numerosity comparison judgements following onset of the central stimulus. All 8 of the contrasts were significantly different from one another, and will each be discussed in turn.

### 5.6.9. ERF contrasts: Black centre

The first comparison of mask and central ERFs was fewer dots with high contrast centre/high contrast surround (LHcsC: Less/High contrast surround Centre), and the empty high contrast surround-annulus that preceded it (LHcsM: Less/High contrast surround Mask). With an F-threshold of 15, there were 2 significant spatio-temporal clusters as seen in figure 2.15A and figure 2.15B *($p$=.01)*. The averaged F-map in figure 5.7A shows a cluster of significant sensors in left pre-frontal region of the head topology. The yellow band seen in the plot of averaged significant cluster time-courses shows that ERF contrasts between LHcsC and LHcsM were significantly different from 80ms to 151ms. Of particular interest was the negative ERF deflection at approximately 130ms following stimulus onset of the averaged cluster trace of LHcsC.

The second significant cluster that resulted from the LHcsC and LHcsM comparison (figure 5.7B) showed an averaged F-map with a cluster of significant sensors localised to the superior parietal (bi-lateral) region of the head topology. The yellow band within the time-course plots showed that the averaged cluster time-courses between LHcsC and LHcsM were significantly different from 166ms to 285ms. From appearance of the ERF trace average of significant parietal sensors there were 2 peak latencies within the LHcsC trace at around 170ms and 260ms and significantly greater in amplitude than the LHcsM trace.

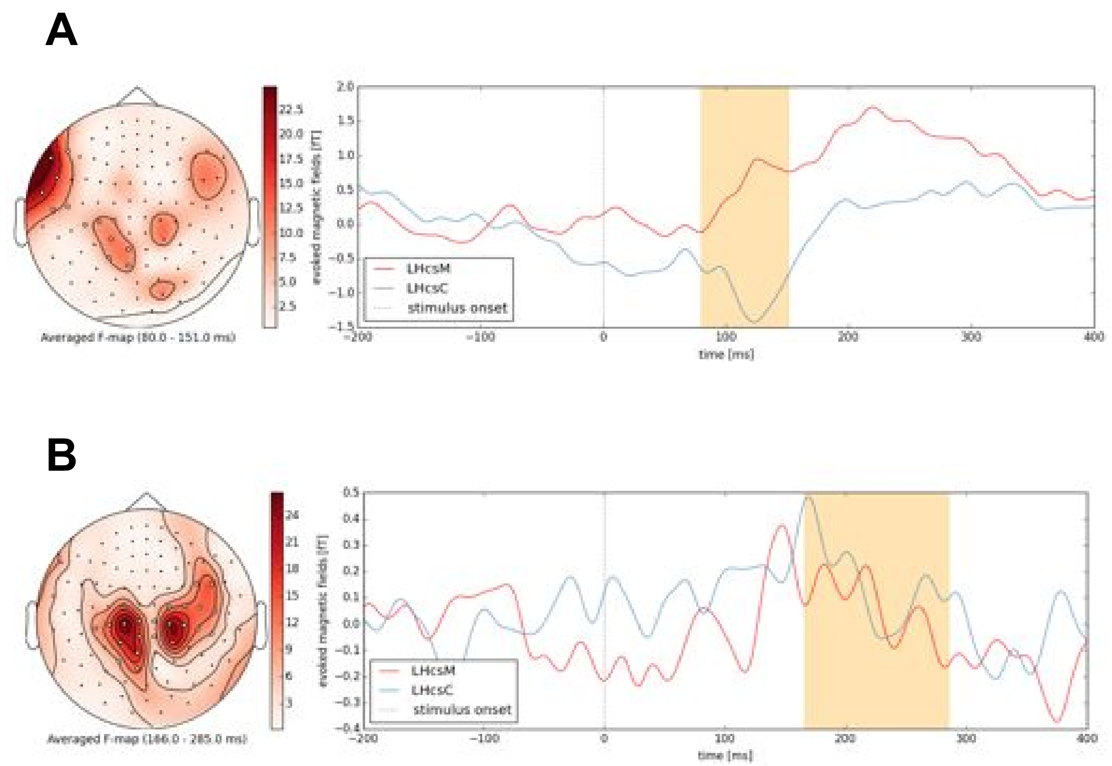



Figure 5.7.Averaged F-maps (left) and cluster time courses for within-group comparisons between surround and central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround mask with black centre for fewer dots (LHcsM); Blue ERF time-series: high contrast surround and high contrast centre with fewer dots (LHcsC). From panel A (cluster #1), it can be seen that the spatio-temporal cluster was localised to left pre-frontal regions of the sensor array. Of particular interest is the time-series of LHcsC, where a negative peak can be seen for this cluster approximately 130ms post stimulus onset. This was conjectured to reflect error-monitoring processes. Panel B (cluster #2) shows that the spatio-temporal cluster was localised within dorsal cingulate regions of the head topography. Dorsal cingulate cortex has been argued to regulate error prediction mechanisms (Luu & Tucker, 2003).

Figure 5.8 shows the 2D topographic field maps within the significant time window for cluster 1 (figure 5.7A). That is, the ERF time-courses for LHcsC and LHcsM compared against one another. For the field topographies of LHcsC, note the negative of electromagnetic dipole distribution around left pre-frontal sensors that peaked around 130ms, and were sustained until 140ms. The onset of superior parietal dipole for LHcsC trace occurred approximately 110ms and, peaked around 130ms. The electromagnetic field topographies for both LHcsC and LHcsM appear to be starkly different from one another, suggesting that there were feed-forward processes at play with the onset of the surround-annulus on its own, and top-down processes recruited with onset of the central stimulus.

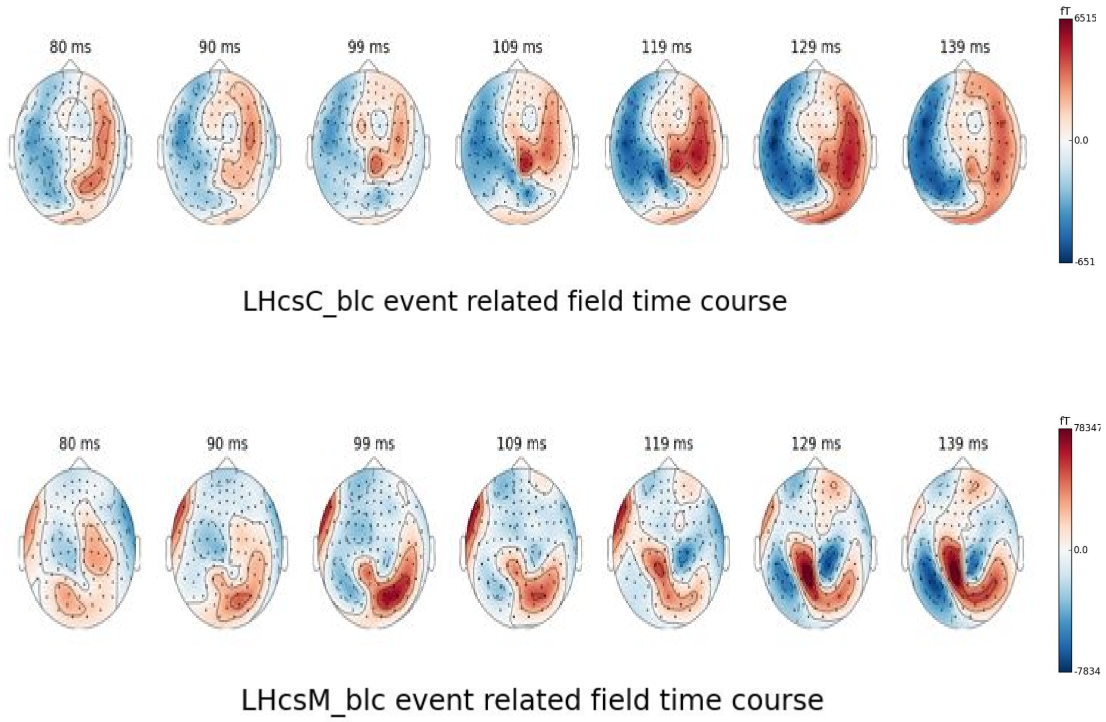



Figure 5.8.Topographic field maps of electromagnetic field responses from figure 5.7 (80ms to 140ms). From 119ms and onward, it can be seen that the differences between LHcsC and LHcsM 2D field distributions were striking. Note that at 129ms, the maximal response of LHcsC was characterised by a negativity distributed across left fronto-parietal regions of the sensor array. The negative peak amplitude at this time instant was greatest from two magnetometers situated at left pre-frontal areas, which supported the notion of a correct related negativity (CRN) type response during comparison of fewer dots under high contrast centre/high contrast surround conditions.

### 5.6.10. Fewer dots with high contrast centre/low contrast surround (LLcsC) and low contrast surround only (LLcsM) comparison

Figure 5.9 shows the averaged F-map with a cluster of significant sensors localised to right posterior parietal region of the head topology *(F-threshold=15, p=.01)*. The yellow band within their time-course plots showed that the averaged cluster time-course between LLcsC and LLcsM were significantly different from 186ms to 258ms. A negative deflection of the LLcsM and LLcsC trace can be seen from 220ms to 230ms, with the LLcsM peak latency (~130ms) being of significantly greater amplitude. Note the absence of spatio-temporal clusters of left pre-frontal sensors as observed from the LHcsC and LHcsM permutations (see figure 5.7). The absence of spatio-temporal clusters around left pre-frontal sensors for the LLcsC and LLcsM statistical contrast, suggests that on average, there was low demand for the allocation of attentional resources during numerosity comparison judgements of fewer dots in the presence of a low contrast surround.

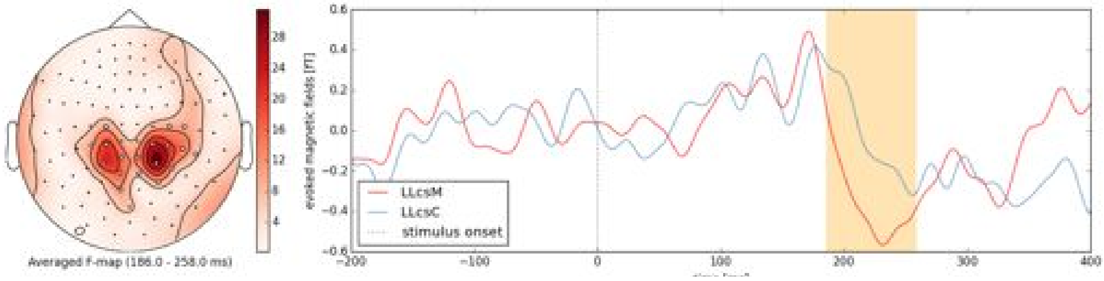



Figure 5.9.Averaged F-maps (left) and cluster time courses for within-group comparisons between surround only and centre/surround stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: low contrast surround mask with black centre for fewer dots (LLcsM); Blue ERF time-series: low contrast surround and high contrast centre with fewer dots (LLcsC). Note that the morphology of LLcsC and LLcsM time series are very similar to one another, only that the negative response peak of LLcsM dips more steeply than LLcsC at ~120ms. Also, the absence of pre-frontally located clusters was indicative that fewer attentional resources were recruited during the comparison of fewer dots under high contrast centre/low contrast surround conditions.

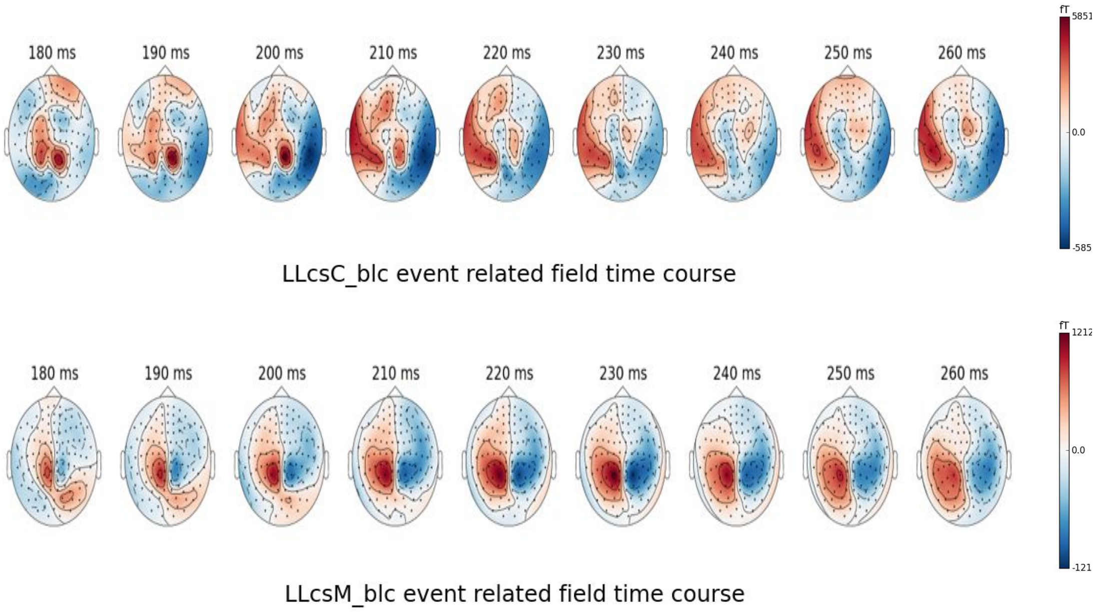



Figure 5.10.Topographic field maps of electromagnetic field responses from figure 5.9 (180ms to 260ms). The time windows of 2D field maps above (180ms to 260ms) were when LLcsC and LLcsM responses were significantly different from one another. Note that the electromagnetic field distribution across time for LLcsC was more complex than LLcsM. That is, the ERF responses for LLcsM appear to be stable across time, where a dipolar response can be seen within the superior parietal/dorsal cingulate region of the sensor array, which varied only in amplitude. In contrast to this, the ERF response distribution of LLcsC appears to be more variable across time, where electromagnetic fluctuations occurred in right posterior parietal and left pre-frontal regions of the sensor array.

Figure 5.10 shows the 2D topographic field maps within the significant cluster time window (186-258ms) of LLcsC and LLcsM ERFs. The most notable difference between these topographic maps is the variation in complexity of both the electromagnetic field distributions across time. Specifically, there is not much variation in the electromagnetic field dynamics across time for the LLcsM condition, where evoked responses following onset of the surround mask were typical of a single sustained parietal dipole that peaked from 210ms to 240ms. The electromagnetic field dynamics for the LLcsC condition however, were much more variable across time, where there was much more response variation in the ERF distribution following onset of the central stimulus region. These observations once again suggest that there were top-down processes involved with the onset of the central stimulus region, and respectively, low-order (sensory) processes involved with the onset of the surround-mask by its self.

### 5.6.11. More dots with high contrast centre/high contrast surround (MHcsC) and high contrast surround only (MHcsM)

The spatio-temporal permutations for the MHcsC and MHcsM contrast resulted in 4 significant clusters *(F-threshold=15, p=.001)*. The averaged F-map of cluster #1 (figure 5.11A) shows a cluster of significant sensors in left pre-frontal region of the head topology – not unlike the averaged F-map observed earlier in figure 5.7A. From the averaged cluster time course plots, it can be seen that MHcsC and MHcsM ERF traces were significantly from 59ms to 83ms. Once again, there was a negative ERF peak at approximately 120-130ms post-stimulus onset of the averaged left pre-frontal cluster trace of MHcsC. The second cluster that resulted from the MHcsC and MHcsM contrast (figure 5.11B) shows an averaged F-map with a cluster of significant sensors localised to the superior parietal (bi-lateral) region of the head topology. The yellow band within the time course plots show that the averaged cluster #2 time-course between MHcsC and MHcsM were significant from 121ms to 261ms. Within this time window, the averaged parietal cluster trace of MHcsM had a positive peak at around 150ms, and conversely, the MHcsC trace comprised a negative peak at the same time instant. The spatial localisation of this cluster group is not unlike the one observed in figure 5.7B (the LHcsC and LHcsM contrast).

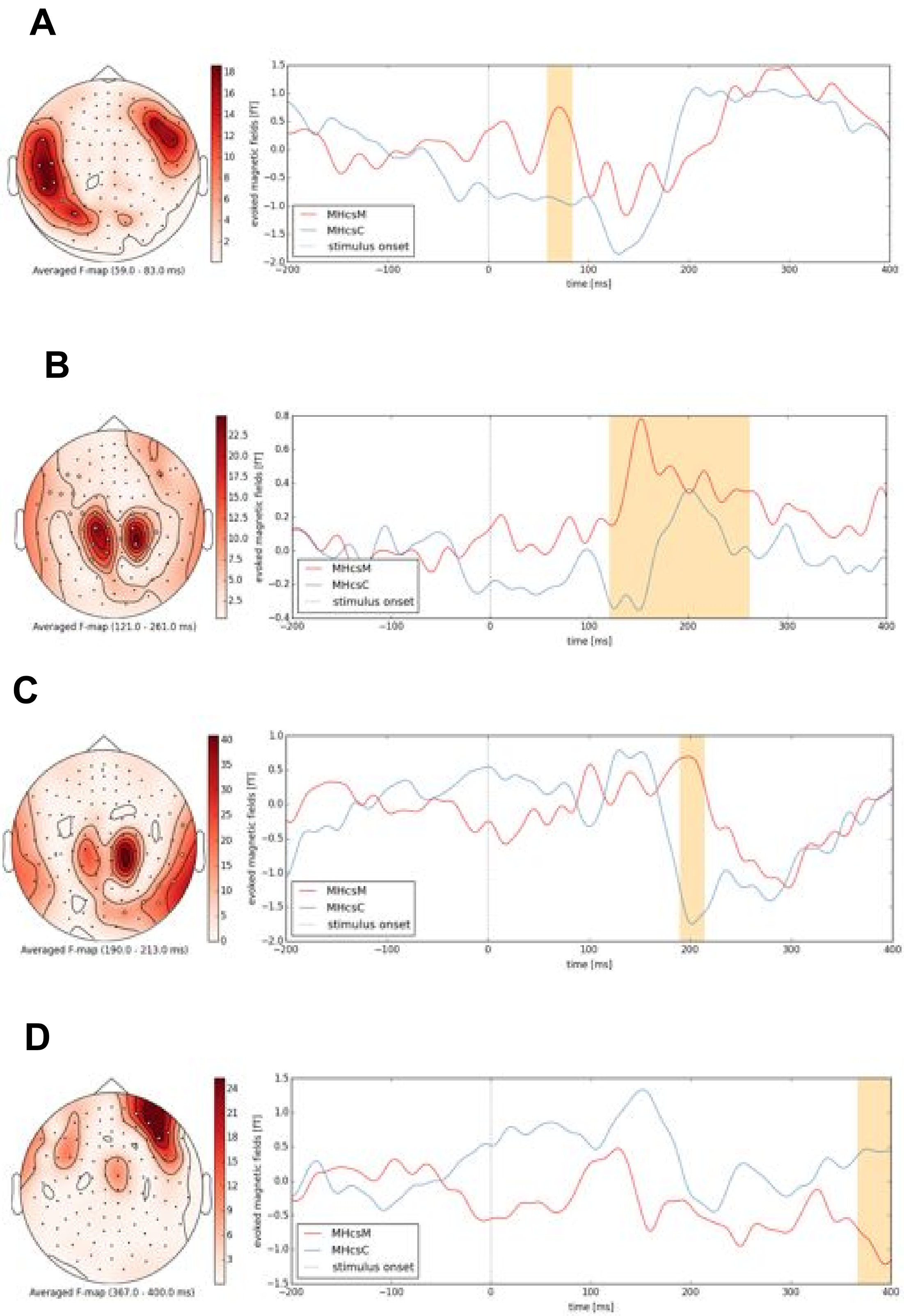



Figure 5.11.Averaged F-maps (left) and cluster time courses for within-group comparisons between surround and central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround mask with black centre for more dots (MHcsM); Blue ERF time-series: high contrast surround and high contrast centre with fewer dots (MHcsC). From panel A (cluster #1), it can be seen that the spatio-temporal cluster was localised to left pre-frontal regions of the sensor array. Of particular interest was the time-series of MHcsC, where there was a negative peak within this cluster approximately 130ms post stimulus onset. This once again, was likely to be a functional reflection of error prediction and monitoring (Holroyd & Coles, 2002).

The third significant cluster from the MHcsC and MHcsM comparison (figure 5.11C) shows an averaged F-map with a cluster of significant sensors localised to right temporal-parietal region of the head topology. The yellow band within the time course plots show that the averaged cluster #3 time-course between MHcsC and MHcsM were significantly different from 190ms to 213ms. Within this significant time window, the averaged right temporal-parietal cluster trace of MHcsC had a steep negative peak at 200ms, and conversely, the MHcsM trace comprised a positive peak at the same time instant. Finally, the fourth significant cluster from the MHcsC and MHcsM contrast (figure 5.11D) shows an averaged F-map with a cluster of significant sensors localised to the right pre-frontal region of the head topology. The yellow band within the time course plots show that the averaged cluster #4 time-course between MHcsC and MHcsM was significantly different from 367ms to 400ms. Within this significant time window, the averaged right pre-frontal cluster trace of MHcsM comprised a negative peak at around 390ms, where as the MHcsC trace appeared to be resting at about 0fT.

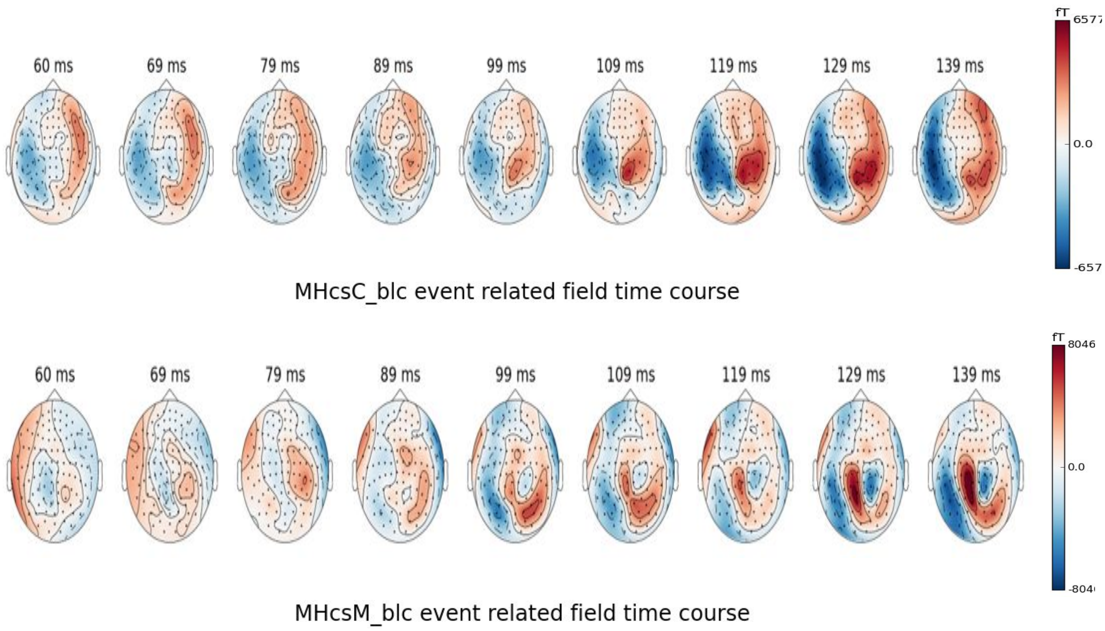



Figure 5.12.Topographic field maps of electromagnetic field responses from figure 5.11 (60ms to 140ms). The time windows of 2D field maps above (60ms to 140ms) were when MHcsC and MHcsM responses were significantly different from one another across all four clusters. The electromagnetic field distribution of the correct related negativity can be seen within the MHcsC time-series from 119ms to 139ms. This response profile was very similar to the one seen in figure 2.16 (LHcsC).

Figure 5.12 shows the topographic (2D) field maps from 60ms to 140ms of MHcsC and MHcsM ERF responses. For the field topographies of MHcsC, note once again the negative electromagnetic dipole distribution around left pre-frontal sensors that peaked around 130ms, and appeared to be sustained until 140ms. Just like the electromagnetic field distribution on LHcsC, a magnetic dipole was localised to superior parietal regions of the sensor topography, which onset around 100ms and peaked at around 130ms.

### 5.6.12. More dots with high contrast centre/low contrast surround (MLcsC) and low contrast surround only (MLcsM)

The spatio-temporal permutations for the MLcsC and MLcsM contrast resulted in 3 significant clusters *(F-threshold=15, p=.001)*. The averaged F-map of cluster #1 (figure 5.13A) shows a cluster of significant sensors in the right pre-frontal region. From the averaged cluster time course plots, it can be seen that MLcsC and MLcsM ERF traces were significantly different from 117ms to 180ms. Most noteworthy was the positive peak latency around 130ms found within the MLcsC ERF trace. Curiously, there appeared to be very little change in the ERF morphology of the MLcsM trace as compared to the baseline period. This observation suggests that the low contrast surround had little effect over higher order processes involved with the numerosity comparison of more dots in right pre-frontal regions.

The second significant cluster that resulted from the MLcsC and MLcsM contrast (figure 5.13B) shows the averaged F-map with a cluster of significant sensors localised to left superior parietal region. The yellow band within the time course plots showed that the averaged cluster #2 time-course between MLcsC and MLcsM were significantly different from 118ms to 149ms. Within this 30ms time window, the averaged parietal cluster trace of MLcsM had significantly greater ERF amplitude than the MLcsC trace. This time, it appeared there was very little change in the ERF morphology of MLcsC trace as compared to the baseline period. This might suggest that there were very few computational resources recruited in left superior parietal regions during the numerosity comparison of more dots in the presence of the low contrast surround, and instead, the wide surround of the low contrast annulus was likely to have had a facilitatory effect upon receptive fields.

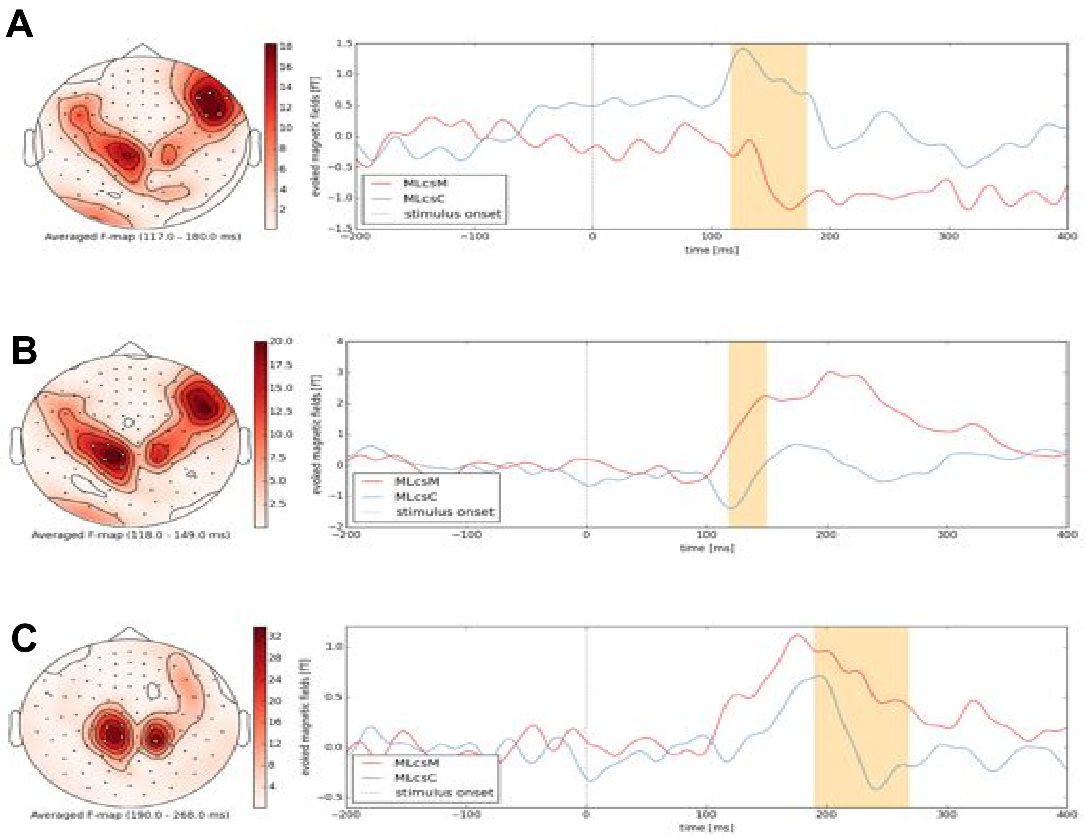



Figure 5.13. Averaged F-maps (left) and cluster time courses for within-group comparisons between surround and central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series (right): low contrast surround mask with black centre that preceded central stimuli with more dots (MLcsM); Blue ERF time-series: low contrast surround and high contrast centre with fewer dots (MLcsC). From panel A (cluster #1), it can be seen that the spatio-temporal cluster was localised to right fronto temporal region of the sensor array, which was likely to reflect the recruitment of entorhinal and para-hippocampal regions during short term recall of the reference set of dots (working memory). The time-series of cluster #1 shows a positive peak response approximately 130ms post-stimulus onset within the MLcsC trace, indicative of working memory processes.

The third significant cluster of the MLcsC and MLcsM contrast (figure 5.13C) shows the averaged F-map with a cluster of significant sensors localised to superior parietal (bi-lateral) regions. The yellow band within the time course plots show that the averaged cluster #3 time-course between MLcsC and MLcsM were significantly different from 190ms to 268ms. Within this 80ms time window, the averaged parietal cluster trace of MLcsM was again of significantly greater ERF amplitude than the MLcsC trace. Of particular interest was the steep negative peak of the MLcsC trace at around 250ms.

Figure 5.14 shows the 2D topographic field maps from 120ms to 200ms of MLcsC and MLcsM ERF responses. It was interesting to note from these comparisons that differences in latency for the onset of magnetic dipoles were localised within the same region of parietal sensors. To elaborate, from observation of the ERF time course of MLcsC, it can be seen that a magnetic dipole occurred within posterior parietal sensors from 120ms post central stimulus onset.

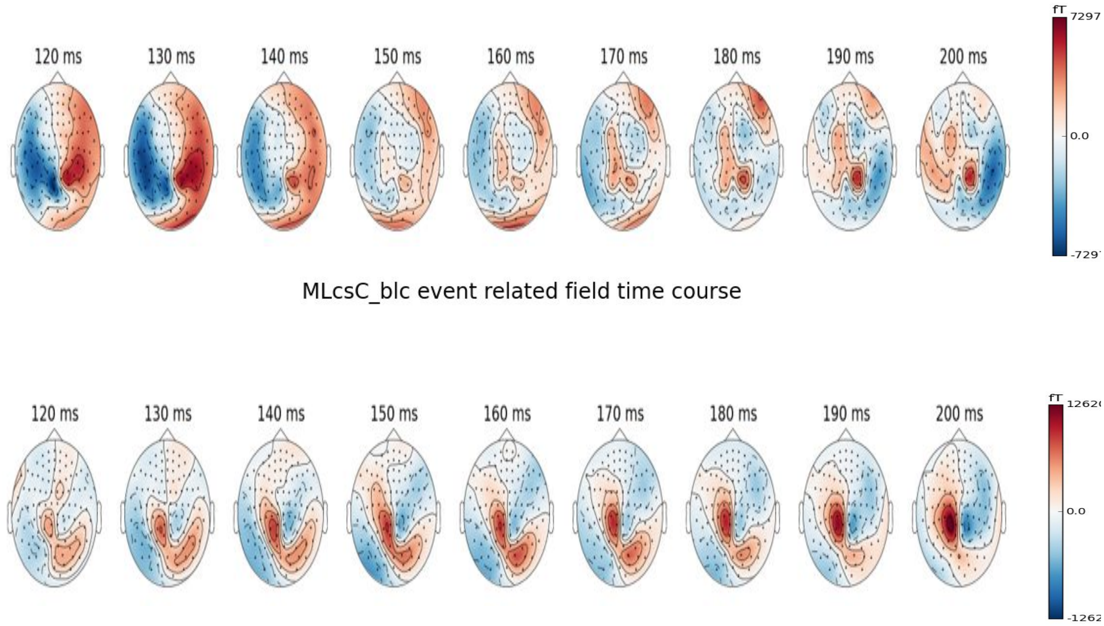



Figure 5.14.Topographic field maps of electromagnetic field responses from figure 5.13 (120ms to 200ms). The time windows of 2D field maps above (120ms to 200ms) were when MLcsC and MLcsM responses were significantly different from one another across all three clusters. An electromagnetic dipole can be seen within posterior parietal/dorsal cingulate regions of the MLcsC time course from 120ms to 130ms. It was likely that this particular response was a functional reflection of response monitoring and error prediction.

In contrast to this, there was also a posterior parietal dipole for ERFs of MLcsM, only that the peak response was from 160ms following the onset of this stimulus. The different time signatures of ERF peak responses contribute further evidence that there were independent cortical systems involved with the onset of surround-mask and the onset of the central stimulus region.

**ERF contrasts: Grey centre**

### 5.6.13. Fewer dots with low contrast centre/high contrast surround (LHcsC) and high contrast surround only (LHcsM)

The spatio-temporal permutations for the LHcsC and LHcsM contrast resulted in two significant clusters *(F-threshold=5, p=.02)*. The averaged F-map of cluster #1 (figure 5.15A) shows a cluster of significant sensors in left pre-frontal region. From the averaged cluster time course plots, it can be seen that LHcsC and LHcsM ERF traces were significantly different from 0ms to 204ms. Most noteworthy was the positive peak latency around 150ms of LHcsM trace. As for LHcsC, the averaged cluster ERF trace appeared to be well below zero and peaked positively at around 200ms.

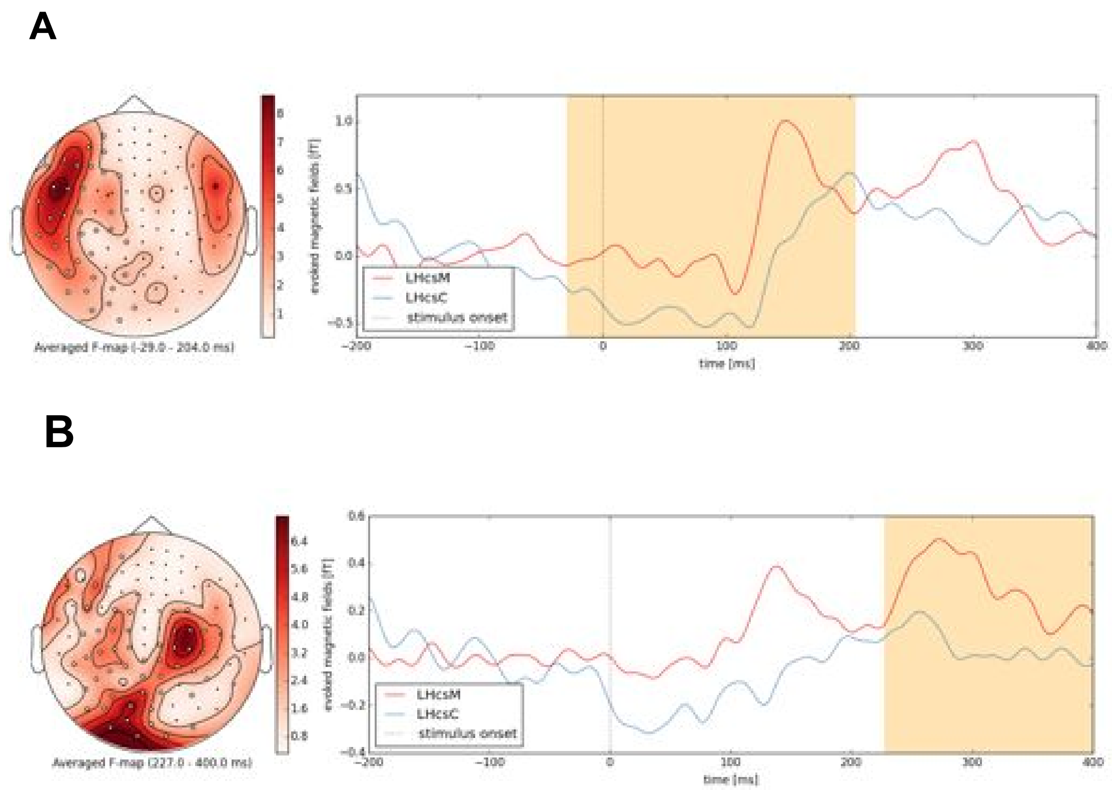



Figure 5.15. Averaged F-maps (left) and cluster time courses for within-group comparisons between surround and central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround mask with grey centre for fewer dots (LHcsM); Blue ERF time-series: high contrast surround and low contrast centre with fewer dots (LHcsC). From panel B (cluster #2), it can be seen that the spatio-temporal cluster was localised to the left occipital region of the sensor array. The spatial localisation of this cluster was possibly generated by the low contrast central region, which had a facilitatory effect upon excitatory regions of RFs in LGN and V1 (Carandini, 2004).

This particular spatio-temporal cluster profile appears to be in stark contrast to those of high contrast centre/high contrast surround, where it would seem counter intuitively that the high contrast surround had an effect upon the recruitment of high-order attentional processes.

The second significant cluster that resulted from the LHcsC and LHcsM comparison (figure 5.15B) shows the averaged F-map with a cluster of significant sensors localised to occipital and right superior parietal regions. The yellow band within the time course plot show that the averaged cluster #2 time-course between LHcsC and LHcsM were significantly different from 227ms to 400ms. Within this time window, the averaged occipital-parietal cluster trace of LHcsM was of significantly greater amplitude than the LHcsC trace. The averaged cluster amplitude of LHcsC was once again resting at approximately 0fT, indicative that there were fewer computational resources recruited during the numerosity comparison of fewer dots during low contrast centre/high contrast surround conditions. It appeared that the high contrast surround was overriding the ERFs from the LHcsC trace however.

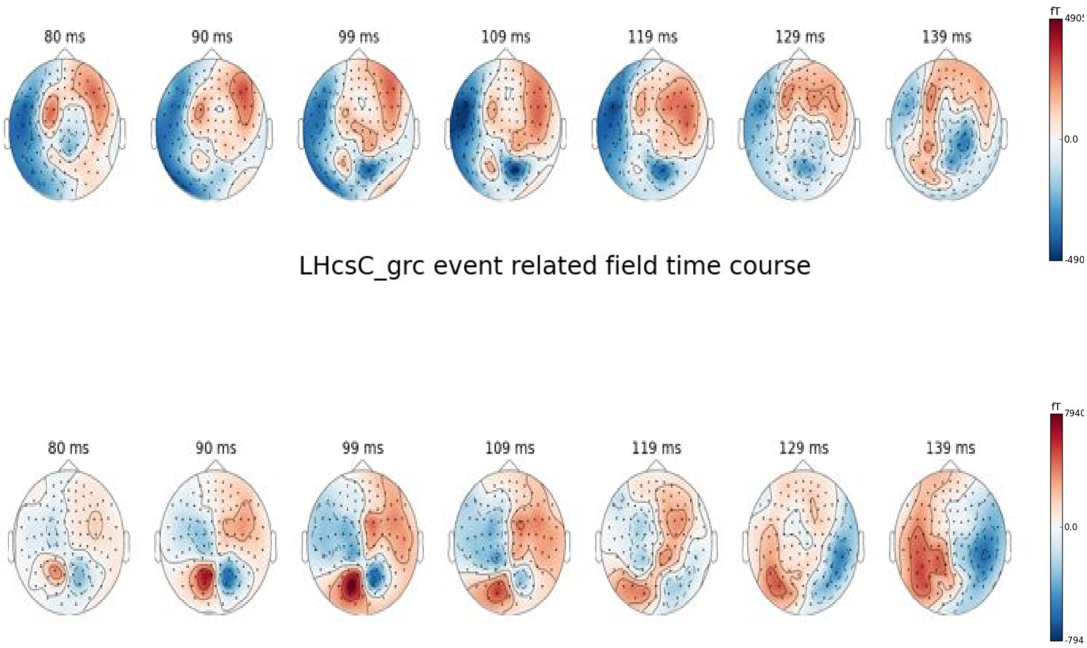


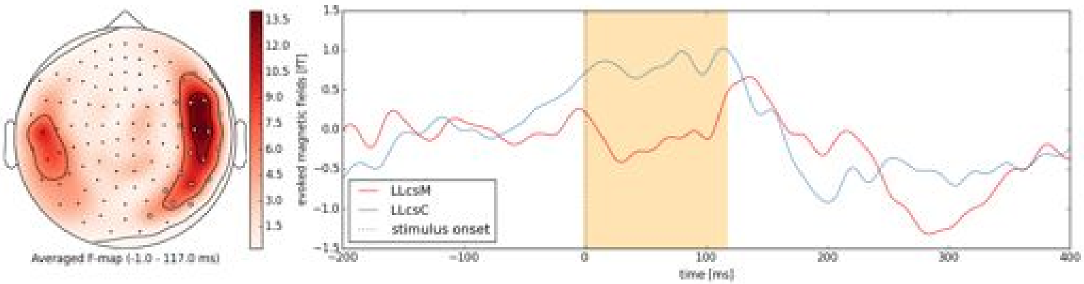

Figure 5.16.Topographic field maps of electromagnetic field responses from figure 5.15 (80ms to 139ms). The time windows of 2D field maps above (80ms to 139ms) were when LHcsC and LHcsM responses were significantly different from one another.

Figure 5.16 shows the 2D topographic field maps from 80ms to 140ms of LHcsC and LHcsM ERF responses. For the field topographies of LHcsC, note the negative electromagnetic dipole distribution of left pre-frontal sensors, which peaked around 110ms then disappeared around 120ms. Upon comparison of the 2D topographic field maps of black centre LHcsC (figure 5.8), it was evident that this left pre-frontal ERF negativity was associated with the high contrast surround, however for the ERFs of grey centre LHcsC, the ERF negativity peak response was markedly earlier (~110ms) than the black centre LHcsC (~130ms). The comparison of these ERF time signatures indicated that the low contrast central stimulus had a facilitative effect upon the ability to make numerosity comparison judgements of fewer dots in the presence of a high contrast surround.

### 5.6.14. Fewer dots with low contrast centre/low contrast surround (LLcsC) and low contrast surround only (LLcsM)

The spatio-temporal permutations for the LLcsC and LLcsM contrast resulted in two significant clusters *(F-threshold=5, p=.02)*. The averaged F-map of cluster #1 (figure 5.17A) shows a cluster of significant sensors in right frontal-temporal regions of the head topology. From the averaged cluster time course plots, it can be seen that LLcsC and LLcsM ERF traces were significantly different fro 0ms to 117ms. Within this time window, the cluster ERF trace of LLcsC was of significantly greater amplitude than the LLcsM ERF, where the trace appeared to be resting at around 0fT for the duration of the significant time window (yellow band). This early ERF response within the frontal-temporal cluster average of LLcsC was likely to have been a functional reflection of recruitment of working memory following onset of the second set of dots (see figure 5.4 for trial sequence) in order to make numerosity comparisons.

A




B

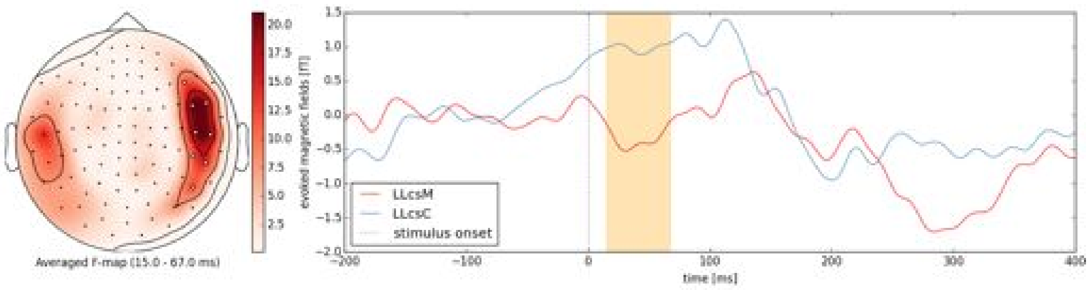



Figure 5.17.Averaged F-maps (left) and cluster time courses for within-group comparisons between surround and central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: low contrast surround mask with grey centre for fewer dots (LLcsM); Blue ERF time-series: low contrast surround and low contrast centre with fewer dots (LLcsC). In comparison to figure 2.15 (LHcsC and LHcsM black centre), it can be seen that the time window to which LLcsC and LLcsM responses were significantly different from one another were earlier. That is, ERF responses during numerosity comparison judgments of fewer dots under low contrast centre /low contrast surround conditions, occurred substantially earlier than those under high contrast centre/high contrast surround conditions.

The second significant cluster that resulted from LLcsC and LLcsM comparisons (figure 5.17B) shows the averaged F-map with once again, a cluster of significant sensors in right frontal-temporal regions of the head topology. The yellow band within the time course plots show that the averaged cluster #2 time-course between LLcsC and LLcsM were significantly different from 15ms to 67ms. The ERF traces of LLcsC and LLcsM appeared to be almost identical to those in cluster #1, only the significant time window was substantially narrower with a slightly later onset (15ms). The only difference was that for cluster #2 of the LLcsC and LLcsM contrast, there were fewer significant sensors. That is, the lateral-occipital sensors within cluster #2 were no longer significant.

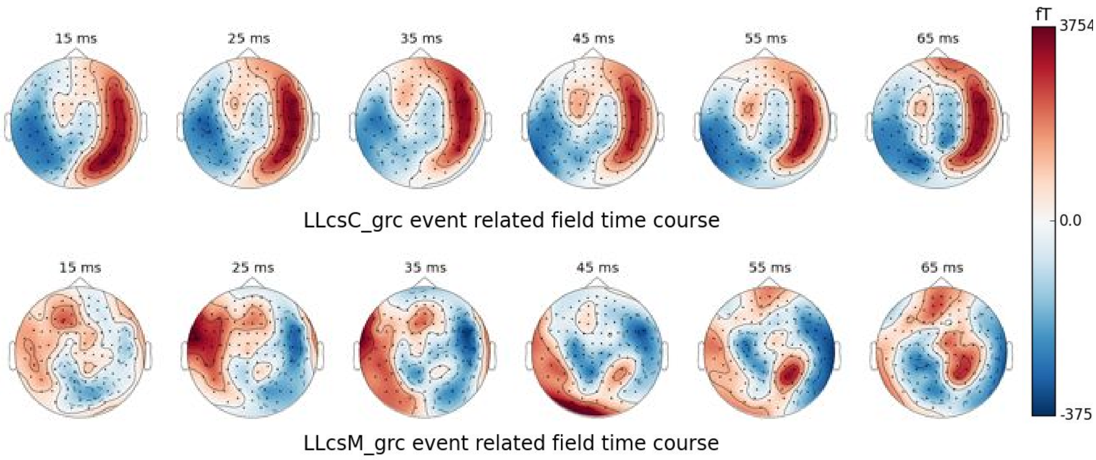



Figure 5.18.Topographic field maps of electromagnetic field responses from figure 5.17 (15ms to 65ms). The time windows of 2D field maps above (15ms to 65ms) were when LLcsC and LLcsM responses were significantly different from one another.

Figure 5.18 shows the 2D topographic field maps from 15ms to 65ms of LLcsC and LLcsM ERF responses. For the field topography of LLcsC, observe the positive electromagnetic field distribution over the right side of the head map. Note that there was a slight spatial shift across time of the peak response amplitude for this positive evoked field, where at 15ms, the LLcsC peak response was localised to right lateral-occipital sensors, and shifted anteriorly toward frontal-temporal sensors at 35ms. The spatial and temporal signatures of ERF field distributions for LLcsC and LLcsM were markedly distinct from one another. The LLcsM ERF maps showed a high amplitude positive peak response at 45ms within occipital sensors, indicative of RF facilitation evoked by the low contrast centre and low contrast surround conditions.

### 5.6.15 .More dots with low contrast centre/high contrast surround (MHcsC) and high contrast surround only (MHcsM)

The spatio-temporal permutations for the MHcsC and MHcsM contrast resulted in two significant spatio-temporal clusters *(F-threshold=5, p=.02)*. The averaged F-map of cluster #1 (figure 5.19A) showed a cluster of significant sensors in left frontal-parietal regions of the head map. From the averaged cluster time course plots, it can be seen that MHcsC and MHcsM ERF traces were significantly different from 164ms to 243ms. Within this time window, there was a positive peak within the averaged cluster trace of MHcsC at approximately 200ms post stimulus onset. In contrast to this, a negative peak within the averaged cluster trace of MHcsM occurred at approximately the same time. As earlier discussed, the positive peak latency within the MHcsC trace of the left frontal parietal cluster average was possibly a functional reflection of enhanced numerosity comparison judgments that were facilitated by the grey central stimulus background.

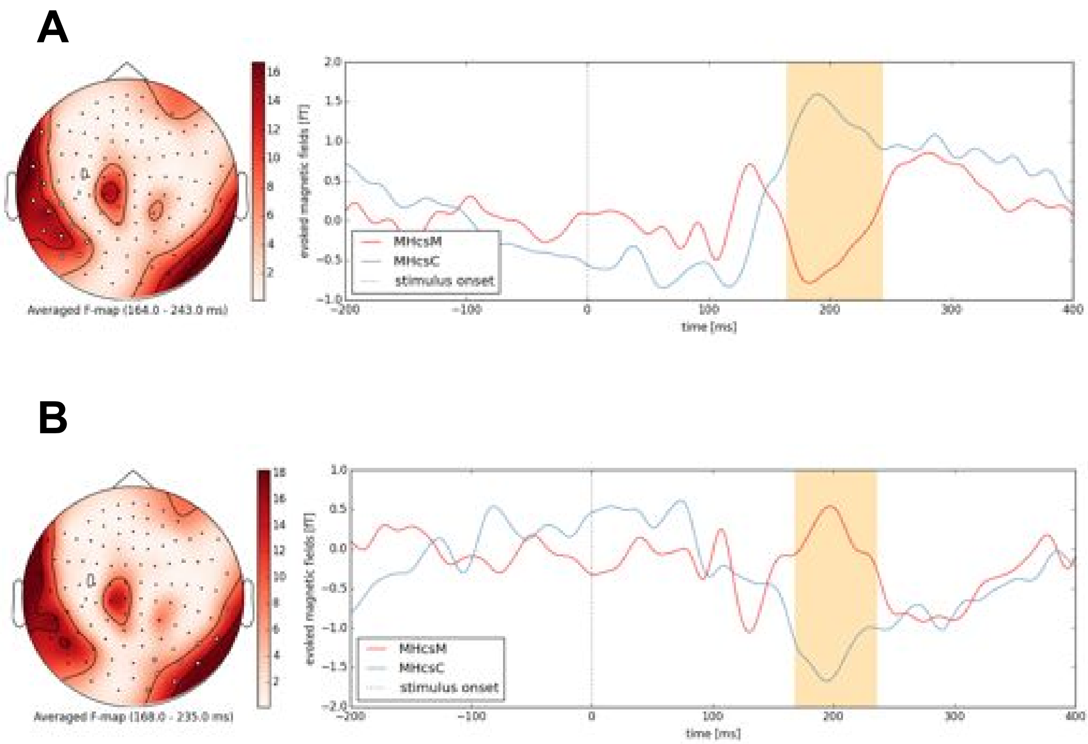



Figure 5.19. Averaged F-maps (left) and cluster time courses for within-group comparisons between surround and central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround mask with grey centre for more dots (MHcsM); Blue ERF time-series: high contrast surround and low contrast centre with more dots (MHcsC). Note that once again, the ERF responses for low contrast centre/high contrast surround conditions resulted in the localisation of significant clusters to occipital regions of the sensor array. Specifically, it can be seen from panel B that the ERF trace of MHcsM occipital cluster comprised of a positive peak response ~200ms post-stimulus onset.

The second significant cluster that resulted from the MHcsC and MHcsM comparison (figure 5.19B) shows the averaged F-map with a cluster of significant sensors in right occipital-parietal regions of the head map. From the averaged cluster time course plots, it can be seen that cluster #2 MHcsC and MHcsM ERF traces were significantly different from 168ms to 235ms. Compellingly, an inverse type pattern emerged for the peak latencies of MHcsM and MHcsC occipital-parietal cluster averages, where the 200ms peak response of MHcsM was positive, and the respective peak response within MHcsC cluster trace was negative at 200ms. It is worth noting that the ERF peak responses observed in cluster A and cluster B both occur at 200ms and possess an almost identical averaged cluster trace and time window of significance.

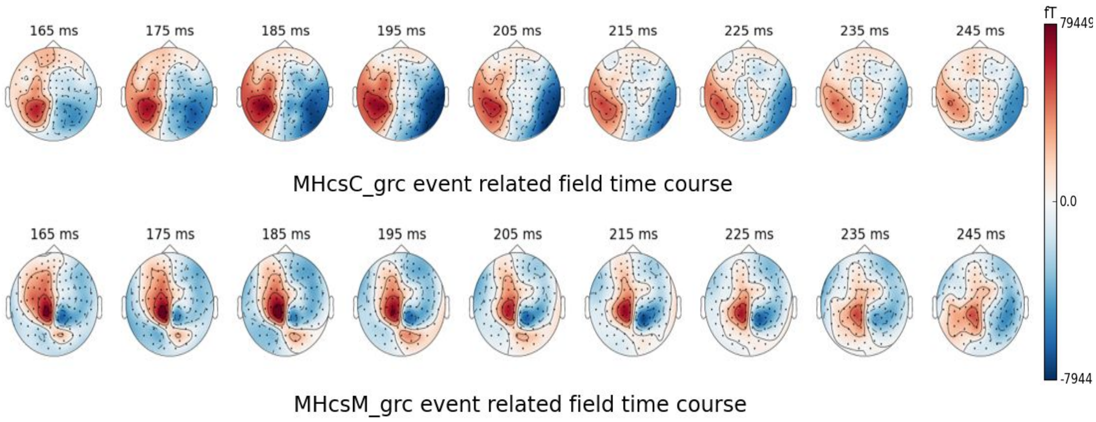



Figure 5.20.Topographic field maps of electromagnetic field responses from figure 5.19 (165ms to 245ms). The time windows of 2D field maps above (165ms to 245ms) were when MHcsC and MHcsM responses were significantly different from one another.

Figure 5.20 shows the topographical field maps from 165ms to 245ms of MHcsC and MHcsM ERF responses. Note for the MHcsC ERF time course maps, there was a positive peak response distributed across left frontal-parietal sensors from approximately 185ms to 200ms. It may be inferred from this particular response that the ability to make numerosity comparison judgements of more dots under high contrast surround conditions, was enhanced or facilitated by the grey background (low contrast) of the central stimulus. That is not to say that the high contrast surround did not impair numerosity comparison judgements of more dots that with low contrast/grey central stimulus region. However, it was conceivable that the high contrast surround did not hinder the recruitment of high-level mechanisms of attentional enhancement.

### 5.6.16. More dots with low contrast centre/low contrast surround (MLcsC) and low contrast surround only (MLcsM) comparison

The spatio-temporal permutations for the MLcsC and MLcsM contrast resulted in two significant clusters *(F-threshold=10, p=.01)*. The averaged F-map of cluster #1 (figure 5.21A) showed a cluster of significant sensors in left temporal-parietal regions of the head map. From the averaged cluster time course plots, it can be seen that MLcsC and MLcsM ERF traces were significantly different from 141ms to 243ms. Within this time window, the signal amplitude of MLcsC averaged cluster was markedly higher than MLcsM. It can be inferred from this observation that, within left temporal-parietal regions of the cortex, there were high-order processes recruited during the numerosity comparison of more dots under low contrast surround conditions, and the surround mask on its own did not elicit a response within this cortical region.

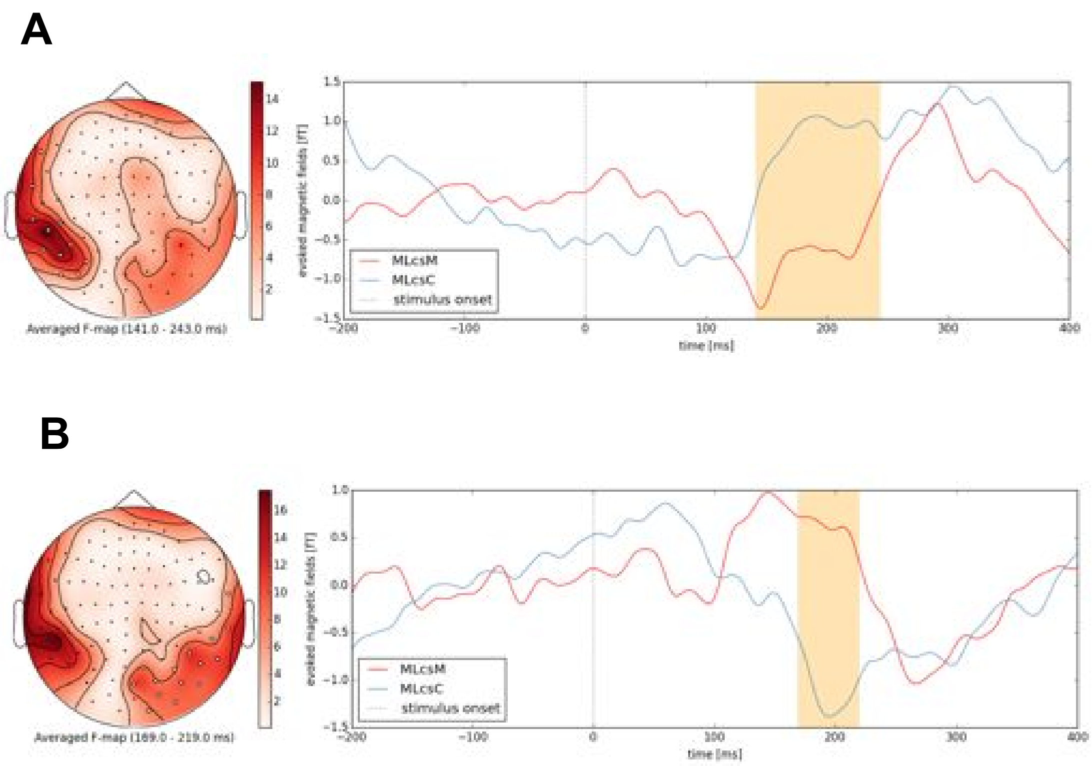



Figure 5.21. Averaged F-maps (left) and cluster time courses for within-group comparisons between surround and central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: low contrast surround mask with grey centre for more dots (MLcsM); Blue ERF time-series: low contrast surround and low contrast centre with more dots (MLcsC).

The second significant cluster that resulted from the MLcsC and MLcsM comparison (figure 5.21B) shows the averaged F-map with a cluster of significant sensors in right temporal-parietal regions of the head map. From the averaged cluster time course plots, it can be seen that cluster #2 MLcsC and MLcsM ERF traces were significantly different from 169ms to 219ms. Within this 50ms time window, the averaged cluster of MLcsC comprised a negative peak at approximately 200ms. In contrast, the response amplitude of MLcsM was positively over 0fT, comprised of a peak response between 100ms and 270ms. These observations indicated that the low contrast surround on its own elicited a positive ERF response within right temporal-parietal regions of the cortex.

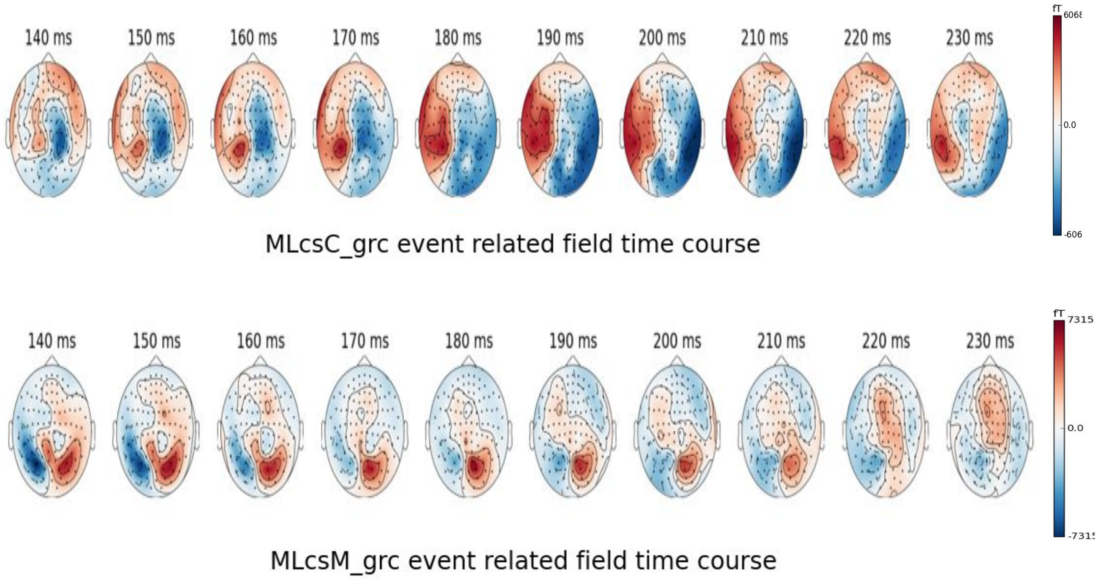



Figure 5.22.Topographic field maps of electromagnetic field responses from figure 5.21 (140ms to 230ms). The time windows of 2D field maps above (140ms to 230ms) were when MLcsC and MLcsM responses were significantly different from one another.

Figure 5.22 shows the topographical field maps from 140ms to 230ms of MLcsC and MLcsM ERF responses. Note that the evoked ERF responses elicited by MLcsM, peaked at around 140-150ms, as evidenced by the occipital-parietal dipole within the specified time window. In contrast to this, the ERF responses that were induced by MLcsC peaked at around 190ms to 200ms, as evidenced by the positive ERF distribution of left temporal-parietal sensors. There was a very obvious difference here, in terms of the electromagnetic response properties involved with sensory processing (MLcsM) and high-order cognitive functions (MLcsC). It may be speculated overall that the low contrast surround was likely to have recruited the mechanisms involved with attentional enhancement, as evidenced by the positive ERF distribution observed in frontal-temporal sensors for MLcsC ERFs.

### 5.6.17. Central stimulus ERF contrasts

Part two of the surround-masking MEG analysis comprised spatio-temporal permutation tests of ERFs following onset of the central stimulus region within the surround-annulus. These statistical contrasts examined differences in the electro-magnetic response properties from the statistically significant paired t-tests implemented earlier on MEG surround-masking RTs (see section 4.8.6). To recapitulate, of the 16 paired t-tests performed on MEG surround-masking RTs, six of them were non-significant. Here, the same statistical contrasts were performed using the spatio-temporal permutation test to examine the electromagnetic response characteristics of significant paired t-tests performed on MEG surround-masking RTs. Of the 10 spatio-temporal cluster tests performed, 7 of them were statistically significant. Each of the significant spatio-temporal cluster tests will be discussed in turn.

### 5.6.18 Uniform centre-surround contrast comparisons

The first two spatio-temporal permutation tests compared differences in ERF response properties between high contrast centre/high contrast surround and low contrast centre/low contrast surround conditions. The spatio-temporal permutation tests for the first contrast – fewer dots with high contrast centre/high contrast surround (LHcsC_blc) and fewer dots with low contrast centre/low contrast surround (LLcsC_grc) resulted in one significant cluster of sensors *(F-threshold=5, p=.03)*. The averaged F-map as shown in figure 5.23

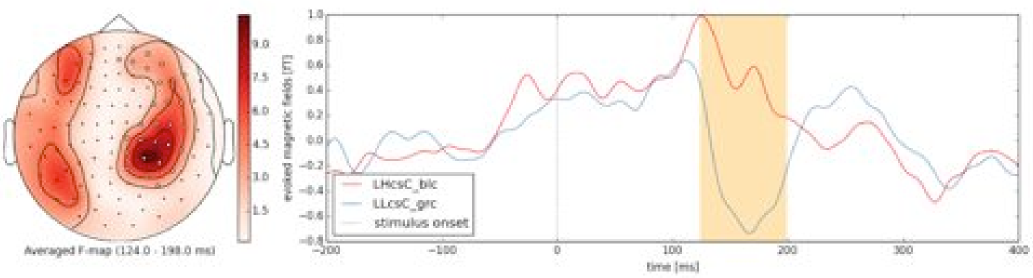



Figure 5.23.Averaged F-maps (left) and cluster time courses for within-group comparisons between central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround/high contrast centre with fewer dots (LHcsC_blc); Blue ERF time-series: low contrast surround/low contrast centre with fewer dots (LLcsC_grc).

revealed that the significant cluster of sensors was localised to right posterior-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that LHcsC_blc and LLcsC_grc ERF traces were significantly different from 124ms to 198ms. Within this significant time window, the averaged right posterior-parietal cluster trace of LHcsC_blc was characterised by 2 positive amplitude peaks at 125ms and ~160ms. Conversely, the LLcsC_grc trace comprised of one negative peak at ~160ms.

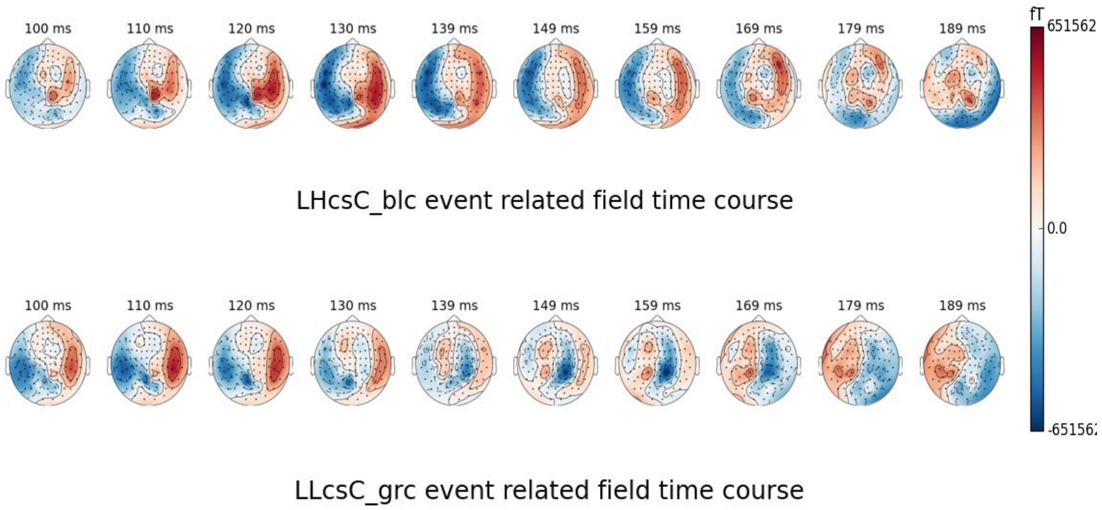



Figure 5.24.Topographic field maps of electromagnetic field responses from figure 5.23 (100ms to 189ms). The time windows of 2D field maps above (100ms to 189ms) were when LHcsC_blc and LLcsC_grc responses were significantly different from one another.

Figure 5.24 shows the 2D topographic field maps from 100ms to 189ms of LHcsC_blc and LLcsC_grc ERF responses. For the field topographies of LLcsC_grc, observe the negative polarity of ERF peaks from 149ms to 159ms localised to right posterior-parietal sensors. Of further interest was the higher response amplitude of positive ERF responses for LHcsC_blc, localised to right frontal-parietal sensors at 130ms as compared to LLcsC_grc responses. These differences in response amplitudes were likely to be a functional reflection of increased attentional load imposed upon observers during the numerosity comparison of fewer dots under high contrast centre and high contrast surround conditions.

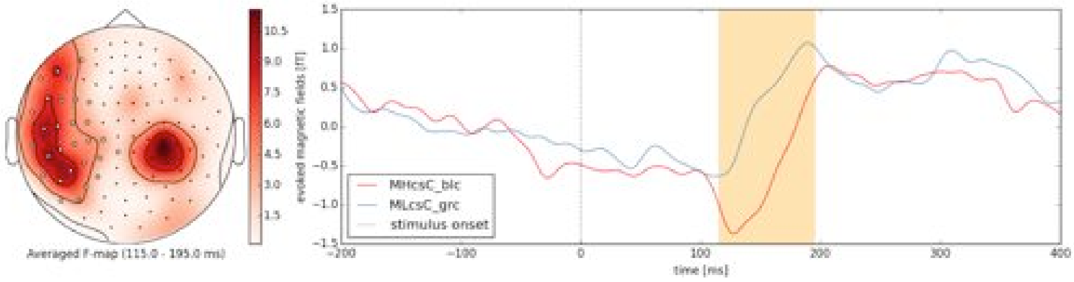



Figure 5.25. Averaged F-maps (left) and cluster time courses for within-group comparisons between central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround/high contrast centre with more dots (MHcsC_blc); Blue ERF time-series: low contrast surround/low contrast centre with more dots (MLcsC_grc). Note from the averaged F-map that one cluster of significant sensors was distributed across left fronto-parietal regions of the array. Of particular interest was the negative peak response within the ERF trace of MHcsC_blc ~130ms post-stimulus onset. As postulated earlier from within group comparisons between surround only and central stimuli with surround (section 4.8.14), this negative peak response was likely to be a functional reflection of decisional uncertainty, error prediction, and response monitoring (Luu & Tucker, 2003; Holroyd & Coles, 2002).

The spatio-temporal permutation tests for the second contrast – more dots with high contrast centre/high contrast surround (MHcsC_blc) and more dots with low contrast centre/low contrast surround (MLcsC_grc) resulted in one significant cluster of sensors *(F-threshold=5, p=.03)*. The averaged F-map as shown in figure 5.25 revealed that the significant cluster of sensors were localised to left frontal-temporal regions of the sensor array. From the averaged cluster time course plots, it can be seen that MHcsC_blc and MLcsC_grc ERF traces were significantly different from 115ms to 195ms. Within this significant time window, the averaged left frontal-temporal cluster trace of MHcsC_blc was characterised by a negative peak latency at ~130ms, and conversely, the MLcsC_grc cluster trace comprised of a positive peak response at around 190ms.

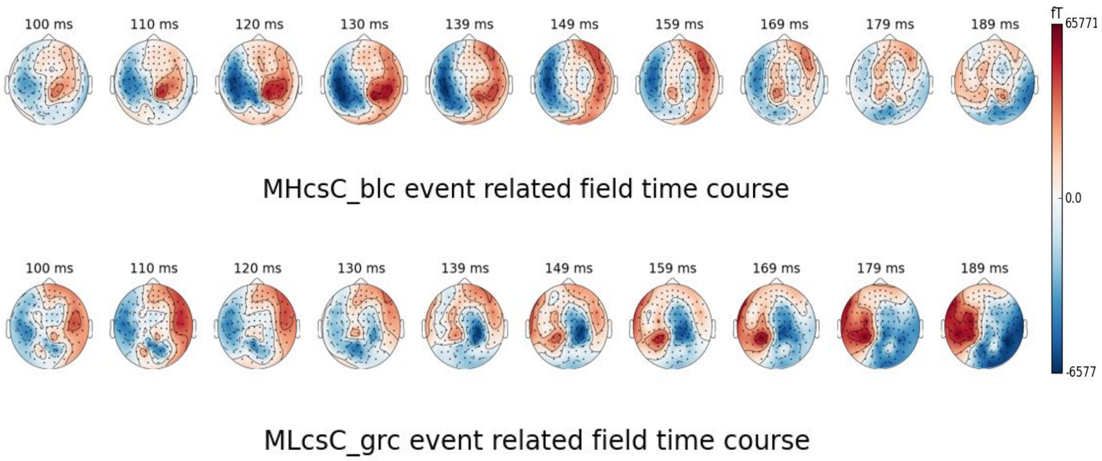



Figure 5.26.Topographic field maps of electromagnetic field responses from figure 5.25 (100ms to 189ms). The time windows of 2D field maps above (100ms to 189ms) were when MHcsC_blc and MLcsC_grc responses were significantly different from one another. Compellingly, a polarity reversal of MHcsC_blc and MLcsC_grc peak responses can be seen at 130ms and 190ms respectively.

Figure 5.26 shows the 2D topographic field maps from 100ms to 189ms of MHcsC_blc and MLcsC_grc ERF responses. Note that at 130ms for the field maps of MHcsC_blc, there was a distributed negative polarity response across left frontal-parietal sensors. Respectively, at 190ms the field maps of MLcsC_grc were comprised of distributed positive polarity responses at the same region of the sensor array. These distinct ERF response signatures across left frontal-parietal sensors between MHcsC_blc and MLcsC_grc were indicative that the centre-surround contrast of the stimulus display had an effect upon the ability to make numerosity comparison judgements of more dots at the high-order attentional level, and not just at the sensory level as earlier postulated.

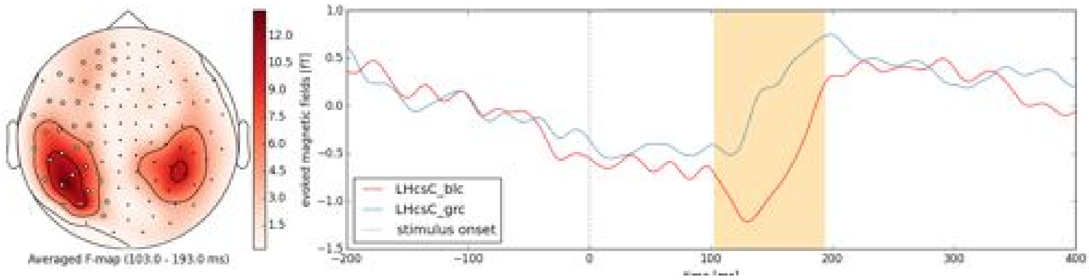
### 5.6.19. Centre contrast effects

The next 3 spatio-temporal permutation tests compared differences of ERF response properties for central stimulus contrasts, holding constant surround contrast. The effect of central stimulus contrasts were examined separately, given that it was found earlier from the MEG surround-masking RT t-tests that central stimulus contrast had the strongest effect upon numerosity comparison judgements, and not the surround-mask exclusively (see sections 4.8.8 and 4.8.9).

The spatio-temporal permutation tests for the third contrast – fewer dots with low contrast centre/high contrast surround (LHcsC_grc) and LHcsC_blc resulted in two significant sensor clusters *(F-threshold=5, p=.02)*. The averaged F-map as shown in figure 5.27A shows a cluster of significant sensors within left temporal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that LHcsC_blc and LHcsC_grc ERF traces were significantly different from 103ms to 193ms. Within this significant time window, the averaged left temporal-parietal cluster trace of LHcsC_blc comprised of a negative peak response at ~130ms post-stimulus onset. The averaged cluster trace of LHcsC_grc on the other hand, was characterised by a positive peak response at around 190ms.

The second significant cluster that resulted from the LHcsC_blc and LHcsC_grc contrast (figure 5.27B) shows an averaged F-map with a cluster of significant sensors localised approximately to right temporal-parietal region of the head map. The yellow band within the time course plot shows that the averaged cluster #2 time course between LHcsC_blc and LHcsC_grc were significantly different from 121ms to 217ms. Within this significant time window, the averaged right temporal-parietal cluster trace of LHcsC_blc comprised of a positive peak response approximately 130ms post-stimulus onset. The averaged cluster trace of LHcsC_grc on the other hand, was characterised by a later negative peak response at approximately 190ms.

A




B

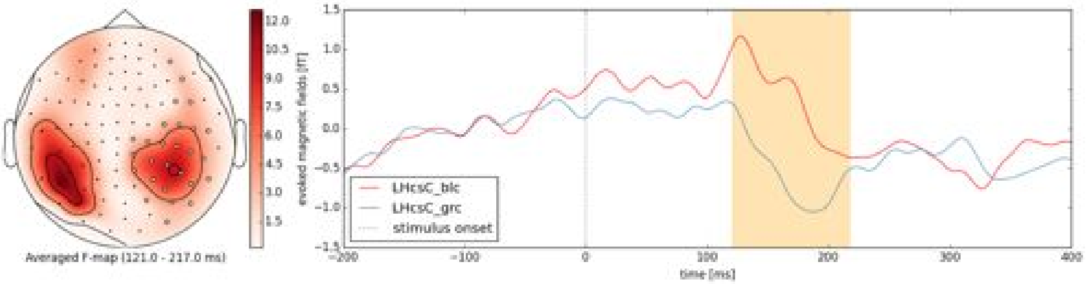



Figure 5.27.Averaged F-maps (left) and cluster time courses for within-group comparisons between central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround/high contrast centre with fewer dots (LHcsC_blc); Blue ERF time-series: high contrast surround/low contrast centre with fewer dots (LHcsC_grc). Panel A shows a similar spatio-temporal cluster profile to that of figure 2.33, with a negative peak response of the left fronto-parietal cluster time-series of LHcsC_blc at 130ms. This suggests that it was the high contrast centre that had a disruptive effect upon numerosity comparison mechanisms.

Figure 5.28 shows the 2D topographic field maps from 100ms to 190ms of LHcsC_blc and LHcsC_grc ERF responses. At 130ms of the LHcsC_blc ERF plots, the negative peak response of the averaged left temporal-parietal (cluster #1) trace can be seen in 2D as the sink region of a posterior-parietal dipole field. At 190ms of the LHcsC_grc ERF plots, the positive peak response of the averaged right temporal-parietal (cluster #2) trace can be seen as the source region of the field within the same location.

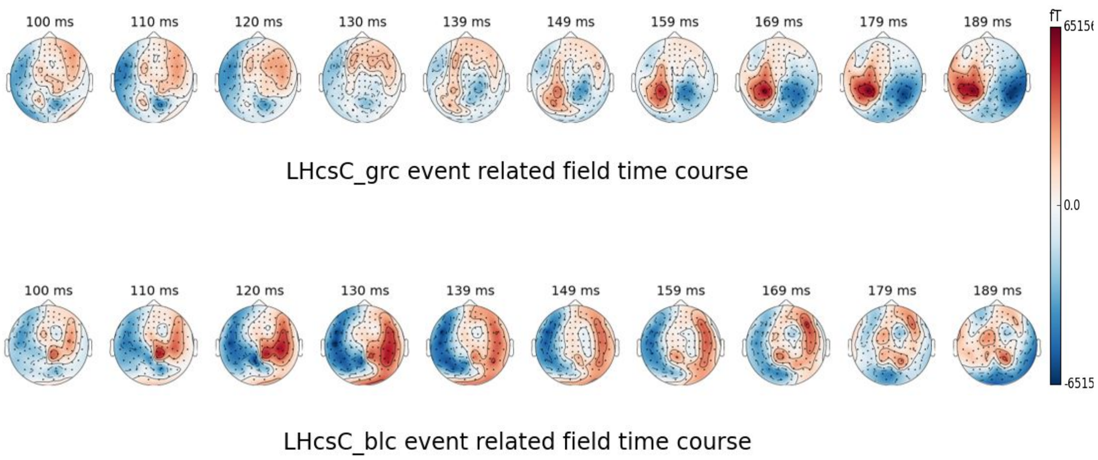



Figure 5.28.Topographic field maps of electromagnetic field responses from figure 5.27 (100ms to 189ms). The time windows of 2D field maps above (100ms to 189ms) were when LHcsC_grc and LHcsC_blc responses were significantly different from one another. The same polarity reversal seen in figure 2.35 of MLcsC_grc and MHcsC_blc peak responses can once again be seen at 130ms and 190ms respectively.

The spatio-temporal permutation tests for the fourth contrast – more dots with low contrast centre/high contrast surround (MHcsC_grc) and more dots with high contrast centre/high contrast surround (MHcsC_blc) resulted in two significant sensor clusters *(F-threshold=5, p=.02)*. The averaged F-map as shown in figure 5.29A, shows a cluster of significant sensors within right temporal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that MHcsC_blc and MHcsC_grc ERF traces were significantly different from 112ms to 210ms. Within this significant time window, the averaged right temporal-parietal cluster trace of MHcsC_blc was characterised by a positive peak response at ~130ms post-stimulus onset. The averaged cluster trace of MHcsC_grc on the other hand, was characterised by a negative peak response at around 190ms.

The second significant cluster that resulted from the MHcsC_blc and MHcsC_grc contrast (figure 5.29B) shows an averaged F-map with a cluster of significant sensors localised to left temporal-parietal region of the sensor array. The yellow band within the time course plot shows that the averaged cluster #2 time courses between MHcsC_blc and MHcsC_grc were significantly different from 119ms to 196ms. Within this time window of significance, the averaged left temporal-parietal cluster trace of MHcsC_blc comprised a negative peak response approximately 130ms post-stimulus onset. The averaged cluster trace of MHcsC_grc on the other hand, was characterised by a later positive peak response at approximately 190ms.

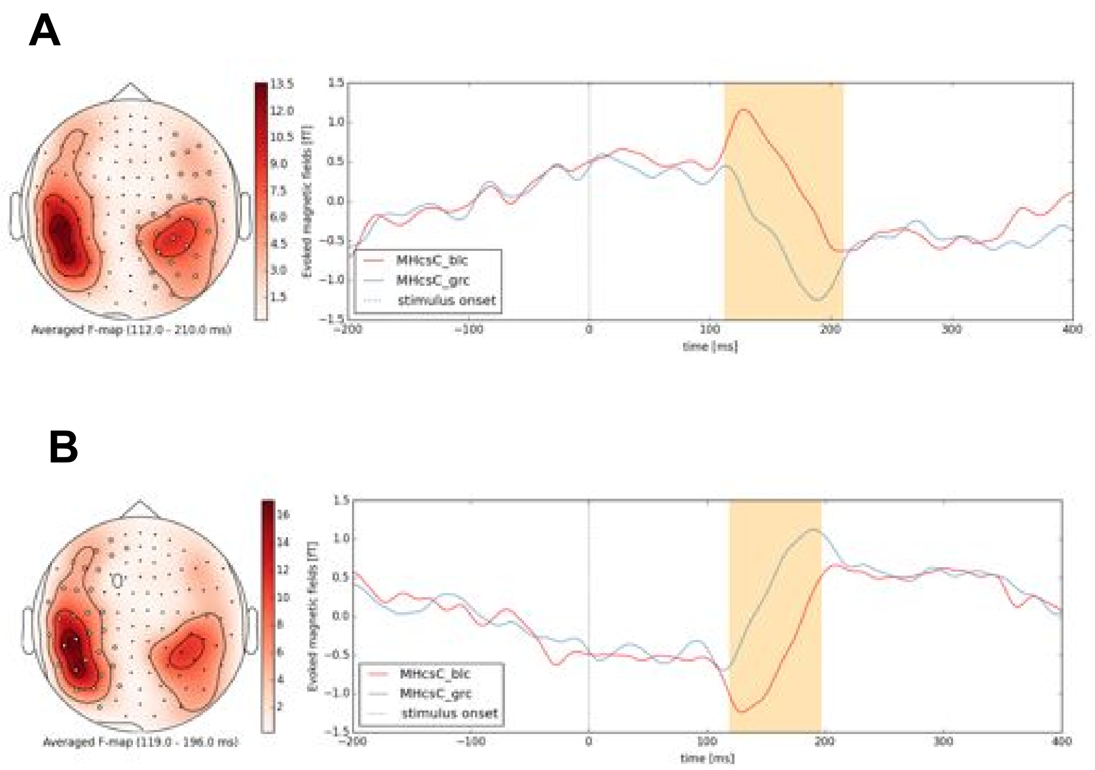



Figure 5.29. Averaged F-maps (left) and cluster time courses for within-group comparisons between central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround/high contrast centre with more dots (MHcsC_blc); Blue ERF time-series: high contrast surround/low contrast centre with more dots (MHcsC_grc). Panel B shows a similar spatio-temporal cluster profile to that of figure 2.35A, with a negative peak response of the left fronto-parietal cluster time-series of MHcsC_blc at 130ms. This once again suggests that it was the high contrast centre that had a disruptive effect upon numerosity comparison mechanisms rather than the high contrast surround.

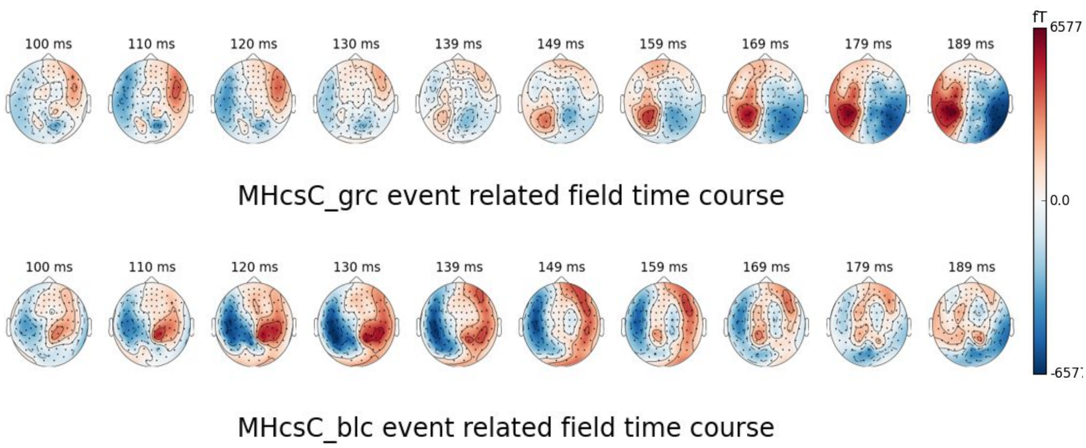



Figure 5.30.Topographic field maps of electromagnetic field responses from figure 5.29 (100ms to 189ms). The time windows of 2D field maps above (100ms to 189ms) were when MHcsC_grc and MHcsC_blc responses were significantly different from one another. The same polarity reversal seen in figure 2.37 of LHcsC_grc and LHcsC_blc peak responses can once again be seen at 130ms and 190ms respectively.

Figure 5.30 shows the 2D topographic field maps from 100ms to 190ms of MHcsC_blc and MHcsC_grc ERF responses. Almost identically to the ERF distribution of LHcsC_blc, at 130ms post-stimulus onset, the ERF distribution of

MHcsC_blc showed a diffuse negative peak response (dipole sink) across left temporal-parietal regions of the sensor array. At 190ms of the MHcsC_grc ERF plots, the positive peak response of the averaged left temporal parietal cluster #2 trace can be seen as the source region of a dipole field that was localised to posterior-parietal regions of the sensor array.

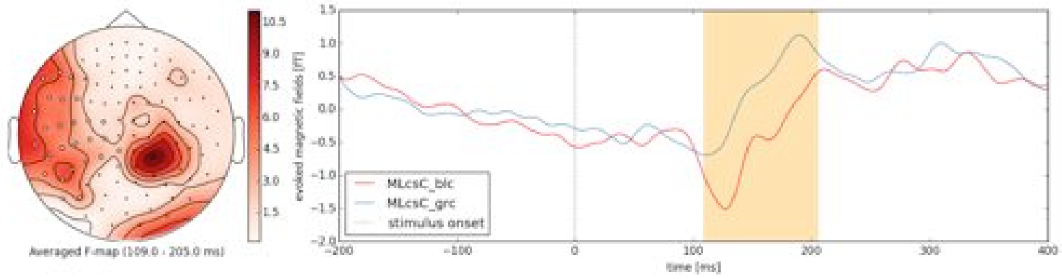



Figure 5.31. Averaged F-maps (left) and cluster time courses for within-group comparisons between central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: low contrast surround/low contrast centre with more dots (MLcsC_blc); Blue ERF time-series: low contrast surround/low contrast centre with more dots (MLcsC_grc).

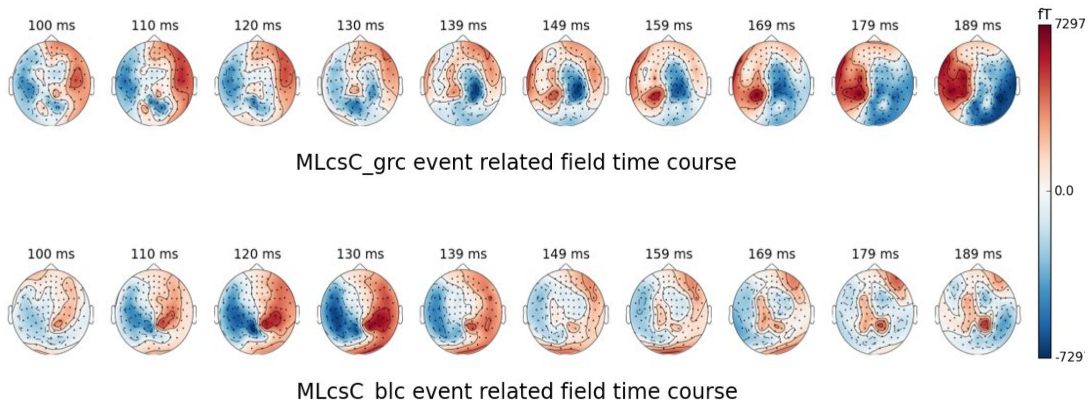



Figure 5.32.Topographic field maps of electromagnetic field responses from figure 5.31 (100ms to 189ms). The time windows of 2D field maps above (100ms to 189ms) were when MLcsC_grc and MLcsC_blc responses were significantly different from one another.

The spatio-temporal permutation tests for the fifth contrast – more dots with high contrast centre/low contrast surround (MLcsC_blc) and MLcsC_grc resulted in one significant cluster of sensors *(F-threshold=5, p=.02)*. The averaged F-map as shown in figure 5.31 revealed that the significant cluster of sensors were localised to left frontal-temporal regions of the sensor array. From the averaged cluster time course plots, it can be seen that MLcsC_blc and MLcsC_grc ERF traces were significantly different from 109ms to 205ms. Within this significant time window, the averaged left frontal-temporal cluster trace of MLcsC_blc was characterised by a negative peak response at ~130ms – respectively, the MLcsC_grc cluster trace was characterised by a positive peak response once again at around 190ms.

Figure 5.32 shows the 2D electro-magnetic field distributions of MLcsC_blc and MLcsC_grc from 100ms to 189ms. Note the sign flip of the magnetic dipole within posterior-parietal sensors for MLcsC_blc at 130ms and MLcsC_grc at 190ms. For MLcsC_blc, the magnetic efflux at 130ms was distributed across right temporal-parietal sensors, and for MLcsC_grc, it was distributed across left temporal-parietal sensors at 190ms. These responses were almost identical to the ones seen for MHcsC_blc and MHcsC_grc – meaning that the central stimulus contrast was having the greatest effect upon the sensory and attentional processes involved with numerosity comparison of more and fewer dots, and not the surround-contrast exclusively.

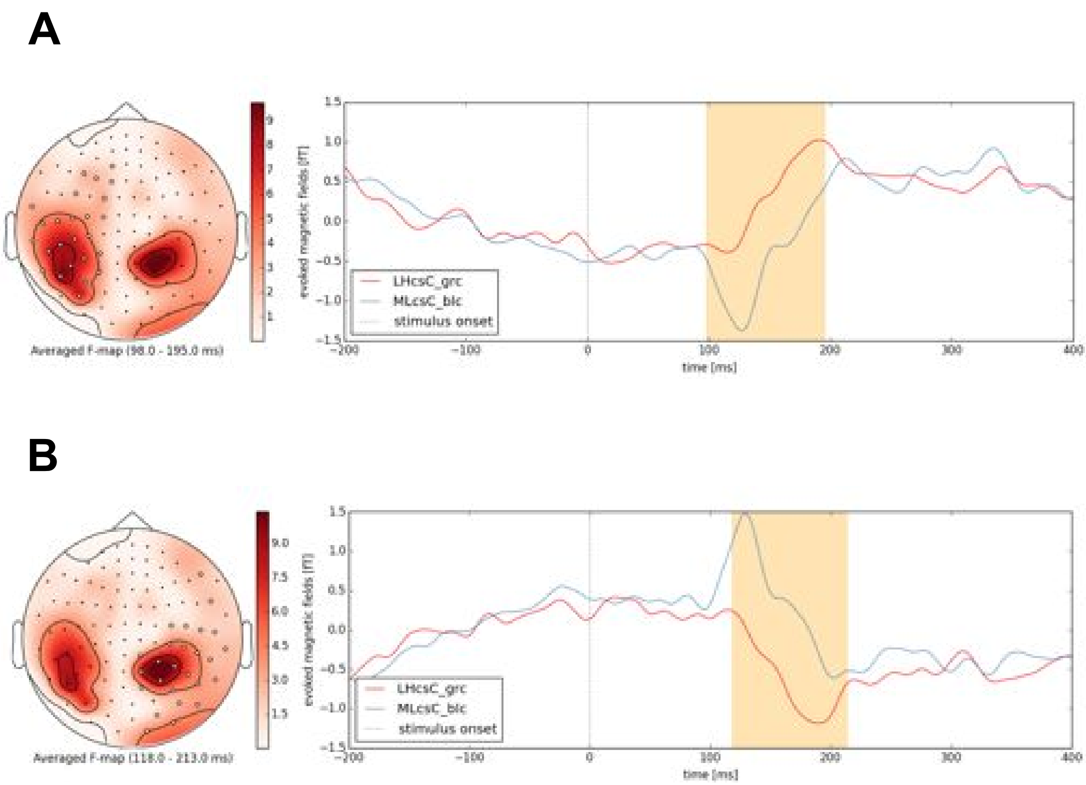



Figure 5.33. Averaged F-maps (left) and cluster time courses for within-group comparisons between central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: high contrast surround/low contrast centre with fewer dots (LHcsC_grc); Blue ERF time-series: low contrast surround/high contrast centre with more dots (MLcsC_blc). Panel A shows a similar spatio-temporal cluster profile to that of figure 5.27A, with a negative peak response of the left fronto-parietal cluster time-series of MHcsC_blc at 130ms. This once again suggests that it was the high contrast centre that had a disruptive effect upon numerosity comparison mechanisms rather than the high contrast surround.

The spatio-temporal permutation tests for the sixth contrast – LHcsC_grc and MLcsC_blc resulted in two significant sensor clusters *(F-threshold=5, p=.02)*. The averaged F-map as shown in figure 5.33A shows a cluster of significant sensors within left temporal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that LHcsC_grc and MLcsC_blc cluster traces were significantly different from 98ms to 195ms. Within this significant time window, the averaged left temporal-parietal cluster trace of MLcsC_blc comprised of a negative peak response at ~130ms post-stimulus onset. The averaged cluster trace of LHcsC_grc on the other hand, was characterised by a positive peak response at around 190ms.

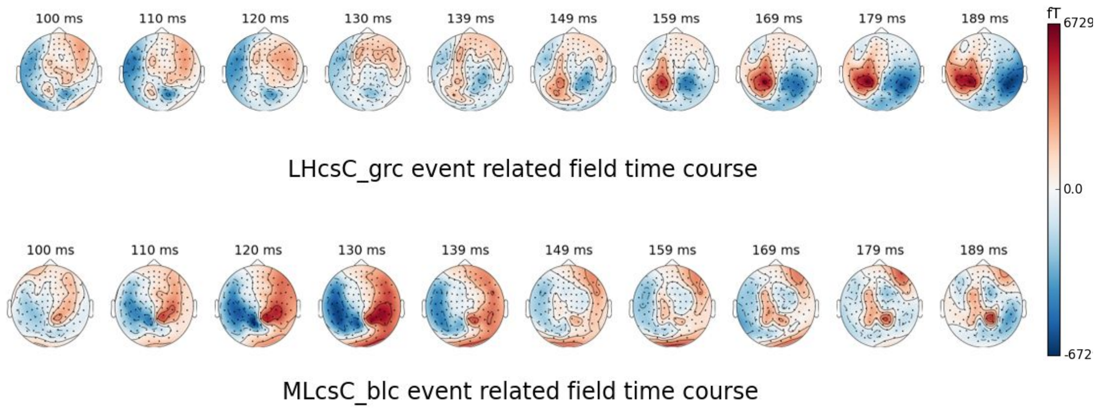
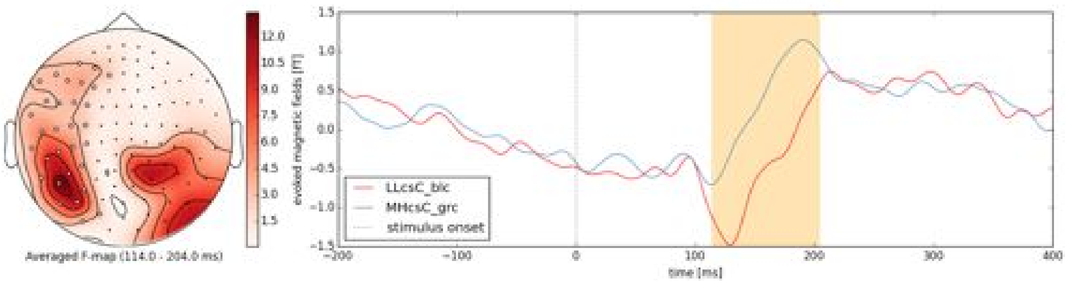



Figure 5.34.Topographic field maps of electromagnetic field responses from figure 5.33 (100ms to 189ms). The time windows of 2D field maps above (100ms to 189ms) were when LHcsC_grc and MLcsC_blc responses were significantly different from one another.

The second significant cluster that resulted from the LHcsC_grc and MLcsC_blc comparison (figure 5.33B) shows an averaged F-map with a cluster of significant sensors localised to right posterior-parietal region of the sensor array. The yellow band within the time course plot shows that the averaged cluster #2 time course between LHcsC_grc and MLcsC_blc were significantly different from 118ms to 213ms. Within this significant time window, the averaged right posterior-parietal cluster trace of MLcsC_blc comprised of a positive peak response approximately 130ms post-stimulus onset. The averaged cluster trace of LHcsC_grc on the other hand, was characterised by a later positive peak response at approximately 190ms.

Figure 5.34 shows the 2D electro-magnetic field responses of MLcsC_blc and LHcsC_grc from 100ms to 189ms. The ERF dynamics involved with this particular contrast had an almost identical spatio-temporal pattern as the one in the previous statistical contrast. That is, as observed with the ERF distribution of MLcsC_grc (see figure 5.31), at 190ms, the electro-magnetic efflux of LHcsC_grc was distributed across left temporal-parietal sensors. It may be inferred from this observation that it was the high contrast centre that had the most disruptive influence upon numerosity comparison judgements.

**A**




**B**

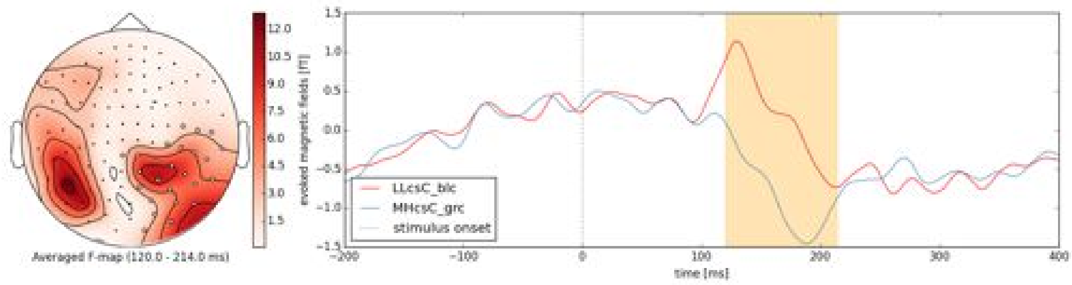



Figure 5.35. Averaged F-maps (left) and cluster time courses for within-group comparisons between central stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: low contrast surround/high contrast centre with fewer dots (LLcsC_blc); Blue ERF time-series: high contrast surround/low contrast centre with more dots (MHcsC_grc). Panel A shows a similar spatio-temporal cluster profile to that of figure 5.33A, with a negative peak response of the left fronto-parietal cluster time-series of LLcsC_blc at 130ms.

The spatio-temporal permutation tests for the seventh contrast – LLcsC_blc and MHcsC_grc resulted in two significant sensor clusters *(F-threshold=5, p=.02)*. The averaged F-map as shown in figure 5.35A shows a cluster of significant sensors within left temporal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that LLcsC_blc and MHcsC_grc cluster traces were significantly different from 114ms to 204ms. Within this significant time window, the averaged left temporal-parietal cluster trace of LLcsC_blc was characterised by a negative peak response at ~130ms post-stimulus onset. The averaged cluster trace of MHcsC_grc on the other hand, was characterised by a positive peak response at around 190ms.

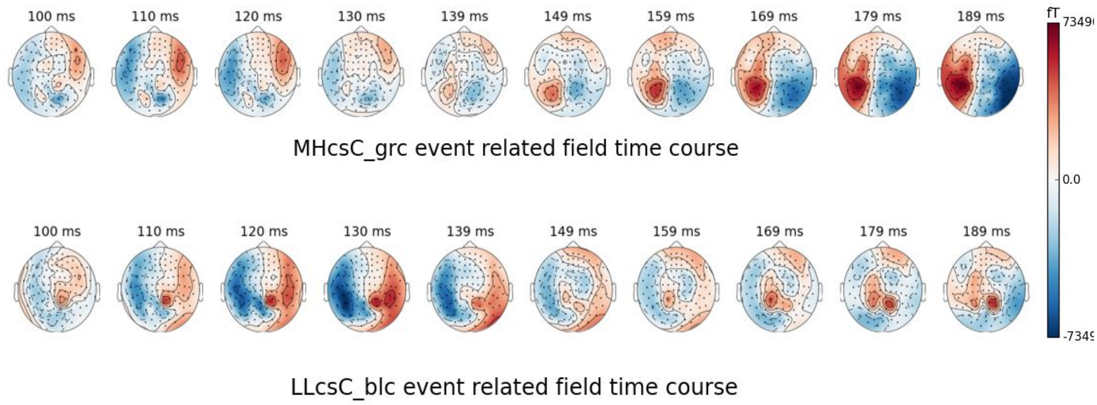



Figure 5.36.Topographic field maps of electromagnetic field responses from figure 5.35 (100ms to 189ms). The time windows of 2D field maps above (100ms to 189ms) were when MHcsC_grc and LLcsC_blc responses were significantly different from one another.

The second significant cluster that resulted from the LLcsC_blc and MHcsC_grc contrast (figure5.35B) shows an averaged F-map with a cluster of significant sensors localised to right occipital-parietal regions of the sensor array. The yellow band within the time course plot shows that the averaged cluster #2 time course between LLcsC_blc and MHcsC_grc were significantly different from 120ms to 214ms. Within this significant time window, the averaged right occipital-parietal cluster trace of LLcsC_blc was characterised this time by a positive peak response approximately 130ms post-stimulus onset. The averaged cluster trace of MHcsC_grc on the other hand, was comprised of a later negative peak response at approximately 190ms.

Figure 5.36 shows the electro-magnetic field responses across the significant time window (100ms to 190ms) for MHcsC_grc and LLcsC_blc. From examination of these plots, it was seen that numerosity of the stimulus display (more/fewer dots) had no effect upon the spatial or temporal characteristics of the ERF response signatures. It appeared instead that the main response peaks at 130ms and 190ms were affected by the contrast of the central stimulus that in turn, influenced the ability to make numerosity comparison judgements.

# 5.7. Discussion

### 5.7.1. Surround-masking MEG analysis (behavioural data)

The following section concerns analysis of the behavioural responses when participants performed the surround-masking of numerosity experiments in the MEG scanner. Given that there were technical problems with the acquisition of button presses (response accuracy), only the RTs of all 8 conditions were analysed. The first analyses performed with this data were 16 paired t-tests (repeated measures), which examined the effects of centre contrast; surround contrast; and numerosity (fewer/more dots) independently. Bivariate correlations were then performed between MEG surround-masking RTs, all WAIS-IV sub-tests, and the computerised task variables. Finally, independent t-tests were performed on MEG surround-masking RTs to determine whether there were WAIS-arithmetic group differences in MEG surround-masking RTs.

**5.7.2. MEG surround masking RT within groups' analysis**

Of the 16 paired t-tests performed, ten were significant. In short, the t-tests that held constant surround contrast of the stimulus display (centre contrast effects), suggested numerosity comparison judgement RTs were most delayed during high contrast centre and high contrast surround conditions – particularly for the numerosity judgements of fewer dots. The ensuing set of hypotheses tests that held constant the centre contrast (surround contrast effects), suggested that central rather than surround contrast affected numerosity comparison judgements. That is, observer RTs were found to be significantly longer when background contrast of the central stimulus was near zero luminance (black) as compared to low luminance (grey). The final set of paired t-tests that compared dot numerosities (fewer/more) amid differences in centre and surround contrasts, suggested that surround contrast and dot numerosities had no effect on numerosity comparison judgement RTs. Rather, it was central stimulus contrast that had the greatest effect on RTs. That is, irrespective of surround contrast or dot numerosities, the RTs of numerosity comparison judgements with black central stimulus regions were markedly delayed compared with judgements with grey central stimulus regions.

In comparing the psychophysical data from experiment one – that is, the mean proportion of correct responses per condition with the behavioural data from the MEG experiments (mean RTs per condition), it became apparent that there were data variations that at first glance appeared discrepant with each other. For example, in experiment one, there was a significant effect found for surround contrast, where the high contrast surround, but not the central stimulus region significantly impaired numerosity comparisons of more dots. A number of explanations can be offered as to why there were effects for centre contrast but not surround contrast within the MEG RT data, where the opposite pattern emerged for experiment one (psychophysics of surround-masking). In contrast to the MEG modified surround-masking stimuli, the onset of surround annulus and central stimuli region in experiment 1 were simultaneous and was presented for 750ms. Onset of the surround annulus for the MEG modified surround-masking experiments however, were 500ms before the central stimuli, which was displayed for substantially longer than experiment one (2000ms).

Thus, the numerosity comparisons of observers in experiment one were limited by briefer centre and surround stimuli duration that was additive toward perceptual ambiguity of numerosities. Alternatively, the absence of surround contrast effects for MEG modified experiments could be attributed to contrast adaptation within the magnocellular channel that innervates the peripheral visual field (Milner & Goodale, 2006). The effects of contrast adaptation have been associated with increased discriminability of perceptually ambiguous stimuli via magnocellular loss of sensitivity to high contrast gain (Solomon, Peirce, Dhruv & Lennie, 2004). In a similar manner, it was possible that prolonged exposure of the high contrast surround (~1,500ms) resulted in reduced sensitivity to high contrast gain of the surround annulus via contrast adaptation. These putative contrast adaptation effects did not, however, appear to completely eliminate the effects of surround-masking for stimuli with the same centre and surround contrasts. For example, numerosity comparison RTs of fewer dots with high contrast centre/high contrast surround stimuli was significantly more delayed than RTs of fewer dots with low contrast centre/low contrast surround conditions. This response time delay was highly significant – by approximately 140ms. These effects were likewise for numerosity comparison RTs of more dots under the same centre/surround conditions, only that the RTs of comparisons for more dots under high contrast centre/high contrast surround conditions were delayed by ~70ms. These findings overall suggest that observers required 70ms to 140ms more time in order to make accurate comparisons of more and fewer dots under high contrast centre/high contrast surround conditions compared to low contrast centre/low contrast surround conditions.

Previous psychophysical experiments that have examined effects of surround-masking on contrast discrimination ability, have reported similar perceptual inefficiencies, where contrast discrimination judgements were severely impaired by the presence of surround stimuli of high contrast gain (Xing & Heeger, 2000;2001; Zenger-Landolt & Heeger,2003). The limited number of neuroimaging investigations into cortical response properties of surround-masking, have indicated that its perceptual consequences – impoverished contrast discrimination of centrally embedded texture regions – were accompanied by a substantial reduction of the BOLD response in V1 that was concluded to be a functional reflection of intra-cortical inhibition (Zenger-Landolt & Heeger, 2003). If intra-cortical inhibition of V1 were the mechanism by which sensory gating resources are saturated by high contrast centre and surround stimuli, it would be well to speculate that delayed RTs for numerosity comparison judgements under these conditions, would have been a result of introduced noisiness in the perceived numerosity of dots within the surround.

### 5.7.3. Correlations between MEG surround-masking RTs and WAIS/computerised tasks

This section of the analysis was an exploratory investigation into the relationship between MEG surround-masking RTs, WAIS-arithmetic, WAIS-digit span total, WAIS-digit span forward, WAIS-digit span backward, WAIS-digit span sequencing, all four magnitude comparison RTs, and the two true/false judgement scores. A positive correlation was found between RTs for fewer dots under high contrast centre/high contrast surround conditions and WAIS-arithmetic scores. There were also positive correlations between RTs for more dots under high contrast centre/high contrast surround conditions, WAIS-digit span backward and WAIS-digit span total scores. These correlations indicated that participants with higher WAIS-arithmetic, WAIS-digit span total, and WAIS-digit span backward scores required more time to make accurate numerosity comparison judgements under high contrast centre/high contrast surround conditions.

Also compelling were the negative correlations between RTs of fewer dots under high contrast centre/high contrast surround stimuli, and all four RTs of the symbolic magnitude comparison task. There were also significantly negative correlations between RTs of more dots under high contrast centre/high contrast surround conditions, RTs for magnitude comparisons of numbers less than 55 with right arrow key press, and RTs for magnitude comparisons of numbers less than 55 with left arrow key-press. Finally, a significantly positive correlation was observed between the RTs for fewer dots under low contrast centre/low contrast surround conditions, RTs for magnitude comparison judgements of numbers more than 55 with left arrow key-press, and RTs for magnitude comparison judgements of numbers less than 55 with left arrow key-press.

These correlations suggested that participants efficient with the magnitude comparison task required more time in order to make accurate numerosity comparison judgements under high contrast centre/high contrast surround conditions. Conversely, participants less efficient with the magnitude comparison task – particularly with left arrow key-presses – required more time in order to make accurate numerosity comparison judgements under low contrast centre/low contrast surround conditions. The correlation analysis between MEG modified surround-masking RTs and true/false judgement scores also revealed a positive correlation between true/false judgement scores for addition/subtraction and multiplication/division conditions, and RTs for fewer dots under high contrast centre/high contrast surround conditions. There was also a positive relationship between true/false judgement scores for multiplication/division problems, and RTs for more dots under high contrast centre/high contrast surround conditions.

The significant correlations observed here – between MEG modified surround-masking RTs and arithmetical ability assessment scores (WAIS-arithmetic and true/false judgements), signified that low-order sensory gating mechanisms disturbed by high contrast centre/high contrast surround stimuli, were related to high order processes involved with numerical cognition. As earlier discussed, it has been argued that the approximate number system is unlikely to be number specific or purely numerical, and that there is no way to measure a pure association between symbolic and non-symbolic numerosity (Liebovich & Ansari, 2016). Instead, high order cognitive control resources are likely recruited to disambiguate numerical from non-numerical dimensions of magnitude as part of non-symbolic number processing (Liebovich & Ansari, 2016). The correlations reported above are in agreement with these postulations, where the contrast level of center and surround stimuli -- a non-numerical parameter of magnitude -- had an influential effect upon the ability to make magnitude comparison judgements across individuals with varying levels of symbolic arithmetical ability.

Sigmundsson, Anholt, and Talcott (2010) were the first group of investigators to report perceptual processing disturbances in children with below average mathematical skills, where psychophysical thresholds for motion sensitivity – a dorsal stream mediated process – was functionally disturbed in ten year olds with mathematical achievement scores in the lowest tenth percentile of their cohort. The findings reported in this dissertation – a positive correlation between numerosity comparison judgements under high contrast centre/high contrast surround conditions and WAIS-arithmetic scores, also suggest that early perceptual processing mechanisms are developmentally awry in those with poor numeric/arithmetical skills.

Perceptual processing disturbances in participants with low numerical/arithmetical ability within the current sample, was evidenced not only by a negative correlation between numerosity comparison RTs under high contrast centre/high contrast surround stimuli, but also a positive correlation between numerosity comparison RTs under low contrast centre/low contrast surround stimuli, and symbolic magnitude comparison RTs with left arrow key-presses. These correlations indicated that participants with slower magnitude comparison RTs were unaffected by the high contrast centre/high contrast surround when making numerosity comparison judgements. Also, participants with slower magnitude comparison RTs for left arrow key-presses required substantially more time to make accurate estimation judgements of fewer dots under low contrast centre/low contrast surround conditions.

It may seem counterintuitive at first to note that participants with low arithmetic skills were advantaged by the high contrast centre/high contrast surround in making numerosity comparison judgements, and then conclude that such observations are likely to reflect perceptual processing disturbances in the participants with poor arithmetical ability. However, in an earlier investigation into surround-masking and contrast discrimination judgements of schizophrenic individuals, Dakin, Carlin, and Hemsley (2005) noted that contrast matching judgement performance of schizophrenics was unaffected by high contrast surround stimuli. Contrast matching judgements of the demographically matched control group, however, were severely impaired by the high contrast surround. From their findings, Dakin, et al., concluded that the superior contrast matching performance of schizophrenics under high contrast surround conditions, was owing toward the failure of a specific visual mechanism, being that of sensory gain attenuation (contextual suppression) rather than a high order cognitive deficit.

A similar effect was observed from a psychophysical study into the functional role of surround-suppression in motion discrimination judgements between schizophrenic and neurotypical observers (Tadin, et al., 2006). To elaborate, there was a negative correlation between stimulus duration thresholds (inspection times) for motion discrimination judgements of high contrast/wide surround drifting Gabors, and schizophrenia negative symptom severity. That is, schizophrenics with more negative symptoms required less stimulus exposure time in order to make accurate motion discrimination judgements. This duration threshold advantage was observed most prominently in schizophrenics with negative symptoms and was associated with weakened surround-suppression.

Overall, participants with low arithmetic/numerical skills were counter intuitively advantaged by their weakened surround-suppressive mechanisms during the comparison of fewer and more dots under conditions that would have otherwise caused a perceptual disturbance. The correlations observed here were concurrent with previous psychophysical literature that revealed functional disturbances of inhibitory mechanisms such as intra-cortical inhibition in V1 and surround-suppression in LGN (Carandini, et al., 2002).

### 5.7.4. MEG surround-masking ERF analysis

Analyses of the MEG ERF responses were made up of 2 parts, where Part 1 compared spatio-temporal cluster responses of surround stimuli with central stimulus responses that onset 500ms later. Part 2 compared the spatio-temporal cluster response differences between centre-surround stimuli during the comparison of fewer and more dots. The purpose of part one was of exploratory origin in order to demarcate the ERF response differences between low-level/sensory processes of surround annulus stimuli, from top-down/high-order responses following onset of central stimuli. The purpose of Part 2 was also of exploratory origin, with statistical comparisons performed on MEG surround-masking RTs. The aim of Part 2 was to note the ERF responses characteristics of statistically significant MEG surround-masking RTs.

### 5.7.5. Mask only and centre contrast ERF comparisons (Part 1)

There were 8 within-group contrasts performed as part of the MEG surround-masking analysis (e.g. high contrast surround with black blank centre and fewer dots with high contrast centre/high contrast surround), where all of these comparisons were significantly different from each other. These significant differences were indicative that effects of the surround annulus were dissociable from effects of the central stimuli. That is, there was a functionally distinct spatio-temporal cluster profile between the surround annulus (mask), and central stimuli across all eight comparisons.

**5.7.6. Spatial characteristics of high contrast surround**

The cluster topography (averaged F-maps) of high contrast surround stimuli showed a consistent response profile distributed across left frontal, temporal, and parietal regions of the sensor array when compared with high/low central contrast and fewer/more numerosities. That is, there were clusters of significant sensors across left frontal-parietal regions when ERF responses from high contrast surround stimuli were compared against ERF responses from high contrast centre/more dots, high contrast centre/fewer dots, low contrast centre/more dots, and low contrast centre/fewer dots. The locus of these significant clusters corresponded approximately to left pre-frontal cortex, left entorhinal cortex, and left inferior parietal regions. In combination with one another, these cortical areas have been proposed to comprise part of the dorsal fronto-parietal network associated with top-down control in attentional selection of sensory information and responses (Corbetta & Shulman, 2002).

The cluster of significant sensors localised to left pre-frontal regions of the array were likely to be associated with recruitment of executive processes in the inhibitory control of making incorrect responses in the decisional stage of making numerosity comparison judgements (Tsushima, Susaki & Watanabe, 2006). Executive functioning in the instance of making numerosity comparison judgements under high contrast surround conditions may have been necessary because of the attentional bottleneck generated by high sensory load (Corbetta & Shulman, 2002; Lavie, 2005). The clusters within left posterior parietal regions of the sensor array were likely to be coupled with pre-frontal areas in a feedback signalling mechanism in the minimisation of decisional uncertainty, or increased saliency of stimulus response mapping (Luu & Tucker, 2003).

From examination of the second set of clusters from high contrast surround and central stimuli comparisons, a different spatial pattern emerged between ERF responses for fewer/more dots with a high contrast centre and fewer/more dots with a low contrast centre. For the high contrast surround/black blank centre comparison with high contrast centre/high contrast surround stimuli that contained fewer or more dots, there was a cluster of significant sensors that were proximal to dorsal/posterior regions of cingulate cortex (see figure 5.7B, and figure 5.11B). Whereas high contrast surround/grey blank centre comparisons with high contrast surround/low contrast centre stimuli with fewer or more dots included clusters of significant sensors near lateral and central regions of occipital cortex, and right posterior parietal cortex (see figure 5.15B, and figure 5.19B).

There is ample fMRI and electrophysiological evidence implicating the cingulate cortex in executive functioning, particularly in the monitoring of errors in instances of conflicting response demands through high attentional load (Luu & Tucker, 2003). It was likely then, that the cluster of significant magnetometers localised to dorsal/posterior cingulate regions, was recruited through the increased task difficulty and increased perceptual capacity limits via high contrast centre and high contrast surround stimuli. Hence, the absence of dorsal/posterior cingulate responses for the comparison of high contrast surround/grey centre with high contrast surround/low contrast centre indicated that fewer attentional and executive resources were required under these conditions during numerosity comparison judgements. The cluster of occipital sensors under high contrast surround/grey centre and high contrast surround/low contrast centre conditions, were likely to be a functional reflection of RF facilitation or summation (Carandini, et al, 2002).

### 5.7.7. Spatial characteristics of the low contrast surround

The significant cluster topography (averaged F-maps) of low contrast surround comparisons revealed a similar activation profile to that of high contrast surround stimuli, where clusters were also observed around dorsal/posterior cingulate regions for low contrast surround/black blank centre and high contrast centre/low contrast surround stimuli (see figure 5.9, and figure 5.13C). As earlier discussed, this cluster profile was possibly a functional reflection of executive processes involved with monitoring of response error in response to increased sensory load by the high contrast centre (Luu & Tucker, 2003).

From examination of comparisons between low contrast surround/blank grey centre and low contrast centre/low contrast surround stimuli with fewer and more dots, there was a distinct absence of significant clusters within dorsal/posterior cingulate and dorsal fronto-parietal regions of the F-maps. This observation indicated that there was little need for executive functions in order to make judgements of fewer or more dots under these conditions, given the little demand imposed upon attentional resources. There was, however, a cluster of significant sensors localised to right occipital-temporal regions that corresponded to lateral-occipital cortex and right temporal parietal junction. These cortical areas have been proposed to form part of the ventral fronto-parietal network in the bottom-up recruitment of stimulus detection (Corbetta & Shulman, 2002).

### 5.7.8. Temporal responses of averaged sensor clusters

The time-series for comparisons between surround stimuli with blank centre and surround/central stimuli (more/fewer dots) were distinguished by differences in the sign and amplitude of peaks within significant clusters. The ERF response characteristics of clusters localised to right occipital and right temporal parietal regions for low contrast surround/blank grey centre stimuli included a positive peak amplitude response at ~140ms (see figure 5.21B). This response was likely to reflect RF spatial summation or facilitation in V1 within lateral occipital complex (LOC) generated by low contrast centre/low contrast surround conditions (Carandini, et al., 2002; Tadin & Lappin, 2005). In contrast to these feed-forward processes, top-down ERF responses of clusters localised to left frontal and parietal regions of high contrast surround/black blank centre stimuli, were also characterised by a positive peak amplitude response at ~70ms (see figure 5.11A). This ERF response was likely to be associated with top-down modulation of attentional control in the resolution of response conflict from perceptual ambiguity (Corbetta & Shulman, 2002; Luu & Tucker, 2003).

### 5.7.9. Centre-surround ERF contrasts (Part 2)

The main purpose of the following analysis was to examine electromagnetic responses accompanied by the earlier within-group comparisons of MEG surround masking RTs. To reiterate, out of the 16 paired t-tests performed on MEG surround-masking RT data, 10 of them were statistically significant. The same within-group comparisons were performed on the respective MEG responses, where 7 out of 10 spatio-temporal cluster tests were significant.

Essentially, the spatio-temporal clusters emergent from these comparisons also indicated a functional role of left dorsal fronto-parietal network, where ERF responses were maximal within left posterior parietal regions of the sensor array. This was evidenced from higher F-values of clusters (>10). There was very little variation in terms of spatial localisation of significant clusters for ERF responses between central stimulus contrasts, surround contrast, and numerosity. There was however, a differentiated response pattern in terms of peak response polarity. That is, the electromagnetic time-series of left fronto-parietal clusters were characterised by a negative peak response at ~130ms after onset of central stimuli with a high contrast centre irrespective of surround contrast. Conversely, left fronto-parietal electromagnetic time-series for central stimuli of low contrast comprised of positive peak responses approximately 190ms post stimulus onset.

### 5.7.10.Temporal response characteristics of high contrast stimuli

From inspection of all 7 significant within-group comparisons, it was apparent there were no significant effects within left fronto-parietal cluster time-series of numerosity. That is, the spatio-temporal response characteristics of numerosity comparison judgements were the same for central stimuli that contained fewer or more dots. One consistent temporal response characteristic however, was the negative peak responses occurring approximately 120ms to 130ms following onset of the high contrast centre stimuli (see figures 5.27A, 5.29A, 5.35A, 5.35B, 5.25). This negative peak under conditions of high attentional demand was not unlike ERP responses from previous studies that have examined temporal and morphological characteristics associated with making task response errors (Coles, Scheffers & Holroyd, 2001; Falkenstein, Hoorman, Christ & Hohnsbein, 2000; Luu & Tucker, 2003; Vidal, Hasbroucq, Grapperon & Bonnet, 2000).

Error related negativity (ERN), also known as ‘error negativity’ (Ne), has been characterised as a negative peak approximately 100ms post button response, and distributed over medial-frontal, parietal, anterior and posterior cingulate areas as shown by source analysis of high density electroencephalography (Luu & Tucker, 2003). Early investigations revealed that the ERN response was maximal within grand averaged ERP trials when participants made incorrect button responses, yet absent on correct trials (Holroyd & Coles, 2002). Yet, following more extensive inquiry into the functional significance of ERN/Ne, it was consistently revealed across studies that this ERP component can also occur for correct responses under stimulus conditions that require attentional monitoring imposed by high task demands (Coles, et al., 2001;

Falkenstein, et al., 2000; Holroyd & Coles, 2002; Luu, Flaisch & Tucker, 2000; Vidal, et al., 2000).

Luu et al., (2000) for example, examined the spatial and temporal response characteristics of ERN/Ne during response conflict of a speeded choice task via the lateralised readiness potential (LRP). The LRP responses across motor cortex (electrodes C3 and C4) for behavioural/button presses of trials that generated response competition (cognitive interference) were examined with their RTs. The RT and LRP data for these trials were averaged and separated into five different response types that were correct, early-late RT, mid-late RT, late-late RT, and incorrect. Of particular interest were the LRPs of late-late RTs of task trials with cognitive interference characterised by higher amplitude peak responses than LRP responses of correct and early-late RTs. From these observations, it was conjectured that the more prolonged an RT was for correct responses with high cognitive interference trials, the more likely it was that motor plans were being executed with the incorrect hand. The medio-frontal ERN/Ne responses for all four correct RT types also indicated that ERN/Ne amplitude also varied as a function of RT lateness, where the ERN/Ne amplitude of correct late-late responses were much higher than correct early-late and correct mid-late responses.

A number of comparisons can be drawn from the main findings of the Luu et al., (2000) study and the RT/ERF data observed here in terms of behavioural/electromagnetic responses for high contrast centre/high contrast surround and low contrast centre/low contrast surround conditions. Firstly, the stimuli that required response monitoring and generated cognitive interference were high contrast central stimuli. These stimulus conditions moreover, were associated with the most prolonged RTs during estimation of more and fewer dots. The prolonged RTs for correct comparison judgements under high contrast centre conditions, were concomitantly associated with negative peak responses within left fronto-parietal networks approximately 120ms to 130ms post stimulus onset. These observations in combination with one another corroborate with the findings of Luu et al., (2000) such that ERN/Ne responses in medio-frontal electrodes were present for correct late-late RTs to stimuli with high cognitive interference and response conflict. Hence, it was reasonable to infer that delayed RTs and negative peak responses for cluster time-series of high contrast central stimuli, were indicative of processes related to response error monitoring of motor planning as postulated by earlier investigators (Coles, et al., 2001; Falkenstein, et al., 2000; Holroyd & Coles, 2002; Luu, et al., 2000; Vidal, et al., 2000).

Given that ERN/Ne response have consistently occurred also for correct trials with high cognitive interference across investigations (Coles, et al., 2001; Falkenstein, et al., 2000; Holroyd & Coles, 2002; Luu, et al., 2000; Vidal, et al., 2000), it has been proposed that this ERP signature may not be a reflection of error detection ipso facto, but rather, high-order executive functions related to response evaluation processes that serve to check whether motor plans are in accord with stimulus-response mapping rules (Luu & Tucker, 2003). According to Luu and Tucker (2003), this ERP response has been labelled as the 'correct related negativity' (CRN), with a topographic distribution same as the ERN/Ne response – fronto-medial regions of the sensor array. The main parameter that distinguishes ERN/Ne from CRN however, is peak amplitude, where ERN/Ne amplitude via error commission (i.e. incorrect button responses) is much higher than CRN responses (Vidal, et al., 2000). A recent MEG investigation revealed that the neural generator of ERN/Ne responses were localised to anterior cingulate cortex as evidenced by source localisation (Keil, Weisz, Paul-Jordanov & Wienbruch, 2010).

Holroyd and Coles (2002) proposed that the ERN/Ne (or CRN) response was a top-down relay from anterior cingulate to pre-frontal cortex via the mesencephalic dopamine pathway. This model postulated an error-monitoring network that comprised of motor controllers (dorso-lateral pre-frontal cortex, amygdala, orbito-frontal cortex); a control filter (anterior cingulate); and an adaptive critic (basal ganglia). The functional role of the control filter was argued to relay predictive error signals toward the appropriate motor controller, which in turn, monitors and adjusts motor plans via the adaptive critic. In generalising the Holroyd and Coles model of error monitoring to the findings observed here, it may be well to speculate that task difficulty generated by high contrast centre and high contrast surround stimuli, recruited the control filter in a feed-back signalling mechanism toward left dorso-lateral pre-frontal cortex to monitor or inhibit motor plans that did not accord with stimulus-response mapping rules – that is, fewer dots/left button press and more dots/right button press.

### 5.7.11. Temporal response characteristics of low contrast stimuli

Curiously, the peak response properties of all left fronto-parietal cluster traces under low contrast centre conditions were characterised by one positive peak response at ~190ms. This positive peak occurred for all stimuli with a low contrast centre in comparison to the high contrast centre response negativity by ~70ms. This response consistency across all low contrast centre conditions suggests that numerosity of dots or surround contrast had no effect upon numerosity comparison judgement RTs. It was worth noting that RTs for low contrast centre ERF responses were significantly earlier than those of the high contrast centre responses. These observations in combination with one another suggested that the low contrast centre had an enhancing effect upon allocation of attentional resources during numerosity comparison judgements of more and fewer dots under low contrast centre (and low contrast surround) conditions. However, the exploratory nature of this MEG investigation, and the lack of a priori assumptions about stimulus modulations of ERF responses, makes it difficult to generalise about the findings and conclusions from prior investigations into neural correlates of numerosity comparison processes.

One ERP investigation into stimulus dependent response modifications during numerosity comparison revealed that the P200 peak amplitude – thought to reflect non-symbolic numerosity processing – was influenced by psychophysical properties that made up the dot arrays rather than numerosity its self (Gebuis & Reynovet, 2012). A number of comparisons can be made between the main findings of this study and the positive peak responses at ~190ms for low contrast central stimuli observed here. Firstly, the positive peak ERF response observed at ~190ms following the onset of low contrast centre stimuli, was within the same temporal window as the P200 response during numerosity processing found in the Gebuis and Reynovet (2012) study. Secondly, no effects of numerosity (or cardinality) were reported here or within the Gebuis and Reynovet (2012) ERP study. That is, the P200 responses during numerosity comparison were modulated by psychophysical cues such as surface area and dot density (Gebuis & Reynovet,2012), and concurrently – the positive electromagnetic response at ~190ms were influenced by low contrast central stimuli. One conclusion drawn from these findings was that irrespective of dot numerosity (fewer or more), the low contrast centre, and to some extent, the low contrast surround had an attentionally enhancing effect upon numerosity comparison.

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# Part 6

# Attentional Filtering and Numerosity Comparison: Magnetoencephalography

# Abstract

The ignoring of uninformative visual input has been established as under guidance of selective attention. Previous neuroimaging experiments have revealed that the functional components of selective attention are a combination of attentional suppression – an inhibitory process, and attentional enhancement – an excitatory process. Here, the contribution of feature based selective attention during numerosity comparison judgements were examined via magnetoencephalography (MEG). The task objective was to make numerosity comparison judgements of two overlapping dot displays that varied in luminance and numerical representation (fewer than or greater than). Upon commencement of each trial, observers were cued as to which dot array to selectively attend by the luminance of a centrally presented cross hair that was either black, grey, or white. Following brief presentation of the stimulus, observers were required to indicate by button response whether the attended array contained fewer or more dots than the simultaneously presented distracter dots. The behavioural response data from this experiment revealed comparison judgements were substantially more difficult when the dots to be attended comprised of contextually incongruent luminance properties. For example, comparison judgements of fewer high luminance target dots amid more low luminance distracter dots were substantially more difficut for observers to make than comparison judgements of more high luminance target dots amid fewer low luminance distracter dots. A spatio-temporal cluster analysis of the accompanying MEG responses indicated that modulations in attentional suppression and attentional enhancement during numerosity comparison judgments were affected by the background luminance of the stimulus display. These findings suggest rudimentary stimulus features such as luminance contrast can modulate high-order attentional mechanisms.

# 6.0. Introduction

As reviewed in part one and part two in this dissertation, there are numerous computational processes that occur in the course of feed-forward and feedback interactions during cortical inhibition. In saying this however, there is no evidence to indicate that sensory filtering or noise exclusion is an exclusively bottom-up process (Carrasco, 2011). There are many neuroimaging and psychophysical investigations into the functional contribution of sensory filtering for selective attention, and the ignoring of highly salient yet contextually irrelevant stimulus features (Andersen & Müller, 2010; Booth et al., 2003; Elahipanah, Christensen, & Reingold, 2008; Gál et al., 2009; Mukai et al., 2007; O'Connor, Fukui, Pinsk, & Kastner, 2002; Schwartz et al., 2005; Tsushima, Sasaki, & Watanabe, 2006; Vidnyánszky & Sohn, 2005; Zhang & Luck, 2009).

According to the Corbetta and Shulman (2002) model of goal directed and stimulus driven attention, there are two functionally separate yet interacting cortical networks involved with top-down (goal-directed) control of spatial or feature based attention, and bottom-up (feed-forward) detection of highly salient stimuli or events. The dorsal fronto-parietal network – comprised of the frontal eye fields (FEF); anterior intra-parietal sulcus (aIPS); posterior intra-parietal sulcus (pIPS); ventral intra-parietal sulcus (vIPS); pre-frontal cortex (PFC) and inferior frontal gyrus (IFG) was postulated to mediate the top-down signalling of spatial, object based and feature based attention. The ventral right fronto-parietal network that comprises of right temporal-parietal junction (rTPJ) and right ventral frontal cortex (VFC), has been shown to modulate feed-forward (bottom-up) signalling with attentional capture by salient stimuli with environmental and behavioural significance.

More recent literature on the neuroimaging of stimulus driven attention has suggested that the reduction of BOLD signal at or below baseline within rTPJ, is a neural marker of the filtering out of highly salient but task irrelevant stimulus information (Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007). This deactivation of rTPJ occurs during inattentional blindness through the saturation of attentional load and visual short-term memory capacity (Todd, Fougnie, & Marois, 2005). These findings are concordant with the load theory of selective attention, where manipulations in peripheral (sensory) and attentional (cognitive) load of distracter to target interference, had modulatory effect upon whether or not observers perceive distracters (Lavie, Hirst, de Fockert, & Viding, 2004).

Thus, a perceptual set with highly salient targets (high perceptual load) amid fewer or lower salience distracters, would facilitate attentional selection in observers, owing to the absence in distracter interference from task irrelevant elements of low salience – the distracters are simply not perceived (Lavie, 2005). Conversely, in a situation related to covert attentional control of task irrelevant distracter suppression, load theory of selective attention posits that in instances where a perceptual set possessing targets of low perceptual load amid distracters too salient to ignore, the capacity limits of attentional selection become saturated not only by distracter interference, but also by increased resource demands upon cognitive load (Lavie, 2005; Lavie et al., 2004).

The neural mechanisms of attentional and sensory load have been well explored over the last 15 years, and these investigations have yielded much insight into the relationship between selective attention and sensory filtering. For example, O' Connor et al., (2002) observed that attentional suppression, or selective ignoring of peripherally presented flickering chequer boards, was characterised by a significant decrease in BOLD signal of lateral geniculate nucleus (LGN) as compared to when observers covertly attended to the same stimulus. The authors concluded from their findings that LGN was likely to have a functional role in the top-down modulation of attentional selection and suppression, where it was previously thought that these were exclusively high-order cognitive functions. Other investigations into activation profiles associated with cognitive and perceptual load have consistently revealed BOLD deactivation of high and low order cortical areas in response to attentional suppression and sensory competition (Pinsk, Doniger, & Kastner, 2004; Schwartz et al., 2005). The observed BOLD deactivations of low order visual areas such as V1 in response to attentional suppression of task irrelevant distracters, has been argued to be a functional reflection of surround suppression (Schwartz et al., 2005), suggestive of a link between sensory filtering and selective attention (Carrasco, 2011).

In view of this, the focus of the following experiment will be upon stimulus driven attention (perceptual load), and its role in the suppression (or ignoring) of high/low salience stimulus features amid task irrelevant distracters. The main rationale of this study was to address the issue of feature-based selective attention, and how this relates to the functional quality of sensory filtering mechanisms during numerosity comparison judgements of non-symbolic number sets. One of the central questions is as follows: is the ability to make accurate comparison judgements during high sensory/perceptual load related to the efficiency or individual differences in sensory gain control mechanisms? Before an answer can be given to such a question it is necessary to discuss the previous psychophysical and neuroimaging literature on feature based selective attention, object based selective attention, exogenous cueing paradigms and cognitive representation of number in the context of attentional suppression.

**6.1. Attentional suppression and the ignoring of high salience distracter competition**

As earlier discussed, stimulus-driven attentional capture is a feed-forward process that serves as a 'circuit breaker' of top-down signals from dorsal fronto-parietal network, so as to orient the locus of attention toward sudden events of high salience (Corbetta & Shulman, 2002). However, it is often necessary in everyday life to ignore or filter out sensory information of high saliency, as it is not always contextually informative or relevant. In this instance, there has been much psychophysical and brain imaging literature that has investigated psychophysical performance and neural responses of task irrelevant distracter suppression. Because of the overwhelming body of literature on this facet of selective attention, discussion will be limited only to the most recent investigations pertaining to feature based selective attention, the ignoring of contextually irrelevant visual information, and sensory filtering associated suppressive responses. Ostensibly, the functional quality to which one can filter out or ignore contextually irrelevant yet salient information has broad reaching implications over essential life skills such as learning, non-verbal communication, abstract comprehension and the achievement of task related goals (Elahipanah et al., 2008; Fukuda & Vogel, 2009, 2011; Gál et al., 2009; Paffen, Verstraten, & Vidnyánszky, 2008).

With this in mind, it is worth noting a novel electroencephalographic (EEG) investigation that related individual differences in working memory capacity with the ability to resist the attentional capture of task irrelevant distracters (Fukuda & Vogel, 2009). The essential findings of this investigation were that individuals with low working memory capacity demonstrated more difficulty in ignoring task irrelevant distracters of high salience during a spatial working memory task, as compared to those with high working memory capacity. Differences in the ability to ignore distracting information was evidenced by a positive correlation between a resistance to attentional capture index (defined as the electrophysiological response amplitude to stimulus probes at distracter present trials) and working memory capacity scores. Furthermore, there was a negative correlation between unnecessary storage of distracters (indexed as the difference in mean electrophysiological response amplitude between distracter present and distracter absent trials) and working memory capacity. There were no significant group differences (high versus low working memory capacity), however, in the electrophysiological peak response amplitudes when targets were selectively attended to during distracter absent trials.

A more recent investigation by Fukuda and Vogel (2011) into the suppression of task irrelevant visual information, revealed that this inability for individuals with low working memory capacity to filter out highly salient yet contextually irrelevant stimuli, was related to a slower visual disengagement of distracters, rather than a deficit in ignoring attentional capture per se. That is, the behavioural data from this study demonstrated that, at the briefest distracter/flanker to target stimulus off-set asynchrony (SOA) of 50ms, there were no significant group differences in attentional capture costs – meaning that visual search performance was equivalently impaired for both high and low working memory capacity individuals. At an SOA of 150ms however, low working memory capacity observers demonstrated significantly greater search performance thresholds than high working memory capacity individuals – suggesting a more prolonged attentional disengagement duration from task irrelevant distracters.

In accord with their earlier investigation into attentional suppression (Fukuda & Vogel, 2009), Fukuda and Vogel (2011) once again found that there were no significant differences between working memory capacity and selectively attending to task relevant target stimuli. It was concluded from these findings that impaired disengagement from, and susceptibility to attentional capture at an early stage of visual processing, was likely to cascade into high-order disturbances in working memory capacity and not the other way around. This preservation in the ability to selectively attend to targets amid distracters during covert search has been observed not only in low working memory capacity (Fukuda & Vogel, 2009; 2011), but also in clinical populations such as in schizophrenia (Elahipanah et al., 2008). From these previously discussed investigations, it can be inferred that the functional quality of top-down attentional modulation when ignoring uninformative or contextually irrelevant information is likely to be determined by how well one can filter out the feed-forward deluge of information arriving into cortex at every instant.

Not only has this attentional suppression phenomena been linked to the functional quality of high-order cognitive mechanisms such as working memory capacity, it has also been evidenced both psychophysically and through fMRI to play a major role in visual perceptual learning (VPL). For example, Vidnyanszky and Sohn (2005) observed that in the course of training observers to selectively attend the motion direction of a task relevant dot population, the attentional suppression of distracter dots drifting in the task irrelevant direction, became more efficient with practice. More specifically, the learning effects noted in this study were operationalized as the strength of motion after effect (stimulus adaptation) evoked by the task irrelevant dots before and after VPL training. The objective of this task was to indicate via key press when observers detected a transient increase in luminance of the task relevant (selectively attended) dot population during the training period of this task. Comparisons of pre and post training of motion after effect duration (the psychophysical threshold) revealed a marked reduction in the distracter dots adaptation time in the post training session. A lower motion after effect duration from distracter dots following VPL training was concluded to reflect task specific learning through the suppression of task irrelevant distracters.

Attentional suppression based VPL has also been shown psychophysically to play a functional role in the modulation of binocular rivalry associated perceptual dominance and suppression (Paffen et al., 2008). As part of this study, observers were trained on a perceptual dominance task of dichoptically presented dot stimuli with task relevant motion in one eye and task irrelevant motion in the other. Task related training required observers to indicate via 2 alternate forced choice (2AFC) as to which of the dichoptically presented dot stimuli possessed faster rightward motion. Before and after binocular rivalry training sessions, observers undertook a motion coherence discrimination experiment in order to determine psychophysical thresholds and gauge the extent of learning. Post training motion coherence thresholds revealed that observers improved significantly on discrimination judgements of task relevant dot motion speed as a result of practice. Most pertinently however, there was a significant learning effect for perceptual dominance of rivalrous motion directions, where percentage of time the task irrelevant motion was perceived decreased as a result of training. This reduction in perception time of task irrelevant motion direction post training was characterised by a significant reduction in mean perceptual dominance of task irrelevant motion. The mean perceptual dominance of task relevant motion post training however, was not significant.

Findings from the Paffen et al., (2008) study were once again concluded to reflect a functional role for inhibitory mechanisms in V1 in the course of learning. Therefore considered at whole, the previously discussed psychophysical experiments suggest that learning may not only involve the enhancement of contextually relevant features, but also the suppression or filtering out of input that is uninformative toward the gist of perceptual gestalt. These investigations, while novel and insightful, are not informative however, of learning dependent changes in cortical circuitry before and after VPL training. There are, nonetheless, a few fMRI investigations that have revealed insight into the BOLD dynamics associated with learning related attentional suppression.

Gal et al., (2009) for example, observed from a motion discrimination task similar to the one used in the Vidnyanszky and Sohn (2005) study, that learning related attentional suppression during the post training period, was characterised by a significant attenuation of BOLD in motion sensitive area V5 (MT+) as compared to the pre-training scanning session. A more recent fMRI investigation into VPL related BOLD dynamics revealed a similar activation profile in occipital-parietal regions following training on a contour detection task of collinear versus orthogonally aligned gabors (Schwarzkopf, Zhang, & Kourtzi, 2009). More specifically, a post training fMRI scan following improved detection of collinearly aligned gabors revealed an associated reduction of BOLD signal within lateral-occipital sulcus (LO) and fronto-parietal (ventral pre-motor) areas as compared to pre-training scans. Conversely, post training scans following improved detection of orthogonally aligned gabors revealed an associated increase of BOLD signal within dorsal visual areas (V3d, V3A and V3B), ventral occipital-temporal region (VOT), LO, posterior fusiform gyrus (pFS) and parietal regions. This reduction in BOLD amplitude as a result of proficient detection of collinear gabors, was postulated by the authors to reflect a cortical gain control mechanism, where by training related enhanced selectivity of the most salient stimulus features is likely to result in a smaller recruitment of neuronal populations.

Compellingly, there were a small number of participants in the Schwarzkopf et al., (2009) fMRI investigation that did not show improved performance on the detection of orthogonally aligned gabors (non-learners). A multi-voxel pattern analysis (MVPA) revealed that before and after training, there was no significant difference in voxel classification accuracies within each of the task related ROIs for non-learners. That is, for non-learners, the fMRI signal remained high in LO and ventral pre-motor areas during post training scans for collinearly aligned contours. From these findings, it is worth noting an earlier investigation into learning related changes in attentional networks that also found observers who failed to demonstrate learning of a contrast discrimination task, also showed no significant difference in BOLD activation patterns before and after training (Mukai et al., 2007). In contrast, participants who demonstrated learning related improvements in this study, showed decreased BOLD activation within post training fMRI scans in extra-striate cortex (BA18 and BA19), IPS, fusiform gyrus and FEF.

In summary, while the learning related BOLD deactivations observed in the Schwarzkopf et al., (2009) and Mukai et al., (2007) studies are not a functional reflection of attentional suppression related filtering, they are nonetheless very valuable in terms of establishing an inferential link between gain control mechanisms in the course of learning and the attentional suppression of highly salient yet contextually irrelevant information. These studies also raise questions about the real world implications related to early learning and individual differences in efficiency of gain control mechanisms by which higher order representations are eventually formed. Could BOLD deactivations that resulted in task irrelevant filtering of distracters (Gal et al., 2009) be functionally linked with learning associated reduction of BOLD signal (Mukai et al., 2007; Schwarzkopf et al., 2009)? In addition, how do these suppressive mechanisms facilitate the extraction of numerically relevant information amid highly salient or contextually incongruent visual input?

### 6.2. Resisting attentional capture of highly salient stimuli or ignoring contextually incongruent information? Distracter interference doesn't always result from high sensory load during selective attention

In some instances, task irrelevant distracter information is more difficult to perceive than targets, yet nonetheless essential in providing the observer with an overall context and perceptual reference. Under these circumstances, attentional suppression can no longer be subject to the effects of overriding salience, but rather, a distracter incongruency type of interference (Lavie, 2005; Stroop, 1935).

Compellingly, Tsushima et al., (2006) observed such a paradoxical effect through a dual-task that was a combination between motion coherence discrimination of random dot kinematograms (RDKs) and rapid serial visual presentation (RSVP) of centrally presented letters/digits. Essentially, the psychophysical data revealed that task irrelevant distracter information at sub-threshold perception (5% motion coherence) resulted in RSVP task performance at chance level. In contrast, task irrelevant motion coherence at supra-threshold perception (>20%) did not result in significantly different performance to that of 0% coherence, that moreover had a facilitatory effect on psychophysical thresholds. That is, the task irrelevant distracters at sub-threshold level of perception (difficult to perceive) induced the greatest level of distracter interference compared to the supra-threshold task irrelevant motion that was much more salient.

The accompanying fMRI data to the Tsushima et al., (2006) study revealed a striking BOLD interaction between motion sensitive V5 and lateral pre-frontal cortex (LPFC) in response to changes in sub-threshold and supra-threshold distracters – the percentage of BOLD signal increased significantly in V5 and remained unchanged in LPFC as compared to the zero motion coherence condition. At 20% motion coherence however, there was a decrease in BOLD signal amplitude in V5 and significant increase within LPFC respectively. It was postulated that the lack of LPFC activation during trials with task irrelevant sub-threshold stimuli, was likely to reflect a disturbance in the attentional suppression of distracters that observers barely perceived.

Such Stroop like interference when ignoring contextually incongruent and task irrelevant input has also been observed during magnitude comparisons of alphanumeric digit arrays of which were varied as a function of numerosity (the number of numerals) and semantic value (Pansky & Algom, 2002). The stimulus display was made up of two 3 X 3 invisible grids paired beside each other that contained a number array of either eights for example in one grid or twos in the other – spaces within the grid that were not occupied by numbers were filled with an asterisk. These magnitude array pairs were either semantically congruent, where for example there were two symbolic 2 digits in one grid and eight symbolic 8 digits in the other; semantically incongruent where there were for example two symbolic 8 digits in one grid and eight symbolic 2 digits in the other. There were also trials that were semantically neutral, where, for example, two symbolic 2 digits appeared in one grid and eight symbolic 2 digits in the other. One final semantically neutral display configuration was organized in such a way that for example, two symbolic 8 digits were displayed in one grid and two symbolic 2 digits in the other. The objective of this task was to indicate via 2AFC which of the 2 grids possessed numerically more elements.

Essential findings of the Pansky and Algom (2002) study were that when observers made numerosity judgements of array pairs (i.e. which array pair had more digits) that were semantically incongruent, response times (RTs) were significantly delayed compared to semantically congruent trials. When observers made numerosity judgements of the numerical value between array pairs (i.e. which array pair had the greatest numerical magnitude) that were semantically incongruent, there were also significantly delayed RTs compared to trials that were semantically congruent. Greater Stroop interference – as evidenced by more prolonged RTs – were observed particularly for comparisons of semantically incongruent numerical magnitude than for comparisons of semantically incongruent numerosity comparisons. From these findings, it was proposed that the Stroop-like interference observed only during semantically incongruent trials, was likely due to a number of factors including the break down of selective attention through attentional reallocation toward task irrelevant variations in the criterial dimensions (numerosity of numerals and magnitude value of numerals). In other words, observers were unable to ignore the task irrelevant dimension that was array numerosity during comparisons of numerical magnitude, and respectively, were unable to ignore task irrelevant variations in numerical magnitude when required to compare the numerosity of arrays. Other disruptive influences resulting in Stroop interference were suggested to stem from the salience of the task irrelevant dimension, where for example, an array with the greatest number of elements within it – irrespective of the numeric value of its contents, would result in an overtake of stimulus driven attentional capture.

The number comparison experiments conducted by Pansky and Algom (2002) were the first to examine the effects of task irrelevant distracter interference on the psychometric performance of numerosity and number value judgements. Also novel were the parametric variations in semantic congruency and stimulus saliency in the context of attentional filtering by means of domain specific variation in numeric representation. That being said, it would be well to speculate about the effects of contextual modulation in numeric representation by means of non-symbolic comparison judgements via feature based selective attention (FBA). There has so far been no numerical cognition investigation that has explored the effects of stimulus saliency, attentional capture and semantic congruency over non-symbolic number comparison judgements. The following experimental protocol aims to address existing gaps in knowledge relating to this.

### 6.3.The present study

The focus of discussion has so far rested mostly upon neural response dynamics of psychophysical/psychometric performance of object based attentional suppression, and the variations in contextual relevance and salience of distracter information. One central question in relation to the following experiment is: how does FBA generalize or translate respective to the Pansky and Algom (2002) investigation into object based attentional suppression of contextually incongruent numeric representation? For the following experiment, alphanumeric digits – as used in the Pansky and Algom (2002) investigation – were replaced with non-symbolic representation of number (dot arrays) that varied as a function of luminance contrast (dim/bright) and numeric representation (less/more). Variations in luminance contrast were parameterized as stimulus saliency given that this feature in particular, possesses non-verbal and spatially invariant content of magnitude. For example, ‘the dots are more bright or less bright’, in contrast to ‘the dots are more numerous or less numerous than some given reference’.

Previous investigations into FBA and attentional filtering have indicated that there is distinct electrophysiological response variation in the duration to which pre-cued stimulus features are attended to and ignored. For example, in a SSVEP (steady state visually evoked potential) investigation into cued shifts of FBA, Andersen and Muller (2010) observed that by attending to or ignoring spatially overlapping RDKs that varied in colour (red or blue) and flicker frequency (11.98Hz and 16.77Hz respectively), a bi-phasic response pattern emerged respective to which RDK sets were attended to or filtered out. That is, when observers were cued to attend to red dots and ignore green dots for example, there was a concomitant rise in SSVEP response amplitude ~220ms after cue onset and inversely related decrease (suppression) in SSVEP response amplitude of dots which were ignored ~360ms after cue onset. Through the different flicker frequencies of attended to and ignored dots, the investigators were able to distinguish attentional suppression from selection by the entrained SSVEP oscillatory responses to red or blue dots. This bi-phasic time course in the enhancement of attended and suppression of ignored dots not only suggests that there are at least two separate neural mechanisms involved with FBA, but also that there is a reciprocal dynamic between attentional filtering and selection of spatially overlapping stimuli in a winner take all process (Desimone & Duncan, 1995).

In similarity to the Andersen and Muller (2010) experiment, the current study used two sets of spatially overlapping RDKs, however, were varied in the numerosity of dots to attend by a 1:2 ratio and by luminance. As in the Fukuda and Vogel (2009; 2011) experiments on the functional role of attentional filtering for working memory, observers were cued as to which set of dots to selectively attend – only in this instance – by a fixation cross that matched the luminance of dots to be attended. The fixation cross appeared prior to onset of the stimulus that was as mentioned, two sets of spatially overlapping dots that varied as a function of luminance contrast and numerosity. The objective of the following experiment was to indicate by a 2AFC protocol as to whether the cued sets of dots were greater or fewer than the contrasting or reference set of dots. As with the Pansky and Algom (2002) investigation into magnitude comparison amid contextually incongruent number representation, the present experiment also contained trials that were contextually incongruent. Only instead of using arrays of numerals as a means to manipulate attentional capture or stimulus salience (as in the Algom and Pansky experimental design), the luminance contrast of dots was here replaced as such a variable within the non-symbolic domain of attentional filtering and enhancement.

There were a total of 16 stimulus configurations that varied in background luminance (zero luminance/black and uniform luminance/grey); dot luminance respective to background (low/high luminance dot contrasts for zero luminance background and zero/low dot contrast for uniform luminance background); and numerosity of dots (less/more than spatially overlapping reference dots). An example of contextual incongruence in making numerosity comparison judgements of dot pairs was less high luminance dots amid more low luminance dots, or less zero luminance dots amid more low luminance dots. Examples of contextual congruence on the other hand, were more high luminance dots amid less low luminance dots, or less low luminance dots amid more zero luminance dots.

In accord with the biased competition model of visual attention (Desimone & Duncan, 1995), high luminance contrast of stimulus features increased the susceptibility towards attentional capture. Therefore, as individual differences in working memory capacity have been shown – dependent on the functional quality of neural mechanisms for attentional filtering (Fukuda & Vogel, 2009; 2011), there are just as likely to be individual differences in the ability to make exogenously cued numerosity comparison judgements of dot arrays, dependent upon the functional quality of contrast gain control mechanisms mediated by receptive field (RF) suppression in LGN and V1 (Carandini, 2004; Carandini, Heeger & Senn, 2002).

The neurophysiological response properties for the following experiment were examined via magnetoencephalography (MEG). Previous MEG investigations into attentional filtering have revealed much about the functional characteristics of visual suppression, and further insight into the identification of distinct electrophysiological markers in its instantiation. For example, from a covert search task, Hopf et al., (2006) found that MEG source current distribution in V1 to V3 during attentional suppression, was characterised by a 'Mexican hat' type topography, where a central excitatory zone possessing a concentrated peak in source current amplitude, was surrounded by an inhibitory region that was characterized by markedly attenuated source current. The central excitatory peak of the attentional response, was suggested by the authors to be a functional reflection of target selection, and the inhibitory surround fall off in source current amplitude as task irrelevant distracter suppression. This centre-surround response was maximal between 130ms and 150ms following stimulus onset. Considered at whole, these observations indicate that the electrophysiological marker for sensory filtering is characterised by attenuation in source current density/amplitude, and that it occurs relatively early on during the process of selective attention in low order visual areas.

## 6.4. Aims and research questions

As evident from the literature reviewed, the functional role of visual inhibitory mechanisms in the attentional suppression of noisy or task irrelevant input has been well established empirically via neuroimaging modalities such as EEG, SSVEP, MEG and fMRI. However, there has so far been no investigation into individual differences of neural responses in the filtering out of highly salient yet contextually irrelevant stimulus features when making non-symbolic number comparison judgements. In fact, the majority of recent investigations into cortical response dynamics associated with numerical cognition have been fMRI investigations rather than MEG studies into such cognitive domains. Therefore, the chief aims of the following experiment were to examine how observers with low and normal arithmetical ability filter out attentionally salient yet irrelevant sensory information, and process contextually incongruent distracters via MEG.

Are observers with normal arithmetical ability more efficient at resisting attentional capture of more numerous high luminance/contextually incongruent dots than observers with low arithmetical ability? If so, what are the functional characteristics of these neural mechanisms that distinguish or demarcate efficient comparison judgements through attentional suppression/sensory filtering across groups? For some trials of this experiment, the reference set of dots (distracters) amid the pre-cued targets to be attended, were not attentionally salient (low luminance). For example, a test stimulus was configured in such a way where there were fewer target high luminance dots amid more low luminance irrelevant dots. As in the fMRI experiments by Tsushima et al., (2006), it was of experimental interest to ascertain whether the contextual incongruity and ambiguous distracter conditions of this particular stimulus configuration could induce a similar type of interference with attentional suppression mechanisms. More specifically, what sort of electromagnetic response dynamics in V1 and fronto-parietal networks could be expected from making numerosity comparison judgements under such stimulus conditions?

One other question in relation to the following experiment was: what sort of electromagnetic response modulations can be expected within rTPJ with respect to attentional capture of high luminance dots which vary as a function of contextual congruency and numeric representation (less/more)? Does the contextually congruent stimulus configuration: More high luminance dots amid less low luminance dots activate rTPJ because of its low attentional load capacity? Also, does the contextually incongruent stimulus configuration: more low luminance dots amid less high luminance dots result in failure to activate rTPJ owing to its high demands on attentional load?

One final research question in relation to the following experiment was: what sort of differences in electromagnetic response properties of early visual areas (e.g. V1) can be expected from the background luminance of displays? That is, how do the electromagnetic responses of zero luminance background differ from uniform (grey) luminance background in sensory areas of visual processing such as V1? Is the effect of high luminance dots/zero luminance background more attentionally salient than zero luminance dots/uniform luminance background?

## 6.5. Method

The exogenous cueing of numerosity comparison (sensory filtering) MEG experiment was undertaken during the same session as the surround-masking experiment. Owing to a technical problem with the button response box, there were 20 out of 34 participants whose behavioural data was not logged. Hence, the response accuracy during performance of this task was analysed with 16 subjects. There were, however, no technical faults with the trigger pulse delivery hardware (Datapixx), and hence the MEG responses from all 34 subjects were included in the analysis.

### 6.5.1. Materials

**MEG task 2B stimuli (sensory filtering)**

The stimuli were once again generated from VPixx software (version 2.70, vpixx.com), and displayed on the same 1920 x 1080 pixel rear projection screen as the surround-masking MEG experiment. The main stimulus of this experiment was made up of a central circular aperture that was 564 x 564 pixels (20 x 20 deg). Within this aperture were two sets of simultaneously presented dots (10 x 10 pixels) that drifted randomly at 2.13 degrees per second (1 pixel per frame). One set of dots within this aperture was of high perceptual salience, and the second set of low salience. The dot sets were also varied by numeric representation, where one set of dots was twice as or half as numerous as the other – that is, a 1:2 ratio between dots sets. There were 4 parametric variations of the main stimulus presentation that were background luminance of the circular aperture (black: 0.30 cd/m$^2$, grey: 40.01cd/m$^2$); numeric representation of the attended to set of dots (fewer/more); difference in saliency between dots (high/low); difference in luminance between set of dots (bright/dim).

The sequence of stimuli within a single trial of this experiment is demonstrated in figure 6.1, where the initial stimulus, a centrally presented cross hair within the circular aperture (100 font size) was displayed for 1000ms. This was replaced by the dot display (main stimulus), which appeared for 150ms. Finally, there was a 150ms gap between presentation of the dot display and the final stimulus made up of static Gaussian noise with 0.5cm granularity. The purpose of the initial cross-hair stimulus was to cue the observer to which set of dots they were to selectively attend. For example, the experimental block that comprised the black ground had either a white (168.33 cd/$m^2$) or grey (40.07 cd/$m^2$) cue. Respectively, the experimental block that comprised the grey ground had either a black (0.30 cd/$m^2$) or grey (15.55 cd/$m^2$) cue.

There were 4 different conditions per experimental block, where the black background ground (zero luminance/dark grey) had 30 trials of the following: fewer low luminance dots (40.07 cd/$m^2$) as target amid more high luminance dots (140.33 cd/$m^2$); more low luminance dots as target amid fewer high luminance dots; fewer high luminance dots as target amid more low luminance dots; and more high luminance dots as target amid fewer low luminance dots. Also, the experimental block with the grey ground (low luminance) had 30 trials each of the following conditions: fewer low luminance dots (15.55 cd/$m^2$) as targets amid more zero luminance (0.30 cd/$m^2$) dots; more low luminance dots as targets amid fewer zero luminance dots; fewer zero luminance dots as targets amid more low luminance dots; and more zero luminance dots as targets amid fewer low luminance dots. The range of dots for both experimental blocks were: minimum 70 and maximum 125 for fewer target dots, and minimum 125 and maximum 250 dots for more target dots.

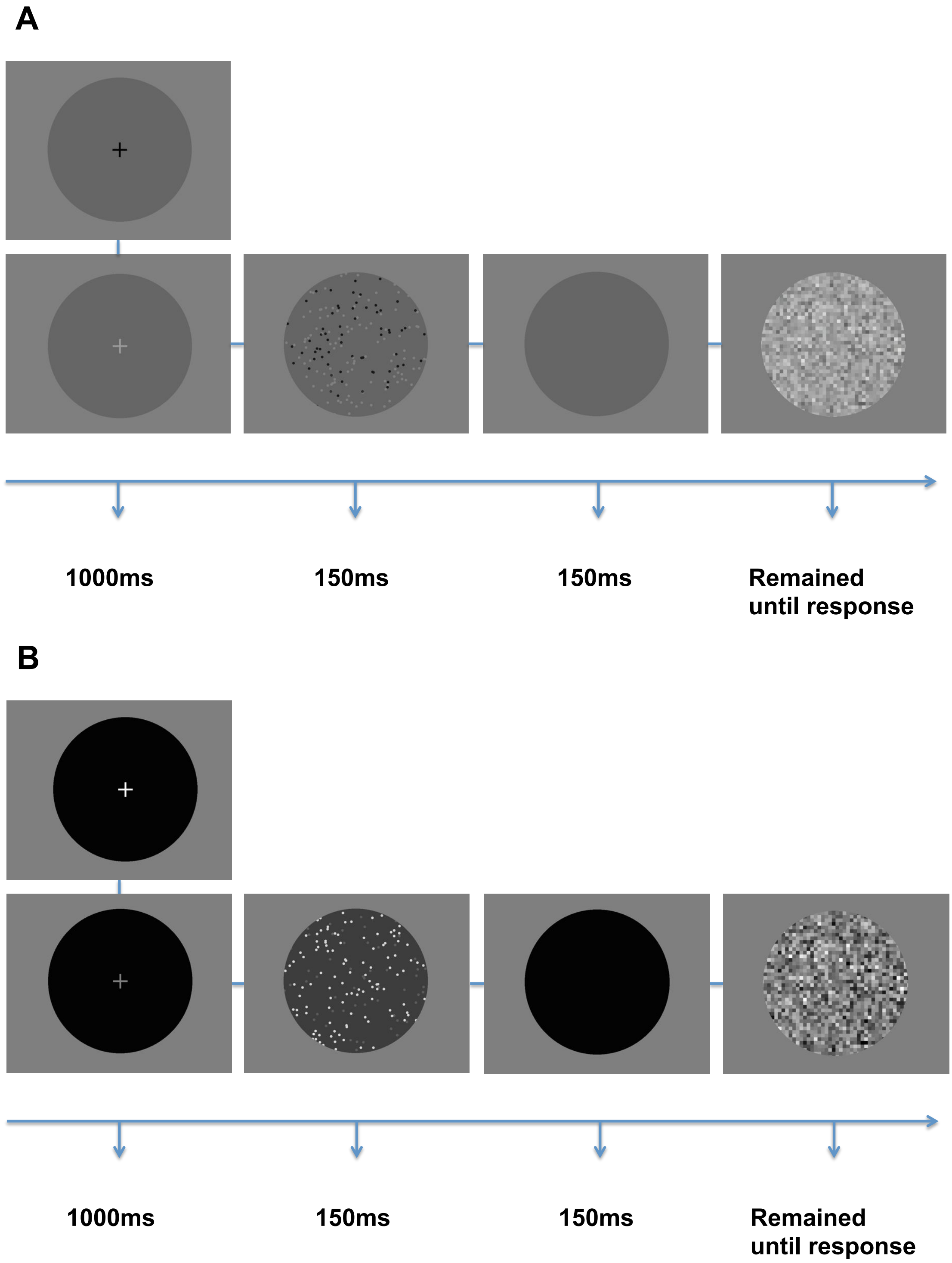


Figure 6.1.Trial sequence of attentional filtering and numerosity comparison experiment. Panel A: Low luminance background stimulus configuration; Panel B: Zero luminance/dark grey stimuli.

The task objective was to indicate via the RESPONSEPixx button box whether the target dot luminance was lesser (left/green button) or greater (right/red button) than the task-irrelevant dot set. Observers were required to respond following onset of the Gaussian noise stimulus. Once observers responded, a new trial commenced. Each condition within an experimental block was fully randomized and lasted approximately 15 minutes.

### 6.5.2. MEG data acquisition

See materials section of part 5 for a detailed description of data acquisition specifications, materials and procedure.

### 6.5.3. MEG data pre-processing

See MEG data pre-processing section of part 4b for detailed description for online filtering specifications, how external noise was removed from the raw data, corrected for head movement, spatially normalized to the common head co-ordinate system, filtering parameters, epoch rejection parameters, and removal of ECG/EOG artefacts. The epoch length for this experiment was a total of 600ms, where tmin was -200ms and tmax was 400ms. The cleaned epochs for each of the events were then averaged into evoked fields per condition and baseline corrected, where evoked fields were standardized to the zeroed out baseline period (-200ms-0ms).

### 6.5.4. Procedure

Once participants completed block 1 and block 2 of the MEG surround-masking experiments, there was a brief resting period (approximately 5 minutes) before going on to complete the following experiments. Each block took approximately 15 minutes to complete.

## 6.6. Results

### 6.6.1. Mean MEG number filtering behavioural responses

For the button (behavioural) responses during comparison judgements of simultaneously presented dot arrays, the proportion of incorrect responses per condition was calculated for each participant. There was, however, a technical problem with the button response box, where behavioural (accuracy) data for only 14 out of the 34 participants was obtained during the MEG data aquisitions. The mean proportion of error for each of the 8 dot luminance/background luminance conditions can be found within table 6.1. A graphic representation of these mean differences can be seen from the bar graphs in figure 6.2.

A series of paired t-tests (repeated measures) was performed in order to independently explore mean response times per condition concerning differences in background luminance and dot saliency; target dot number and representational congruity; target and distracter dot luminance; and dot number and target/distracter dot salience. The t-tests performed here were not post-hoc or family-wise comparisons, where each hypotheses test performed was completely independent from one another. Independence was determined by Pearson's *r* correlations, which revealed a non-significant relationship between variables for each t-test performed. Paired t-tests instead of ANOVAs were performed on the data in order to ensure consistency with the within groups comparisons performed here and in section 6.6.6.

Table 6.1.Mean and standard deviation of comparison judgment proportions

| | **Background** | | | |
|---|---|---|---|---|
| | **Grey background** | | **Black background** | |
| **Dot brightness** | Mean | *SD* | Mean | *SD* |
| **Low saliency** | Grey dots | | Grey dots | |
| Less dots | .24 | *(.15)* | .26 | *(.14)* |
| More dots | .50 | *(.22)* | .48 | *(.21)* |
| **High saliency** | Black dot | | White dot | |
| Less dots | .36 | *(.16)* | . 33 | *(.13)* |
| More dots | .19 | *(.11)* | .21 | *(.14)* |

N=14

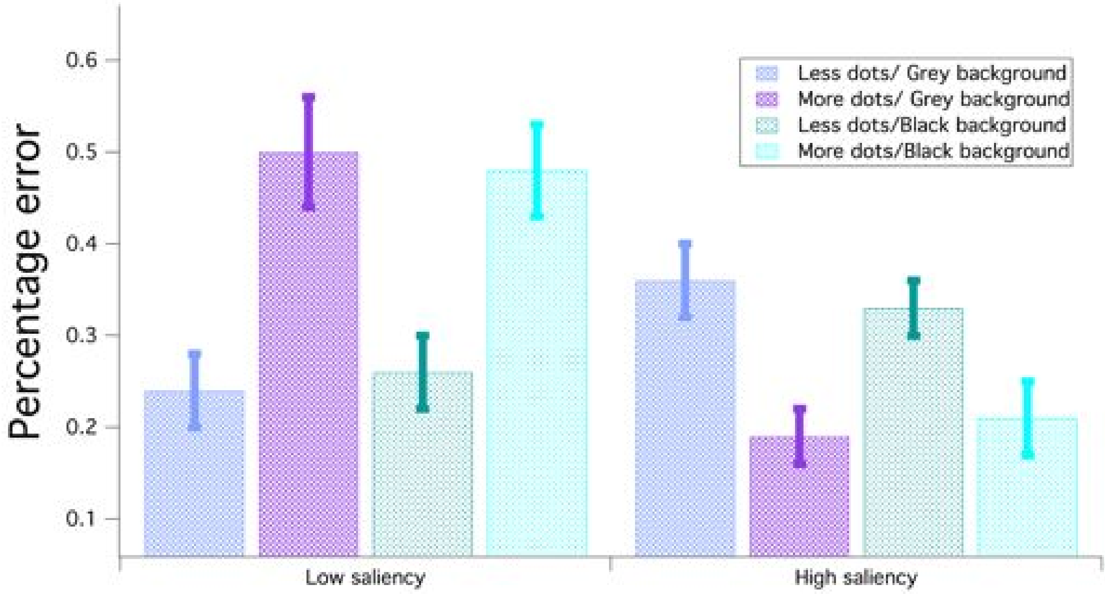


Figure 6.2.Bar graph of mean and standard error proportion. The lines in the centre of the bar are the standard error. It can be seen that the greatest proportion of error was when participants made comparisons of more low luminance (low saliency) target dots amid fewer high luminance distracter dots under grey background (low luminance) conditions. Respectively, the lowest proportion of error was when participants made comparisons of more high luminance (high saliency) target dots amid fewer low luminance distracter dots under grey background conditions.

### 6.6.2.Contrasts between background luminance and dot saliency

The first four paired t-tests compared mean differences between error proportions of comparison judgements for fewer/more dots of high/low saliency amid background luminance (black/grey). Findings revealed that there were no significant differences between mean error proportions for fewer low luminance (grey) target dots amid more higher luminance (white) distracter dots with black background (LLld_zlg) and fewer low luminance target dots amid more zero luminance (black) distracter dots with grey background (LLld_llg); more low luminance target dots amid fewer higher luminance distracter dots with black background (MLld_zlg) and more low luminance target dots amid fewer zero luminance distracter dots with grey background (MLld_llg); fewer high luminance target dots amid more low luminance distracter dots with black background (LHld_zlg) and fewer zero luminance target dots amid more low luminance distracter dots with grey background (LZld_llg); and nor the contrast between more high luminance target dots amid fewer low luminance distracter dots with black background (MHld_zlg) and more zero luminance target dots amid fewer low luminance distracter dots with grey background (MZld_llg).

The non-significant differences between the LLld_zlg/MLlld_zlg and LLls_llg/MLld_llg contrasts suggested that the background luminance had no effect upon the perceived numerosity of target or distracter dots.

### 6.6.3.Contrasts between target dot number (fewer/more) and representational congruity

The next four paired t-tests compared the mean error proportion scores between fewer and more dots, holding constant background luminance and target dot saliency. There was a significant difference between mean error proportion of LLld_zlg and MLld_zlg, where observer error in making comparisons of fewer dim dots amid twice as many bright dots, were 22% lower than comparison judgements of more dim dots amid half as many bright dots *(t(13)=4.03,p=<.0005, 1-tailed)*. There were also significant differences between the mean error proportions of LHld_zlg and MHld_zlg, where observer error rates in making comparison judgements of more bright dots amid half as many dim dots, were 12% lower than numerosity comparison judgements of fewer bright dots amid twice as many dim dots *(t(13)=2.21,p=.023, 1-tailed)*.

Akin to the preceding contrasts with zero luminance background, there was a significant difference between mean error proportions of LLld_llg and MLld_llg, where observer errors rate in making comparison judgements of fewer dim target dots amid twice as many black dots, were 26% lower than comparison judgements of more dim target dots amid half as many black dots *(t(13)=3.5,p=.002, 1-tailed)*. There were also significant differences between the mean error proportions of LZld_zlg and MZld_zlg, where error in making comparison judgements of more black target dots amid half as many dim distracter dots, were 17% lower than comparison judgements of fewer black target dots amid twice as many dim distracter dots *(t(13)=4.34,p=<.0005, 1-tailed)*.

The significant differences between the LLld_zlg/LLld_llg and MLld_zlg/MLld_llg contrasts – that is, less error during comparisons of fewer low saliency (dim) dots amid twice as many high saliency (black/white) dots, suggests there was a representational congruity between ‘fewer’ and ‘low salience’ dots that required recruitment of attentional enhancement mechanisms. Conversely, the significant differences between LHld_zlg/LZld_llg and MHld_zlg/MZld_llg contrasts – that is, less error during the comparison of more high salience dots amid half as many low salience dots, suggests that fewer high saliency distracter dots induced cognitive interference effects during these conditions.

### 6.6.4.Contrasts between target and distracter dot Luminance

The next set of paired t-tests compared mean proportion of error scores between bright and dim target dots, holding constant dot numerosity and background luminance. There were no significant differences between mean error proportion comparisons of LLld_zlg and LHld_zlg. However, there was a significant difference between the mean error proportions of MLld_zlg and MHld_zlg, where observer error rates in making comparison judgements of more bright target dots amid half as many dim dots, were 27% lower than comparison judgements of more dim target dots amid half as many bright dots *(t(13)=4.29,p=<.0005, 1-tailed)*.

There were also significant differences between mean error proportion scores of LLld_llg and LZld_llg, where observer error rates in making comparison judgements of fewer dim target dots amid twice as many black distracter dots, were 12% lower than comparison judgements of fewer black target dots amid twice as many dim distracter dots *(t(13)=2.79,p=.005, 1-tailed)*. Finally, there were highly significant differences between MLld_llg and MZld_llg, where observer error rates in making comparison judgements of more black target dots amid half as many dim distracter dots, was 31% lower than numerosity comparison judgements of more dim target dots amid half as many black distracter dots *(t(13)=6.15,p=<.005, 1-tailed)*. The significant differences between MLld_zlg/MLld_llg and MHld_zlg/MZld_llg contrasts – that is, less error during comparisons of more high salience target dots amid fewer low salience distracter dots, once again suggested that observers capitalised upon the representational congruity between ‘more’ and ‘high salience’ dots that were recruited as part of the cortical mechanisms of attentional selection.

### 6.6.5.Contrasts between dot number and target/distracter dot salience

The final set of t-tests compared the mean proportion of error score differences between fewer/more dots with high/low salience distracter dots, holding constant the background luminance. There were no significant differences between mean proportion of error for comparisons between LLld_llg and MZld_llg or LLld_zlg and MHld_zlg. There were, however, significant differences between the mean error scores of LZld_llg and MLld_llg, where observers error rates in making comparison judgements of fewer black target dots amid twice as many dim distracter dots, were 14% lower than comparison judgements of more dim target dots amid half as many black distracter dots *(t(13)=2.17,p=.024, 1-tailed)*. Likewise, there were also marginally significant differences between the mean error scores of LHld_zlg and MLld_zlg, where observers error rates in making comparison judgements of fewer bright target dots amid twice as many dim distracter dots, were 14% lower than comparison judgements of more dim target dots amid half as many bright distracter dots *(t(13)=2.45,p=.014, 1-tailed)*.

Overall, cognitive interference effects were demonstrated during number comparison judgements of target dots that did not match congruently with their saliency. These interference effects were seen for example, during comparison of more dim target dots amid fewer high salience distracter dots, and fewer high salience target dots amid more low salience distracter dots. It was uncertain whether these cognitive interference effects were attributed to disturbances in attentional suppression induced by representational incongruities, or capacity limitations in sensory load. These problems will be addresses in the next section of this analysis.

### 6.6.6.Spatio-temporal cluster analysis of ERF sensory filtering responses

Analyses of the evoked fields were performed by means of within-groups spatio-temporal permutation F-test in sensor space with magnetometers using MNE-python (version 0.9.0) analysis tool (Gramfort, et al., 2013). The statistical contrasts performed here examined differences in electromagnetic response properties of statistically significant paired t-tests earlier implemented on the mean proportion of error scores for each of the 8 stimulus conditions.

To recapitulate, of the 16 paired t-tests performed on error proportion scores, seven were non-significant. Here, the same statistical contrasts were performed using the spatio-temporal cluster test to examine ERF differences in significant paired t-tests performed on error scores. Of the 9 spatio-temporal cluster tests performed, none of them were significant. Because of this, spatio-temporal cluster contrasts were performed on the remaining 7 possible combinations of statistical contrasts. Out of these, there were only 4 significant spatio-temporal permutation tests that were significant.

The following four spatio-temporal permutation tests contrasted differences in ERF response properties between luminance background (zero/low) and target dot luminance, holding constant the target dot numerosity. Noteworthy was that there were no significant differences in the behavioural responses – that is, the numerosity comparison error proportion rate for the following significant statistical comparisons.

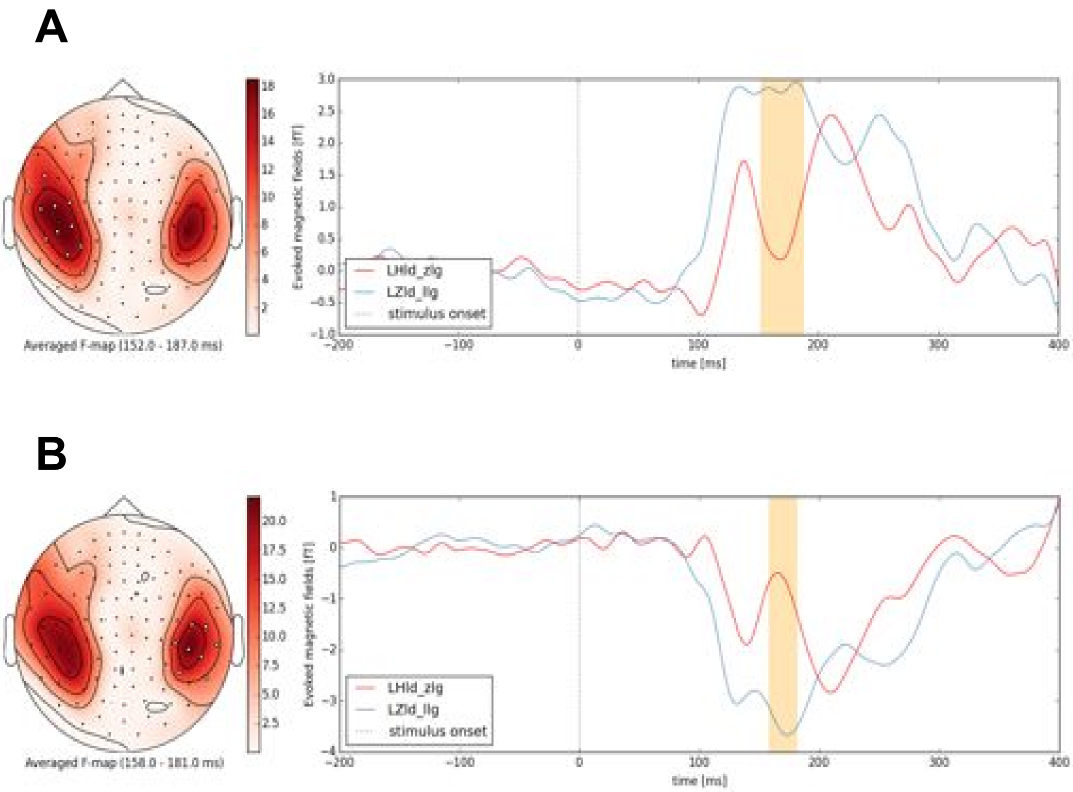


Figure 6.3.Averaged F-maps (left) and cluster time courses for within-group comparisons between zero and low luminance ground stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: fewer high luminance target dots amid more low luminance distracter dots with zero luminance ground (LHld_zlg); Blue ERF time-series: fewer zero luminance target dots amid more low luminance distracter dots with low luminance ground (LZld_llg). From panel A (cluster #1), it can be seen that the spatio-temporal cluster was localised to left pre-frontal regions of the sensor array. Of particular interest was the time-series of LHld_zlg, where a negative peak can be seen for this cluster approximately 160ms post stimulus onset. From panel B (cluster #2), it can be seen that the spatio-temporal cluster was localised to right pre-frontal regions of the sensor array. Of particular interest was the time-series of LHld_zlg, where a positive peak can be seen for this cluster approximately 160ms post stimulus onset. It was apparent that the spatio-temporal profile of cluster A and B are part of a dipole type evoked response.

The spatio-temporal permutation tests for the first contrast – LHld_zlg and LZld_llg resulted in two significant spatio-temporal clusters (F-threshold=10, p=.01). The averaged F-map in figure 6.3A shows a cluster of significant sensors in left temporal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that LHld_zlg and LZld_llg cluster traces were significantly different from 152ms to 187ms. Within this significant time window, the averaged left temporal-parietal trace of LHld_zlg was characterised by a negative peak response approximately 170ms post-stimulus onset. The averaged cluster trace of

LZld_llg on the other hand, was characterised as sustained positive response for the duration of the significant time window.

The second significant cluster that resulted from the LHld_zlg and LZld_llg contrast (figure 6.3B) shows an averaged F-map with a cluster of significant sensors localised to the right temporal-parietal region of the sensor array. The yellow band within the time course plot shows that the averaged cluster-2 time course between LHld_zlg and LZld_lld were significantly different from 158ms to 181ms. Within this significant time window, the averaged right temporal-parietal trace of LHld_zlg was comprised of a positive peak response approximately 170ms post-stimulus onset. The averaged cluster trace of LZld_llg respectively, was comprised of a negative peak response also at 170ms.

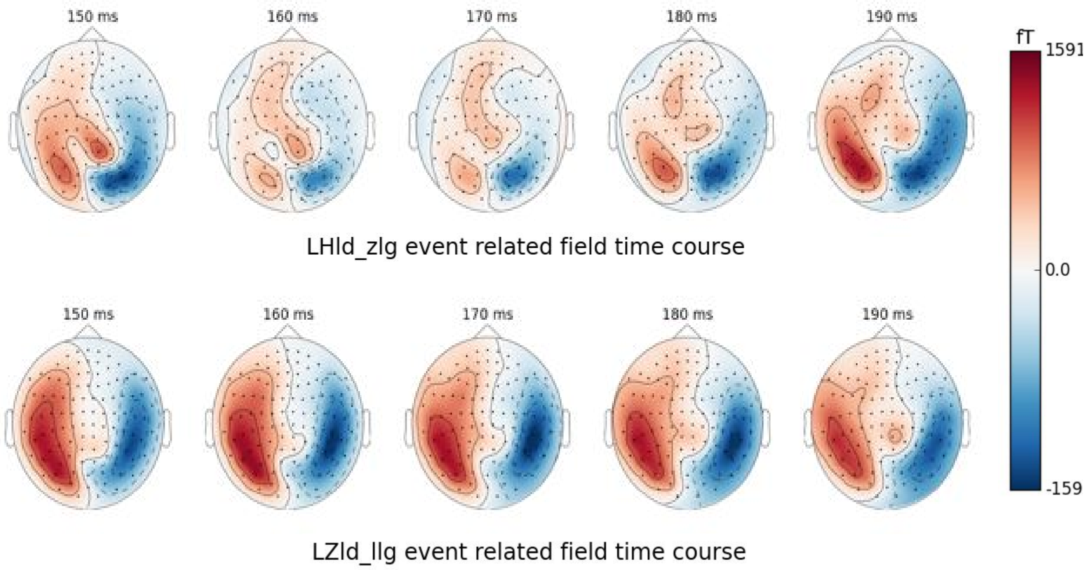


Figure 6.4.Topographic field maps of electromagnetic field responses from figure 6.3 (150ms to 190ms). The time windows of 2D field maps above (150ms to 190ms) were when LHld_zlg and LZld_llg responses were significantly different from one another. Note that the electromagnetic dipole of LZld_llg was of substantially greater amplitude than LHld_zlg. Both of these conditions were equally salient and were moreover contextually incongruent. Hence, these amplitude differences between occipito-parietal dipoles were likely attributed to differences in background luminance, where the low luminance background induced RF facilitation and the zero luminance ground induced RF suppression (Carandini, 2004).

Figure 6.4 shows the topographic field maps from 150ms to 190ms for LHld_zlg and LZld_lld. For the ERF topography of LZld_llg, note that the response amplitude of the electromagnetic field distribution across time was markedly greater than that of LHld_zlg. The low amplitude responses observed for the LHld_zlg ERF topography was likely attributed to RF suppression induced by the zero luminance background. In contrast, the low luminance background of LZld_llg was likely to have induced RF facilitation in V1 (or earlier) as evidenced by the higher amplitude ERF response distribution.

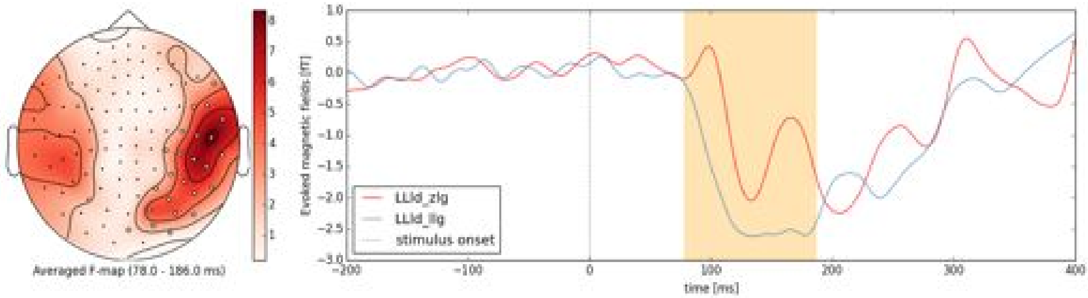


Figure 6.5.Averaged F-maps (left) and cluster time courses for within-group comparisons between zero and low luminance ground stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: fewer low luminance target dots amid more high luminance distracter dots with zero luminance ground (LLld_zlg); Blue ERF time-series: fewer low luminance target dots amid more zero luminance distracter dots with low luminance ground (LLld_llg). It can be seen that the spatio-temporal cluster was localised to right temporal-parietal regions of the sensor array. Of particular interest was the time-series of LLld_llg, where a negative peak can be seen for this cluster from 160ms to 190ms post stimulus onset. Given that the spatio-temporal cluster was localised to right temporal-parietal regions of the sensor array, it was likely that the ventral fronto-parietal network was recruited in order to select the most perceptually salient stimuli (Corbetta & Shulman, 2002).

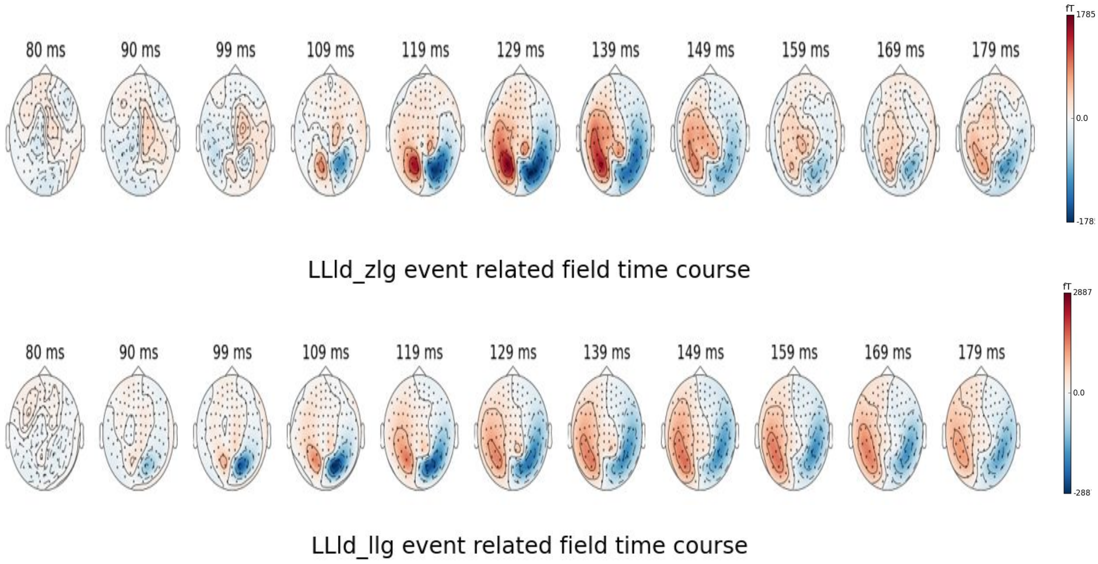


Figure 6.6.Topographic field maps of electromagnetic field responses from figure 6.5 (80ms to 179ms). The time windows of 2D field maps above (80ms to 179ms) were when LLld_zlg and LLld_llg responses were significantly different from one another.

The spatio-temporal permutation tests for the second contrast – LLld_zlg and LLld_llg resulted in one significant spatio-temporal cluster (F-threshold=5, p=.02). The averaged F-map in figure 6.5 shows a cluster of significant sensors in right temporal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that LLld_zlg and LLld_llg cluster traces were significantly different from 78ms to 186ms. Within this significant time window, the averaged right temporal-parietal trace of LLld_zlg comprised two positive peak responses that occurred at approximately 100ms and 170ms post-stimulus onset. The averaged cluster trace of LLld_llg in contrast, involved a sustained negative response that peaked from approximately 120ms to 180ms.

Figure 6.6 shows the topographic field maps from 80ms to 179ms for LLld_zlg and LLld_llg ERF responses. For the ERF response characteristics of LLld_zlg, note the occipital-parietal dipolar structure from 119ms to 139ms. It possessed a similar spatial and temporal signature to that of LLld_llg, however of greater amplitude. The similar spatio-temporal signature of this ERF contrast suggests that there were similar cortical processes involved with the comparison of fewer low salience target dots amid twice as many high salience distracter dots – irrespective of background luminance

The spatio-temporal permutation tests for the third contrast – MHld_zlg and MZld_llg resulted in one significant spatio-temporal cluster (F-threshold=5, p=.02). The averaged F-map in figure 6.7 shows a cluster of significant sensors in left frontal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that MHld_zlg and MZld_llg cluster traces were significantly different from 134ms to 194ms. Within this significant time window, the averaged left frontal-parietal trace of MHld_zlg was characterised by a negative peak response approximately 160m post-stimulus onset. In contrast, the averaged cluster trace of MZld_llg comprised of a positive peak response at approximately the same time window (160ms).

Figure 6.8 shows the topographic field maps from 135ms to 185ms of MHld_zlg and MZld_llg ERF responses. For the ERF topography of MZld_llg, note that like LZld_llg, the response amplitude of the electromagnetic field distribution across time was markedly greater than that of MHld_zlg. Once again, the high amplitude dipolar response within the sensor array of the MZld_llg time course was possibly a functional reflection of RF facilitation in V1 (or earlier) induced by the low luminance background.

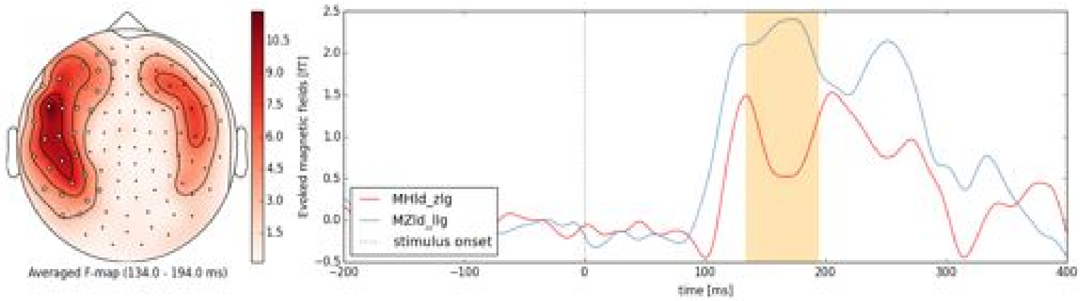


Figure 6.7.Averaged F-maps (left) and cluster time courses for within-group comparisons between zero and low luminance ground stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: more high luminance target dots amid fewer low luminance distracter dots with zero luminance ground (MHld_zlg); Blue ERF time-series: more zero luminance target dots amid fewer low luminance distracter dots with low luminance ground (MZld_llg). It can be seen that the spatio-temporal cluster was localised to left pre-frontal regions of the sensor array. Of particular interest is the time-series of MHld_zlg, where a negative peak can be seen for this cluster approximately 160ms post stimulus onset.

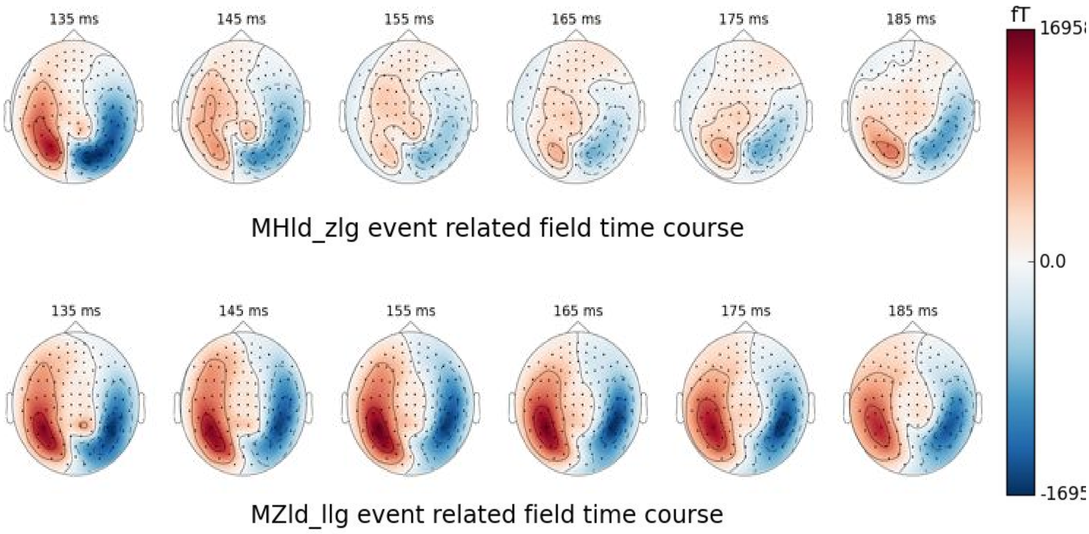


Figure 6.8.Topographic field maps of electromagnetic field responses from figure 6.7 (135ms to 185ms). The time windows of 2D field maps above (135ms to 185ms) were when MHld_zlg and MZld_llg responses were significantly different from one another. Note that the electromagnetic dipole of MZld_llg was of substantially greater amplitude than MHld_zlg. Both of these conditions were equally salient and were moreover contextually incongruent. Hence, these amplitude differences between occipito-parietal dipoles were likely attributed to differences in background luminance, where the low luminance background induced RF facilitation and the zero luminance ground induced RF suppression (Carandini, 2004).

The spatio-temporal permutation tests for the fourth contrast – MLld_zlg and MLld_llg resulted in two significant spatio-temporal clusters (F-threshold=10, p=.01). The averaged F-map in figure 6.9A shows a cluster of significant sensors in right temporal-parietal regions of the sensor array. From the averaged cluster time course plots, it can be seen that MLld_zlg and MLld_llg cluster traces were significantly different from 152ms to 184ms. Within this significant time window, the averaged right temporal-parietal trace of MLld_zlg comprised a positive peak response approximately 160ms post-stimulus onset. The averaged cluster trace of MLld_llg was respectively comprised of a negative peak response at approximately the same time instant.

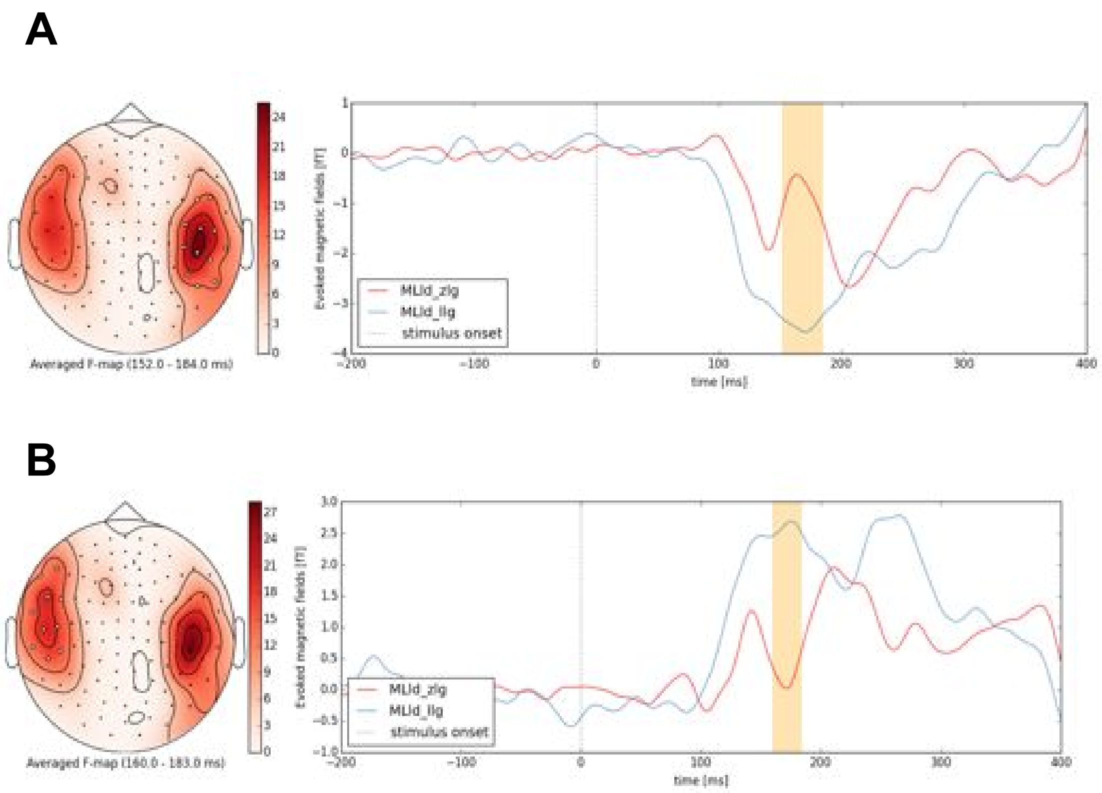


Figure 6.9.Averaged F-maps (left) and cluster time courses for within-group comparisons between zero and low luminance ground stimuli (magnetometers). The yellow/orange band within the right panel denotes the duration at which the time-series were significantly different. Red ERF time-series: more low luminance target dots amid fewer high luminance distracter dots with zero luminance ground (MLld_zlg); Blue ERF time-series: more low luminance target dots amid fewer zero luminance distracter dots with low luminance ground (MLld_llg). It can be seen that the spatio-temporal cluster was localised to right temporal-parietal regions of the sensor array. Of particular interest was the time-series of MLld_llg, where a negative peak can be seen for this cluster approximately170ms post stimulus onset. Given that the spatio-temporal cluster was localised to right temporal-parietal regions of the sensor array, it was likely that the ventral fronto-parietal network was recruited in order to select the most perceptually salient stimuli (Corbetta & Shulman, 2002).

The second significant cluster that resulted from the MLld_zlg and MLld_llg contrast (figure 6.9B) shows an averaged F-map with a cluster of significant sensors localised to the left frontal-temporal region of the sensor array. The yellow band within the time course plot shows that the averaged cluster-2 time course between MLld_zlg and MLld_llg were significantly different from 160ms to 183ms. Within this significant time window, the averaged left frontal-temporal trace of MLld_zlg was this time was characterised by a negative peak response approximately 160ms post-stimulus onset. The averaged cluster trace of MLld_llg was characterised by a positive peak response also at 160ms.

Figure 6.10 shows the topographic field maps of MLld_zlg and MLld_llg from 140ms to 190ms. There appeared to be consistency in the ERF response distribution across all four contrasts that indicated zero luminance (black) background had a suppressive effect upon evoked electromagnetic fields within parietal-occipital regions of the sensor array. This suppressive type response was evidenced by lower amplitude of the dipole distribution as compared to the ERF responses from stimuli with a low luminance background.

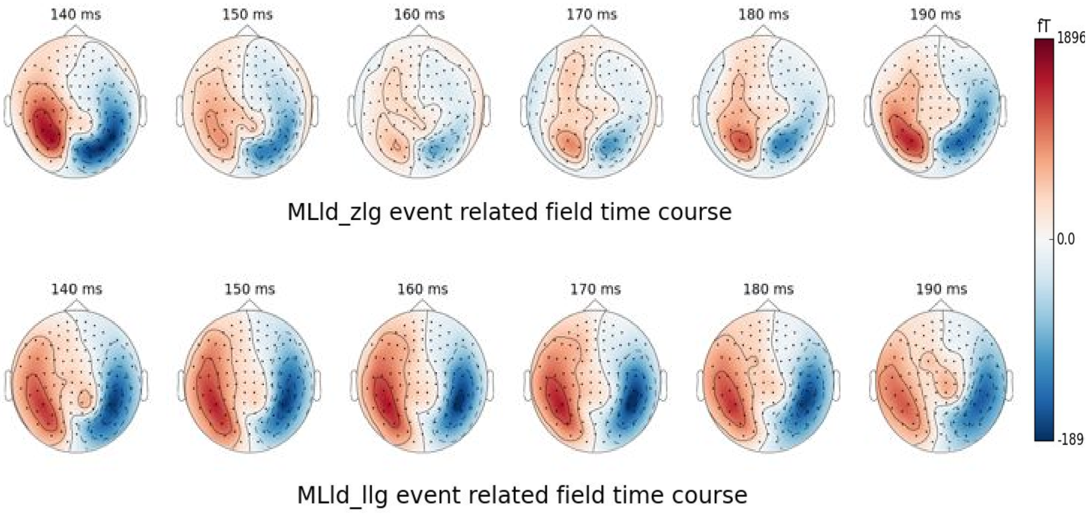


Figure 6.10.Topographic field maps of electromagnetic field responses from figure 6.9 (140ms to 190ms). The time windows of 2D field maps above (135ms to 185ms) were when MLld_zlg and MLld_llg responses were significantly different from one another. Note that the electromagnetic dipole of MLld_llg was of substantially greater amplitude than MHld_zlg. Both of these conditions were equally salient and were moreover contextually incongruent. Hence, these amplitude differences between occipito-parietal dipoles were likely attributed to differences in background luminance, where the low luminance background induced RF facilitation and the zero luminance ground induced RF suppression (Carandini, 2004).

# 6.7. Discussion

## 6.7.1. Behavioural analysis (proportion of error)

The essential findings from this data – that comparison judgements of target dot arrays were easier under conditions where there was a semantically congruent match between numerosity representation and target dot saliency, suggests a functional role for feature based selective attention in the distinction between fewer and more dots within the display. This conclusion was arrived at from an earlier conjecture that the locus of covert feature based attention is likely to occur by means of a ‘winner take all’ process, where attentional selection (or enhancement) of the most relevant stimulus representation overrides the task-irrelevant or perceptually redundant stimulus components within a display (Carrasco, 2011; Desimone & Duncan, 1995).

This biased competition model of visual attention (Desimone & Duncan, 1995), can be generalised to the main findings of this experiment in the following respect: In the correct selection of more high luminance target dots amid fewer low luminance distracter dots for instance, the representation of more dots was the winning feature of attentional resources because of its higher level of salience and contextual congruity between luminance and numeric representation.

The other essential findings from this data – that numerosity comparisons of target dot arrays were substantially more difficult under conditions where a contextually incongruent match occurred between numerosity representation and target dot saliency suggests a transient disruption in the neural mechanisms involved with attentional and sensory suppression in filtering out irrelevant psychophysical properties uninformative about numerosity of target dots. This conclusion was warranted by earlier psychometric and neuroimaging investigations that noted a similar type of Stroop interference for stimuli with representational incongruence. Pansky and Algom (2002) for example, observed a similar numerical interference effect to the one noted here, where RTs for magnitude comparison judgements of displays that involved a contextual mismatch between numerosity of digits and their numerical representation, were substantially more delayed than displays that were congruent between symbolic and non-symbolic representation of cardinality.

More specifically, Stroop interference effects were most prominent with displays when observers were required to indicate which of two arrays contained a greater non-symbolic numerosity of alphanumeric digits that were representationally 'fewer' along the number line (e.g. an array of eight alphanumeric 2 digits compared to an array of two alphanumeric 8 digits). These cognitive interference effects were not unlike the ones observed within this investigation, where error was much higher for instance, when observers were required to make numerosity comparison judgements of more low luminance target dots amid half as many high luminance distracter dots.

Pansky and Algom (2002) concluded from their findings that the Stroop like interference observed from magnitude comparison judgements of contextually incongruent pairs of number arrays, was attributed to salience of the numerical dimension to be ignored, where attentional capture of more numerous digit arrays were more difficult to resist than those with fewer elements – irrespective of the cardinal representation of digits/elements within the target array. In a similar manner, the proportion of error during comparison judgements of target dots that were highly salient (e.g. high luminance) yet contextually irrelevant to their numeric representation were likely to be higher from a similar interference upon the discriminability between fewer and more dots.

One of the first neuroimaging investigations into the effects of luminance on symbolic numerical comparisons (Cohen-Kadosh, Cohen-Kadosh & Henik, 2008), also found from their accompanying behavioural/RT data, a Stroop like interference when the luminance of alphanumeric digits were contextually incongruent with their numeric representation. More specifically, magnitude comparison RTs were significantly delayed when digits of greater numerical value were of low luminance and respectively, when digits of lower numerical value were of higher luminance. On the other hand, magnitude comparison RTs were significantly faster when digits of greater numerical value were of higher luminance, and for when digits of lower numerical value were of lower luminance. In view of the similarity of this data to the main findings observed for the current experiments, it may be inferred that the non-spatial dimensions of magnitude such as luminance generates cognitive interference during processing of magnitude difference, irrespective of whether numeric representation is expressed in terms of symbolic (alphanumeric digits) or non-symbolic (dot arrays) representations of number.

One limitation upon the analysis of comparison judgement response accuracy was a technical problem with the button response box, where the proportion of errant responses could only be calculated for 14 out of 34 participants. Hence, there was not a sufficient amount of statistical power to perform more complex analyses such as correlations, regressions or ANCOVAs with other variables in this investigation such as WAIS-arithmetic scores, or true/false judgement scores. Nonetheless, 16 paired t-tests (repeated measures) were performed on the behavioural data for all 8 conditions. Of the 16 paired t-tests performed, 9 of them were significant, which showed that overall, there were fewer estimation comparison errors when there was a congruent match between the salience of the attended to dots and their numerosity representation. For example, the mean error for comparison judgements of more high luminance (bright) target dots amid fewer low luminance (dim) distracter dots, was significantly lower than those for fewer bright target dots amid more dim distracter dots.

Neither the background luminance of the stimulus display or polarity of the high salience dots (black or white) had an effect upon the perceived saliency of dots or the error proportion of comparison judgements. That is, white/high luminance dots were equally salient as black/zero luminance dots, evidenced by the non-significant differences between comparison judgement error rates between more/fewer white target dots amid fewer/more dim distracter dots, and more/fewer black target dots amid dim fewer/more distracter dots. In terms of differences in background luminance of the stimulus display – that is, grey (mid luminance) of black (zero luminance), there was also no influence upon the perceived salience or numerosity of target dots. This was evidenced by the non-significant differences between proportion of error scores for comparison judgements of fewer/more dim target dots amid more/fewer high luminance distracter dots against a black background, and fewer/more dim target dots amid more/fewer black distracter dots against a grey background.

In conclusion, it has been indicated elsewhere that feature based selective attention occurs by means of perceptual enhancement of the attended to stimulus features, with a concomitant suppression of the ignored task-irrelevant features (Andersen & Müller, 2010). In relation to this, it has been conjectured that attentional selection and noise exclusion (sensory suppression) are not mutually exclusive processes, and that these mechanisms in combination with one another serve to enhance the contextual information within the locus of attention by means of filtering out perceptually uninformative visual input via external noise exclusion (Carrasco, 2011). In the instance of the cognitive interference effects observed from this experiment – that is, a higher proportion of error for comparison judgements of fewer high luminance target dots amid more low luminance distracter dots for example, was therefore attributed to conflict between attentional suppression and enhancement mechanisms, where selection and noise exclusion may have occurred simultaneously within the locus of attention. The electromagnetic dynamics of these processes are discussed in the following section.

### 6.7.2. Spatio-temporal cluster analysis (MEG analysis)

The purpose of the following analysis was to examine electromagnetic response differences associated with the earlier within-group comparisons of behavioural data previously discussed (the error proportion of comparison judgements across all 8 conditions). To reiterate, out of the 16 paired t-tests performed on the mean error proportion of comparison judgements for all 8 conditions, 9 of them were significant. The same comparisons were performed on the MEG data that corresponded to the behavioural responses (button presses), where zero out of the nine permutations performed were significant. From this, a separate spatio-temporal cluster analysis was performed, with 4 within-group contrasts that examined differences in ERF response characteristics between background luminance and salience of dots. All 4 of these spatio-temporal cluster tests were significant where no mean group differences were observed for the t-tests performed on their respective behavioural responses.

It was uncertain as to why there were no significant differences between error proportions for numerosity comparison judgements of fewer high luminance target dots amid more low luminance distracter dots against a black background and fewer zero luminance target dots amid more low luminance distracter dots against a grey background for example, when the MEG spatio-temporal permutation tests for these behavioural responses were significant. There were two of these spatio-temporal cluster tests that compared ERF responses for contextually congruent stimuli (fewer low luminance target dots amid more bright distracter dots against a black background/ fewer low luminance target dots amid more black distracter dots against a grey background and more high luminance target dots amid fewer low luminance distracter dots against a black background/ more zero luminance target dots amid fewer low luminance distracter dots against a grey background), and the other two respectively, compared ERF responses for contextually incongruent stimuli (more low luminance target dots amid fewer bright distracter dots against a black background/ more low luminance target dots amid fewer black distracter dots against a grey background and fewer high luminance target dots amid more low luminance distracter dots against a black background/ fewer zero luminance target dots amid more low luminance distracter dots against a grey background).

From inspection of the spatio-temporal cluster plots of contextually incongruent ERF responses (see figure 6.4, and figure 6.9), it was apparent that significant ERF responses were characterised by differences in polarity of peak amplitudes within the significant time window (~150ms to ~190ms). That is, the averaged left posterior parietal cluster traces for stimuli with a grey/low luminance background comprised a positive high amplitude peak response, and respectively, stimuli with a black/zero luminance background were characterised by negative peak responses approximately 180ms post stimulus onset. These differences in peak responses for within group comparisons of contextually incongruent ERF responses, suggests that the background luminance of stimuli had a modulatory effect upon the neural mechanisms involved with attentional enhancement and attentional suppression, where other parameters such as differences in polarity of high salience target dots (black or white); numerosity of target dots (fewer or more); and salience of distracter dots did not appear to influence the differences in ERF responses. Attentional suppression and attentional enhancement were implicated with these responses because of the spatial localisation of significant clusters that were proximal to the left dorsal fronto-parietal areas (Corbetta & Shulman, 2002).

There was a common spatial pattern across the four permutation tests performed. The spatial localisation of significant clusters for the contextually congruent and incongruent within-group comparisons were situated within left fronto-parietal regions of the sensor array. It may be inferred from this observation that attentional response gain to target dots was enhanced by the low luminance background and attenuated by the zero luminance background – that is, attentional enhancement by the low luminance background was likely to have increased the amplitude of neural responses within left fronto-parietal regions of the cortex, and respectively, attentional suppression by the zero luminance background was likely to have decreased neuronal responses in the parietal cortex (Carrasco, 2011). If the dorsal fronto-parietal network had a functional role in attentional enhancement (increased response gain) during numerosity comparison of target dots, then the low luminance background was likely to have had a contribution toward the mechanisms involved with stimulus selection (Corbetta & Shulman, 2002).

In conclusion, given that the spatio-temporal permutation tests or within-group comparisons of ERF responses between contextually congruent and incongruent stimuli were non-significant, it was not possible to make inference about the functional role of sensory filtering in the suppression of unattended distracter dots. However, Cohen-Kadosh, et al., (2008) noted a similar effect from their fMRI investigation into the cortical responses associated with magnitude comparison interference via manipulations in luminance of the digits to be compared. More specifically, there was a significant main effect found for contextual congruity of magnitude comparison behavioural data, where RTs for trials that contained contextually incongruent stimuli (e.g. bright digits that were numerically lower compared with dim digits that were numerically higher) were significantly delayed compared to contextually congruent trials. For the concomitant fMRI responses to these stimuli, there was however, a different pattern of congruity effects emergent, where BOLD activation or right intra-parietal sulcus and right middle frontal gyrus were modulated by incongruities in luminance comparison judgements and not numerical comparison judgements as observed from the RT data.

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# Part 7

# General discussion and conclusion

## 7.1. Reiteration of investigative purposes and main findings

Based on previous psychophysical and psychometric investigations into processing of non-symbolic representation of number, it was postulated here and elsewhere that the neural mechanisms involved with numerosity comparison of large perceptual sets beyond the subitization range, involved the recruitment of low-order sensory areas such as V1 rather than high-order areas that sub-serve attentional resources such as pre-frontal cortex (Burr & Ross, 2008; Burr, Turi & Anobile, 2010; Ross & Burr, 2010; Vetter, Butterworth & Bahrami, 2008). By this reasoning, there is a given qualia for any perceived numerosity, where comparison of these perceptual sets are gleaned by their statistical descriptors such as mean and variance of the display – a putatively independent process that occurs in primary sensory areas (Burr & Ross, 2008; Ross & Burr, 2010).

It has not been explicitly specified as to how sensory processes of numerosity comparison occur in the brain, or by what mechanism(s) drive them. The use of the term ‘sensory process’ here, refers to the organization of afferent input into a meaningful and coherent percept. By this reasoning, one of the chief aims of this doctoral dissertation was to address this gap in understanding about spatial and temporal response characteristics associated with low-order and perceptual processes associated with ‘visual sense of number’ as postulated by Burr and Ross. One underlying assumption of this dissertation was that the sensory processes associated with numerosity perception were partly driven by the neural mechanisms involved with surround suppression – the attenuation of unessential visual information (Jastrzebski, Crewther & Crewther, 2015).

Given that there has been growing empirical evidence that suggests psychiatric disorders such as schizotypal personality disorder, full-blown schizophrenia, and autism spectrum disorder are commonly characterised by a functional anomaly of inhibitory mechanisms in lateral geniculate nucleus (LGN) and V1 (Dakin, Carlin & Hemsley, 2005; Tadin et al., 2006; Sutherland & Crewther, 2010), and that these same psychiatric disorders have also been linked with poor arithmetical skills (Meaux, Taylor, Pang, Vara & Batty; 2014; Weiser et al., 2003), one other principal aim of this dissertation was to ascertain whether there was a correlation between the functional quality of sensory gating mechanisms, and the extent of schizotypal/autistic traits, and arithmetical ability.

This dissertation was made up of four main studies in attempt to address the knowledge gap between early visual processing mechanisms, and how they are putatively involved with the perception of numerosity (Burr & Ross, 2008; Ross & Burr, 2010). The main purpose of the first study (psychophysics) was to ascertain whether surround-masking had a disruptive effect upon the comparison of numerosity. Given this was found, it was concluded that sensory gating resources were likely to functionally contribute to numerosity comparison processes. The main purpose of study two (cognitive and behavioural assessments) was to firstly assay the extent of schizotypal/autistic traits across participants, then to additionally measure their arithmetical and cognitive ability. A correlation analysis between SPQ/AQ scores and the cognitive assessment variables revealed that there was no significant relationship between any of the 9 SPQ sub-scales and arithmetical ability tests such as WAIS-arithmetic sub-test, WAIS-digit span, or computerised tasks. There were nonetheless significant correlations between the AQ sub-scales; WAIS digit-span sub-tests; and magnitude comparison RTs, which suggested that participants with AQ tendencies such as poor attentional shifting showed impairment in making magnitude comparison judgements, and the recall of digit strings in sequential order.

The main purpose of study three was an exploratory investigation into the electromagnetic response properties evoked by numerosity comparison judgements during surround-masking. A correlation analysis between MEG surround-masking RTs; WAIS-arithmetic sub-test scores; magnitude comparison RTs; and true/false judgement scores revealed an unexpected relationship between arithmetical ability and the disruptive effect of surround-masking on numerosity comparison, where, good/normal arithmetical skills were associated with slower RTs for numerosity comparison judgements during high contrast centre and high contrast surround conditions. These novel findings indicated that there was a link between the functional quality of sensory gating or inhibitory mechanisms, and numerosity comparison ability. Contrary to Burr et al., (2010), that estimation of numerosity does not require attentional resources, a within-groups spatio-temporal cluster analysis on MEG surround-masking responses revealed a significant cluster of sensors localised approximately to left pre-frontal and parietal regions of the sensor array. These findings indicated that indeed, attentional resources were quite high, especially during numerosity comparison judgements under high contrast centre and high contrast surround conditions.

Finally, the main purpose of study four was also an exploratory investigation into the functional role of feature-based selective attention, attentional suppression, and attentional enhancement during numerosity comparison. Essential findings were that numerosity comparison judgements were most difficult when the target dots to be compared contained contextually incongruent psychophysical properties – that is for example, more dim target dots amid fewer bright distracter dots. The within-groups spatio-temporal cluster analysis of MEG responses for this experiment revealed that the background luminance of the stimulus display had a modulatory effect upon the mechanisms involved with attentional enhancement and attentional suppression. The effect of luminance on attentional enhancement and attentional suppression was evidenced by the significant cluster of sensors localised to left pre-frontal and posterior parietal regions of the sensor array.

### 7.2. What do the main findings from each experiment suggest overall?

Overall, from each of the four experiments performed, it was possible to conclude that a link existed between the functional quality of sensory gain control mechanisms in V1 and LGN (Carandini, Heeger & Senn 2002), numerosity comparison ability (number acuity), and high-order arithmetical computation. This relationship was evident from the significant correlations between MEG surround-masking RTs and performance on cognitive assessments. More specifically, MEG surround-masking RTs for numerosity comparison judgements under high contrast centre and high contrast surround conditions, correlated positively with WAIS-arithmetical ability scores; true/false judgement scores, and negatively with magnitude comparison judgement RTs. These significant correlations suggested that participants, who were more competent at solving arithmetical problems and faster in making magnitude comparison judgements, were most adversely affected by making comparison judgements under these conditions.

Compellingly, MEG surround-masking RTs for numerosity comparison judgements under low contrast centre and low contrast surround conditions correlated positively with magnitude comparison RTs, which concomitantly indicated that participants who were slower in making magnitude comparison judgments required substantially more time in making accurate judgements under low contrast conditions. Overall, these correlations corroborate with the notion that high order cognitive representations of number are dependent somehow upon low-order and perceptual processes involved with numerosity comparison judgements. The sensory processes involved with numerosity comparison judgements moreover, were indicative as partly driven by surround suppression – the attenuation of redundant visual input.

It begs the question as to what can be concluded about the counterintuitive relationship found between the functional quality of sensory gating resources and high-order numerical ability – it was consistently apparent from correlation analyses that participants with lower arithmetical ability made more rapid judgements under high contrast conditions and slower magnitude comparison judgements under low contrast conditions than participants with higher arithmetical ability. One likely explanation was derived from two earlier psychophysical investigations into the perceptual consequences of surround-masking (centre-surround antagonism) in schizophrenic patients and neurotypical controls.

Both studies noted a similar advantage in psychophysical performance of schizophrenics under conditions that caused perceptual disturbances in the control groups (Dakin et al., 2005; Tadin et al., 2006). Dakin et al., (2005) for instance, noted that unlike neurotypical participants, contrast matching judgements of the schizophrenia group were unaffected by surround-masking. Accordingly, Tadin et al., (2006) also found that schizophrenic participants with the weakest surround suppression (poor inhibitory control) showed superior performance on motion discrimination judgements under high contrast and wide surround conditions than the neurotypical control group.

In conclusion, the participants with low arithmetical ability in this sample appeared to possess a similar type of perceptual processing abnormality in the inhibitory control of high contrast gain stimuli that was evident in schizophrenia. None of the participants in this sample, however, were schizophrenic, and the mean SPQ total score of this population was within the low to normal range. This observation suggests that such perceptual processing deficits can occur in the absence of psychotic (i.e. schizophrenia) or developmental disorders (i.e. ASD). While the origins of weak surround suppression mechanisms remain to be elucidated in detail, there has been magnetic resonance spectrographic evidence to suggest that it is a likely consequence of deficient GABA concentrations in V1 (Yoon et al., 2010).

### 7.3. Numerosity comparison judgements and executive functioning

Based on the postulation of Burr and Ross (2008), that "the visual system has the capacity to estimate numerosity and that it is an independent primary visual property", it was tentatively hypothesised here that the spatial localisation of significant sensor clusters for MEG surround-masking ERF responses, would be situated within occipital and parietal regions of the sensor array. Occipital and parietal responses were expected on the premise that numerosity comparison and inhibitory gain control mechanisms (sensory filtering) have been evidenced via fMRI to be mediated by these cortical areas (Nieder & Dehaene, 2009; Zenger-Landolt & Heeger, 2003). In other words, numerosity comparison judgements were expected to recruit low-level sensory processes and not high-order executive processes related for example, to attentional enhancement and attentional suppression.

Contrary to this however, the significant clusters across all seven within-group comparisons were localised approximately to left pre-frontal, parietal and cingulate regions of the sensor array. This unexpected spatio-temporal cluster profile was indicative that indeed, high-order executive functions were at play in the allocation of attentional resources during numerosity comparison judgements. It was uncertain however, as to how these putative attentional resources were allocated, or as to what executive processes were driving them. One can still speculate nonetheless, that there was wide spread surround-suppression in V1 generated by the high contrast centre/high contrast surround conditions, resulting in saturation of sensory gating resources. Consequently, the perceptual noisiness induced by overwhelmed sensory gating mechanisms, recruited additional high-order processes related to decision-making and error monitoring (Luu & Tucker, 2003; Holroyd & Coles, 2002).

This dissertation is the first investigation into the functional contribution of the perceptual noise exclusion mechanisms during the comparison of non-symbolic numerosity. Unexpectedly, the spatio-temporal cluster analysis on ERF responses revealed that sensory processes evoked via surround masking (i.e. contrast gain saturation), had a modulatory effect upon executive functioning and sensory processing. It remains to be elucidated however, as to whether these high-order processes were executed in response to attentional enhancement/suppression (Carrasco, 2011; Corbetta & Shulman, 2002), or the monitoring of predictive error signals (Holroyd & Coles, 2002).

To conclude from this, the absence of significant sensor clusters within occipital regions of the sensor array was by no means indicative of absence in sensory processing during numerosity comparison judgements. Rather, the impoverishment of inhibitory gain control mechanisms via surround-masking, yielded a tenable model of the developmental origins of dyscalculia. That is, greater cognitive effort may be required from dyscalculics when making numerosity comparison judgements because of a perceptual defect in the reduction of external noise (Jastrzebski et al., 2015; Lu & Dosher, 1999; Sigmundsson et al., 2010).

### 7.4. The recruitment of attentional resources during numerosity comparison

One other primary assumption of this dissertation was that the execution of numerosity comparison judgements required minimal cognitive effort and hence, the recruitment of high-order and attentional resources would be redundant under such conditions. This assumption was based on psychophysical evidence suggestive that numerosity comparison judgements well above the counting range were impervious to manipulations in attentional load (Vetter et al., 2008; Burr et al., 2010). Contrary to this however, the spatial localisation of significant clusters for comparisons between ERF responses of high and low contrast conditions were situated within pre-frontal and parietal regions of the magnetometer array. The spatial localisation of significant clusters for these comparisons indicated that attentional resources were indeed recruited during numerosity comparison judgements.

In this instance, variations in attentional load during numerosity comparison judgements appeared to be modified by centre/surround contrast parameters. For example, attentional load during numerosity comparison judgements was observed to be greatest under influence of the high contrast centre/high contrast surround, and almost absent for low contrast centre/low contrast surround conditions. These observations were apparent from the differences in peak electro-magnetic responses within left fronto-parietal clusters between these conditions. That is, the peak amplitude responses for numerosity comparison judgements under high contrast conditions, whilst negative, were much higher than the positive peak responses for judgements under low contrast conditions.

The peak ERF responses within fronto-parietal regions to numerosity comparison judgements in the presence of surround-masking were quite early – from 130ms to 190ms. In contrast to this, a recent MEG investigation into the neural mechanisms involved with numerosity estimation of autistic and neurotypical individuals revealed that executive processes within superior frontal gyrus of neurotypical participants occurred approximately 400ms post stimulus onset (Meaux, Taylor, Pang, Vara & Batty, 2014). In this investigation, numerosity estimation mechanisms were revealed by source imaging analysis to be made up of four main spatial and temporal signatures, starting with early occipital within 80ms to 120ms; temporal sources within 120ms to 290ms; parietal sources within 120ms to 400ms; and finally, frontal sources within the 400ms to 500ms time window. The early occipital sources were concluded to reflect extraction of perceptual properties within the array to be estimated – a sensory process. Temporal and parietal sources were moreover postulated to subserve processes related to the individuation of dot arrays and the integration of visuo-spatial information with numerical representation. Finally, late frontal sources were concluded to reflect executive processes such as decision-making and error monitoring of numerosity estimation judgements.

The main findings from the MEG surround-masking of numerosity comparison experiments corroborate with the findings of Meaux et al., (2014), where both investigations noted that estimation judgements require attentional resources – evidenced from the spatial localisation of electro-magnetic responses within frontal regions. However, there was wide variability in the temporal signatures of frontal peak responses between these investigations, where attentional modulation was observed to be relatively late for the Meaux et al. MEG study (400ms>) and unexpectedly early within this dissertation (130ms to 190ms). One other main difference between the spatial and electro-magnetic response profile between these investigations, was that there were early occipital sources associated with numerosity estimation judgements within the Meaux et al. study, where as there was a noticeable absence in occipital responses for the spatio-temporal cluster profile of the MEG surround-masking data presented here. It was uncertain as to why there were such differences in spatial and temporal response profiles for numerosity processing mechanisms between these two investigations. However, one may still conclude that both MEG investigations in combination with one another provide evidence that attentional load and sensory load are not mutually exclusive processes.

### 7.5. Future research directions

It was of paramount interest to examine whether there were definitive markers in the electromagnetic responses that would distinguish inhibitory from excitatory processes within early visual areas. Also of particular interest was to explore how individual differences in peak responses for numerosity comparison judgements within occipital sensors related to variations in RTs across high and low contrast conditions. However, it was not possible to determine a distinct bio-marker of the inhibitory mechanisms that were likely recruited during sensory filtering for numerosity judgements given that a) there were no significant sensor clusters observed within occipital regions for any of the MEG experiments performed, b) the spatial resolution of electro-magnetic field responses were not adequate enough to localise neural generators associated with inhibitory mechanisms, given that the type of MEG analysis was performed with magnetometers in sensor space (spatio-temporal cluster analysis).

One other major research limitation was that it was not possible to examine what type of relationship existed between peak amplitudes of electro-magnetic responses in occipital sensors; response times for MEG surround-masking judgements; and proportion of error rates for comparison judgements under selective attention. Because of this limitation, it was not possible to make inference about the functional quality of sensory gating resources across individuals, and its relation to individual differences in numerosity judgements.

In view of this, future investigations will feature a multiple regression analysis with for example, MEG surround-masking high contrast RTs as the dependent variable, and high contrast MEG surround-masking ERF peak responses; WAIS-arithmetic sub-test scores; magnitude comparison RTs; and true/false judgement scores as the predictor variables. The aim of this proposed analysis is to ascertain the unique variance explained by each predictor in the model upon the independent variable. That is, a multiple regression analysis upon each of these significantly correlated variables, will enable an insight into which predictor within the model contributed most prominently towards the response times for comparison judgements under high contrast conditions. From these findings, a hierarchical regression could be performed in order to establish a causal link between predictors and the dependent variable. For instance, a 2 stage hierarchical model with MEG surround-masking high contrast RTs as the dependent variable; high contrast MEG surround-masking ERF occipital peak responses at stage 1; and ERF fronto-lateral peak responses at stage 2 would enable the observation as to whether occipital or pre-frontal peak responses have mediating or direct effects upon numerosity judgement RTs under high contrast conditions.

**7.6 Conclusion**

The main postulation of this dissertation was that numerosity comparison judgements are likley to recruit the neural mechanisms involved with the elimination of redundant visual input (sensory filtering). One other central argument of this dissertation was that developmental dyscalculia may be partly explained by aberrant sensory filtering mechanisms.

This dissertation comprised of the first MEG exploratory analysis into the functional contribution of visual sensory gain control mechanisms in the effective comparison of non-symbolic numeric representations (i.e. more than or fewer than). This was achieved by manipulation of the psychophysical properties well known to modulate centre and surround regions of receptive fields within the geniculo-striate relay (Carandini, 2004; Carandini et al., 2002). Unexpectedly however, the spatio-temporal cluster analysis of contrast dependent electro-magnetic response differences revealed that numerosity comparison judgements were vulnerable to variations in attentional rather than sensory load, as evidenced by the localisation of significant sensor clusters within fronto-parietal rather than occipital-parietal regions of the magnetometer array.

As demonstrated by experiment 1 – the psychophysical effects of surround-masking on comparison judgements – performance was significantly compromised by the centre and surround stimuli with high contrast gain. From this observation, it was conjectured that a functional defect in the inhibitory control of unessential visual input was a likely contributor towards poor numerosity skills as apparent in developmental dyscalculia (Halberda et al., 2007; Piazza et al., 2010). A correlation analysis between the computerised task variables (magnitude comparison RTs and true/false judgement scores); cognitive assessment variables (WAIS-arithmetic sub-test scores and WAIS-digit span sub-test scores); and MEG surround-masking RTs revealed that indeed, there was a significant relationship between arithmetical ability and numerosity comparison RTs that varied as a function of contrast (high/low). Essentially, the significant correlations indicated that participants with normal arithmetical ability were markedly impaired at making numerosity comparison judgements under high contrast centre/high contrast surround conditions. Curiously, the comparison judgement RTs of participants with low arithmetical ability appeared to be uninfluenced and even advantaged by the high contrast centre/high contrast surround conditions.

Based on previous psychophysical investigations into the effects of surround suppression upon contrast discrimination and motion direction judgements of schizophrenic observers, it was concluded here that the counter-intuitive RT advantage observed for low arithmetic participants during judgements under high contrast centre/high contrast surround conditions, could be attributed to weakened inhibitory RF mechanisms in LGN and V1, given that schizophrenic participants – as with low arithmetic participants – were impervious to the deleterious effects on perceptual processing by surround-masking (Dakin et al., 2005; Tadin et al., 2006; Yoon et al., 2010). The essential findings from this dissertation have raised new questions regarding individual differences in numerosity comparison ability, and how the anomalous development of sensory gating mechanisms impact the ontological progression of number sense development, mathematical competence, and the cognitive representation of number. Further inquiry into these processes will adopt a neuroconstructivist perspective with respect to individual differences in numerical competence within clinical populations such as schizotypal personality disorder.

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# Appendix A: Surround-masking (Psychophysics)

Email from Swinburne ethics comitee for approval of these experiments:

>>> Resethics 12/03/12 2:09 PM >>>

To: Prof David Crewther/Ms Nicola Jastrzebski/Ms Laila Hugrass, FLSS

Dear David and Nicola

SUHREC Project 2012/016 The effects of centre-surround inhibition through surround masking on number perception
Prof David Crewther, FLSS; Ms Nicola Jastrzebski, Ms Laila Hugrass
Approved Duration: 7/03/2011 to 7/03/20 14 [Adjusted]

I refer to the ethical review of the above project protocol undertaken on behalf of Swinburne's Human Research Ethics Committee (SUHREC) by SUHREC Subcommittee (SHESC1). Your responses to the review, as emailed on 23 February 2012, were put to a SHESC1 delegate for consideration.

I am pleased to advise that, as submitted to date, the project has approval to proceed in line with standard on-going ethics clearance conditions here outlined. Please would you separately forward a copy of the finalised consent instruments for inclusion in the record as soon as practicable.

- All human research activity undertaken under Swinburne auspices must conform to Swinburne and external regulatory standards, including the National Statement on Ethical Conduct in Human Research and with respect to secure data use, retention and disposal.

- The named Swinburne Chief Investigator/Supervisor remains responsible for any personnel appointed to or associated with the project being made aware of ethics clearance conditions, including research and consent procedures or instruments approved. Any change in chief investigator/supervisor requires timely notification and SUHREC endorsement.

- The above project has been approved as submitted for ethical review by or on behalf of SUHREC. Amendments to approved procedures or instruments ordinarily require prior ethical appraisal/ clearance. SUHREC must be notified immediately or as soon as possible thereafter of (a) any serious or unexpected adverse effects on participants and any redress measures; (b) proposed changes in protocols; and (c) unforeseen events which might affect continued ethical acceptability of the project.

- At a minimum, an annual report on the progress of the project is required as well as at the conclusion (or abandonment) of the project.

- A duly authorised external or internal audit of the project may be undertaken at any time.

Please contact the Research Ethics Office if you have any queries about on-going ethics clearance, citing the SUHREC project number. Chief Investigators/Supervisors and Student Researchers should retain a copy of this email as part of project record-keeping.

Best wishes for the project.

Yours sincerely

Keith Wilkins
for Kaye Goldenberg
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*******************************************
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SWINBURN UNIVERSITY OF TECHNOLOGY

## Consent information statement
## What effect does a high contrast surrounding stimulus have upon number perception?

**Principal investigator:** Prof. David Crewther.
**Student investigators:** Ms Nicola Jastrzebski and Ms Laila Hugrass.

Our eyes can play tricks on us sometimes, so what is seen might not be an actual representation of whatever is being perceived. This is partly because the brain has to do a lot of work filtering out unnecessary information – sometimes the limit for this filtering process is exceeded by high information processing demands. When information processing limits are exceeded, sometimes the brain makes errors in coding these physical components of visual information and hence perceptual discrimination becomes impoverished and difficult.

### What is this project about and why it is being undertaken?

The central aim of this investigation is to examine what effect imposing capacity limits on the information filtering system – of the peripheral visual field – has upon the ability to make number estimation judgements of stimuli presented in the central area of the visual field. This psychophysical procedure is commonly known as the 'surround-masking' or 'surround-inhibition' paradigm. Previous surround-masking experiments have demonstrated that contrast matching judgements of centrally presented stimuli is greatly impaired only when embedded in a high-contrast surround stimulus. Hence, this research is being conducted in order to ascertain whether surround-masking effects are generalizable to estimation judgements of number sets. Moreover, this research forms part of the first named student investigators PhD research project (Nicola Jastrzebski). Ms Hugrass has kindly assisted in the development of some of the experiments used in this investigation and will collaborate in any publications that may result from these experiments.

### What participation will involve.

Participation in this study involves firstly completion of a demographic questionnaire, the informed consent form and then some simple computer based tasks that test arithmetic reasoning. Participation then involves undertaking a series of computer based psychophysical tests/experiments under various contrast conditions. Irrespective of contrast condition(low contrast centre/high contrast surround), the task objective is to indicate – by two alternate choice of keyboard response – whether a central region of the visual field contains more or less dots than a reference number of dots. Participation in this study (which is greatly appreciated) is on the basis of your voluntary consent, and may take approximately 2 hours.

#### Participant rights and interests – Privacy & Confidentiality

Given that participation is voluntary, you are free to withdraw at any point of this investigation without explanation. The information you provide as part of this investigation will be held confidential and retained securely in the principal investigators office. All information provided (informed consent, demographics, experimental data) will be replaced by codes that de-identify the participant from their data.

#### Research output

The potential findings emergent from this investigation may enable a better understanding of the sensory and perceptual processes involved with number sense. This may have potential benefits in the devise of remediation programs targeted at disorders in learning mathematics. The findings moreover will form part of the first named student investigators PhD thesis and may be published in a scientific journal.

**If you would like further information about this project, please do not hesitate to contact:**

**Prof. David Crewther**
**Advanced Technologies Centre (ATC) ATC929 Swinburne University of technology**
**Tel No: 9214 5877**
**Email: dcrewther@swin.edu.au**

This project has been approved by or on behalf of Swinburne's Human Research Ethics Committee (SUHREC) in line with the *National Statement on Ethical Conduct in Human Research*. If you have any concerns or complaints about the conduct of this project, you can contact:

Research Ethics Officer, Swinburne Research (H68),
Swinburne University of Technology, P O Box 218, HAWTHORN VIC 3122.
Tel (03) 9214 5218 or +61 3 9214 5218 or resethics@swin.edu.au

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## Consent for participation

**What effect does a high contrast surrounding stimulus have upon number perception?**

### Principal Investigator(s):

**Prof. David Crewther, Ms Nicola jastrzebski, Ms Laila Hugrass**

1. I consent to participate in the project named above. I have been provided a copy of the project consent information statement to which this consent form relates and any questions I have asked have been answered to my satisfaction.

2. ***In relation to this project, please circle your response to the following:***
   - I agree to complete a brief demographics questionnaire **Yes** **No**
   - I agree to complete computer based psychophysical tasks **Yes** **No**
   - I agree to make myself available for further information if required in relation to this project **Yes** **No**
   - I agree to undertake tasks that evaluate arithmetic skills **Yes** **No**

3. I acknowledge that:
   (a) my participation is voluntary and that I am free to withdraw from the project at any time without explanation;
   (b) the Swinburne project is for the purpose of research and not for profit;
   (c) any identifiable information about me which is gathered in the course of and as the result of my participating in this project will be (i) collected and retained for the purpose of this project and (ii) accessed and analysed by the researcher(s) for the purpose of conducting this project;
   (d) my anonymity is preserved and I will not be identified in publications or otherwise without my express written consent.

By signing this document I agree to participate in this project.

**Name of Participant:** ………………………………………………………………………………

**Signature & Date:** ……………………………………………………………

# Appendix B: Surround-masking (MEG/Part 5) and Attentional-Filtering and Numerosity Comparison (MEG/Part 6)

Email from Swinburne ethics comitee for approval of these experiments

**From:** Keith Wilkins
**Sent:** Monday, 15 July 2013 6:30 PM
**To:** David Crewther; Nicola Jastrzebski
**Cc:** RES Ethics; FLSS Research
**Subject:** SUHREC Project 2013/006 Ethics Clearance

To: Prof David Crewther/Ms Nicola Jastrzebski, FLSS

Dear David and Nicola

**SUHREC Project 2013/006 The effects of surround masking inhibition on number perception: A magnetoencephalographic (MEG) and fMRI investigation.**

Prof David Crewther, FLSS; Ms Nicola Jastrzebski

Approved Duration: 15/07/2013 to 15/07/2014 [Adjusted]

I refer to the ethical review of the protocol for the above project by Swinburne's Human Research Ethics Committee (SUHREC). Your responses to the review were as per several emails (some with attachments) between 18 March and 13 July 2013, latter emails in response to feedback and latter information superseding previous information as applicable. The consent instruments effectively approved for use are those attached to your emails of 13 July 2013.

I am pleased to advise that, as submitted to date, the project has approval to proceed in line with standard on-going ethics clearance requirements here outlined

- All human research activity undertaken under Swinburne auspices must conform to Swinburne standards, including external regulatory standards such as the current *National Statement on Ethical Conduct of Human Research* and with respect to secure data use, retention and disposal.

- The named Swinburne Chief Investigator/Supervisor remains responsible for any personnel appointed to or associated with the Swinburne student project being made aware of ethics clearance conditions, including research and consent procedures or instruments approved. Any change in chief investigator/supervisor requires timely notification and appropriate endorsement.

- The above project has been approved as submitted for ethical review by or on behalf of SUHREC. Amendments to approved procedures or instruments ordinarily require prior ethical appraisal/clearance. SUHREC must be notified immediately or as soon as possible thereafter of (a) any serious or unexpected adverse effects and any redress measures; (b) proposed changes in protocols; and (c) unforeseen events which might affect continued ethical acceptability of the project.

- At a minimum, an annual report on the progress of the project is required as well as at the conclusion (or abandonment) of the project.

- A duly authorised external or internal audit of the project may be undertaken at any time.

Please contact the Research Ethics Office at Swinburne Research if you have any queries about the Swinburne ethical review, citing the SUHREC project number. Copies of clearance emails should be retained as part of project record-keeping.

Best wishes for the project.

Yours sincerely

Keith

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Keith Wilkins

Secretary, SUHREC & Research Ethics Officer

## Email from research and ethics officer that approved removal of fMRI from the protocol:

**From:** Keith Wilkins
**Sent:** Wednesday, 29 January 2014 2:07 PM
**To:** David Crewther; Nicola Jastrzebski
**Cc:** RES Ethics
**Subject:** SUHREC Project 2013/006 Ethics Clearance for Modifications (1)

To: Prof David Crewther/Ms Nicola Jastrzebski, FLSS

Dear David and Nicola

**SUHREC Project 2013/006 The effects of surround masking inhibition on number perception: A magnetoencephalographic (MEG) investigation.**

Prof David Crewther, FLSS; Ms Nicola Jastrzebski

Approved Duration: 15/07/2013 to 15/07/2014 [Modified January 2014~~2013~~]

I refer to your request concerning modifications to the protocol approved on 15 July 2013, as per your email of 26 January 2014 with progress report and applicable revised documentation attached. The request was put to a SUHREC delegate for consideration.

I am pleased to advise that, as modified to date, the project has approval to continue in line with ethics clearance conditions previously communicated and reprinted below.

Please contact the Research Ethics Office if you have any queries about on-going ethics clearance, citing the SUHREC project number. Copies of clearance emails should be retained as part of project record-keeping.

As before, best wishes for the project.

Yours sincerely

Keith

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Keith Wilkins

Secretary, SUHREC & Research Ethics Officer

SWINBURNE UNIVERSITY OF TECHNOLOGY

# The effects of surround masking inhibition on number perception: A magnetoencephalographic (MEG) investigation.

**Principal investigator:** Prof. David Crewther.
**Student investigator:** Ms Nicola Jastrzebski.

One of the many brain processes for learning how to read or count involves the removal of unessential visual information – this process is named sensory filtering. It has been suggested among researchers that a defect in the brain's sensory filtering processes may induce distortions in the organization of what is being perceived, which is likely to have a negative impact upon learning, cognitive development, and attention . Sensory filtering defects have been observed in Autism Spectrum Disorders (ASD) and schizophrenia – these findings have been evidenced through psychophysics (experiments that test functioning of the visual pathways).

## What is this project about?

Schizophrenic type symptoms, such as frequent feelings of mistrusting other people (paranoia), or frequent loss in train of thought (disorganized thinking) can occur in people who are not mentally ill. The schizophrenic type symptoms which occur in the absence of full blown psychosis are named schizotypal personality traits. There is a growing body of clinical studies which indicate that people with a high level of schizotypal traits also have an associated disorder in learning arithmetic concepts (developmental dyscalculia). The extent of schizotypal traits can be measured by the schizotypal personality questionnaire (SPQ) – a self report evaluation of schizotypal traits in non-clinical populations. People with schizophrenia and high SPQ scores have both been found to have sensory filtering defects. From these observations, we aim to investigate what relationship exists between SPQ scores, arithmetic reasoning/skills and sensory filtering functioning of the visual system. The sensory filtering system will be tested through 2 separate psychophysical procedures, one is commonly known as the 'surround-masking' paradigm which will involve making number estimation judgements in the presence of a high-contrast surround stimulus. The second psychophysical test is a measure of the ability to ignore irrelevant visual information when making simultaneous number estimation judgements. These tasks are very simple to complete.

While psychophysical experiments as such have revealed much insight into the information processing limits on visual perception, they are not very informative about the underlying brain processes which occur as a result of this type of visual stimulation. Magneto-encephalography (MEG) – a brain imaging technique that measures electro-magnetic changes in response to sensory stimulation – will enable a more informative observation of the brain processes involved with sensory filtering while undertaking the surround masking experiments.

## Why is this project being undertaken?

- To examine what effect imposing capacity limits on the information filtering system has upon the ability to make number estimation judgements. This visual perceptual experiment is commonly known as the 'surround-masking' paradigm.
- **Why?** *Previous surround-masking experiments have demonstrated that contrast matching judgements of centrally presented stimuli is greatly impaired only when embedded in a high-contrast surround stimulus.*
- To examine the associated changes in neural activity for these tasks with magneto-encephalography (MEG).
- **Why?** *The high contrast surrounding stimulus has a negative effect upon the brains sensory filtering processes. The implementation of MEG will enable an examination of the brains biological events which occur for errors in coding physical components of visual information.*

• To investigate whether there are differences in performance of surround masking tasks between participants with high and low scores on the Schizotypal personality questionnaire (SPQ) and the Autism Spectrum Quotient (AQ), and whether there are biological differences in the sensory-filtering processes induced through the high contrast surround.

• **Why?** *We wish to distinguish the types of perceptual anomaly exhibited between those with high SPQ and those with high AQ scores.*

• To examine what effect the brightness of stimuli (luminance) has on the ability to ignore irrelevant sensory information when making number estimation judgements in people with high and low SPQ scores.

• **Why?** *The brightness of visual information has a strong impact upon brain activity involved with sensory filtering – the brighter a stimulus is, the harder it is to ignore. Also, the brightness of stimuli places demands upon the brains sensory filtering processes.*

• To examine the associated changes in neural activity during sensory filtering of highly salient (bright), however irrelevant visual information between high and low SPQ individuals through MEG.

• **Why?** *We wish to examine the associated changes in neural activity associated with filtering out salient yet irrelevant visual information between individuals with high and low SPQ traits.*

• To investigate whether there are differences in arithmetic ability between participants with high and low SPQ scores.

• **Why?** *There is a growing body of clinical studies which indicate that people with a high level of schizotypal traits also have an associated disorder in learning arithmetic concepts (developmental dyscalculia). We expect that this will not be so in those with high AQ scores.*

**What does it mean if I have a high SPQ or AQ score?**
Obtaining a 'high' SPQ or AQ score simply means that you possess an above average level of schizotypal or autistic personality traits than the general population, and is by no means an indicator of fully blown psychiatric illnesses schizophrenia or autism. If however you have any further concerns or questions about your SPQ or AQ score, please contact the Swinburne psychology clinic for low cost counselling and referral services (03 9214 8653).

Swinburne Psychology Clinic:
**Email:** psychclinic@swin.edu.au
**Phone:** (03) 9214 8653
**Location:** Level 4, George Swinburne Building, Wakefield St (Hawthorn)

Swinburne students are entitled to free counselling through the campus student development and counselling services:

Swinburne student development and counselling

**Phone:** (03) 9214 8025
**Location:** Level 4, George Swinburne Building, Wakefield St (Hawthorn)

## What participation will involve.

**This study is made up of 5 main components:**

1. The first part involves completion of an online version of the Schizotypal personality questionnaire (SPQ) and Autism spectrum quotient questionnaire (AQ) included with some demographic questions.
2. The second part involves completion of some simple computer based tasks that test arithmetic reasoning, Ravens advanced progressive matrices, a pen and paper based

evaluation of non-verbal intelligence, the Wechsler adult intelligence scale (WAIS) subscale which evaluates arithmetic reasoning and the previously mentioned psychophysical tests.

3. The third part involves taking MEG recordings of changes in brain activity whilst undertaking a series of surround-masking psychophysical experiments. Irrespective of contrast condition(low contrast centre/high contrast surround), the task objective is to indicate – by keyboard response, whether a central region of the visual field contains more or less dots than a reference number of dots. The MEG recording session should take approximately 45 minutes. During the MEG recording, you will be in a magnetically shielded room (MSR) with the door shut. You will be in communication with the investigators via intercom for the duration of the MEG recordings. MEG is a completely non-invasive technique, meaning that all testing is done on the outside of the body. Bringing metal into the recording room can be a danger to the very sensitive equipment. Hence you **must not bring any metal into the room**. If you have metal implants, you may not be able to participate. Please read the MEG Information form and complete the questionnaire.
4. The fourth part involves taking MEG recordings of changes in brain activity whilst undertaking a different psychophysical task which is a test of ability in the ignoring of salient but irrelevant visual information during estimation judgements. This MEG scanning session will take place on a separate day from the previously mentioned testing session.
5. The fifth part involves undergoing an MRI (magnetic resonance imaging) scan to obtain an image of the brain that will take no longer than 15 minutes. The conditions inside the MRI magnet are somewhat constricted which may be distressing to those with claustrophobia. In the unlikely event that you should feel any cause for anxiety in the course of fMRI scanning you are free to withdraw at any time without explanation. The likelihood of increased risk from the MRI scanning process has been associated with magnetic metal implants. Bringing metal into the scanner can be dangerous because of the very strong magnetic field (please refer to the attached MRI pre-scan information sheet). Therefore, you **must not bring any metal into the MRI scanner.** If you have metal implants, you may not be able to participate. Prior to going into the MRI scanner, you will be screened by the radiographer to make sure that you can safely be put into the scanner. During the MRI scanning process there is a chance that a previously unknown medical condition may be detected. If this occurs, you will be notified and referred to a specialist. Please read the MRI information sheet (MRI-14) and complete the associated questionnaire.

Participation in this study (which is greatly appreciated) is on the basis of your voluntary consent, and may take overall 2.5-3 hours. ***As part of the visual perception experimental procedures, participants will be exposed to high contrast visual stimuli which have been known on occasion to induce migraines in those who suffer them and seizures for those with epilepsy. Therefore, if you suffer from migraine or epilepsy, unfortunately you cannot participate in this study.***

**What is the likelihood of experiencing psychological or physical discomfort as a result of participating in this study?**

There is very little risk in this study. All electrical equipment complies with current safety standards and there is no foreseeable discomfort to the participant.

However, if you feel like you need a break or would like to discontinue the study, you may do so without any explanation.

In the unlikely event you need medical assistance a referral will be provided or you can contact Swinburne Health Services on 9214 8483. Alternatively, for counselling contact:
Swinburne psychology clinic:
**Email:** psychclinic@swin.edu.au
**Phone:** (03) 9214 8653
**Location:** Level 4, George Swinburne Building, Wakefield St (Hawthorn)

Participant rights and interests – Privacy & Confidentiality
Given that participation is voluntary, you are free to withdraw at any point of this investigation without explanation. The information you provide as part of this investigation (informed consent, demographics), will be held confidential and retained securely. All identifying

information in  experimental data will be replaced by codes that de-identify the participant from their data.

**Research output**
The potential findings emergent from this investigation may enable a better understanding of the inhibitory processes at risk in schizophrenia and how it affects number sense. The findings moreover will form part of the student investigators PhD thesis and may be published in a scientific or medical journal.

**If you would like further information about this project, either prior to continuing, or after participating (in the way of feedback or debriefing), we would be pleased to provide it. Please do not hesitate to contact:**

**Prof. David Crewther**
**Advanced Technologies Centre (ATC) ATC929 Swinburne University of Technology**
**Tel No: 9214 5877**
**Email: dcrewther@swin.edu.au**

This project has been approved by or on behalf of Swinburne's Human Research Ethics Committee (SUHREC) in line with the *National Statement on Ethical Conduct in Human Research*. If you have any concerns or complaints about the conduct of this project, you can contact:

Research Ethics Officer, Swinburne Research (H68),
Swinburne University of Technology, P O Box 218, HAWTHORN VIC 3122.
Tel (03) 9214 5218 or +61 3 9214 5218 or resethics@swin.edu.au

SWINBURNE UNIVERSITY OF TECHNOLOGY

**Project Title:**
**The effects of surround masking inhibition on number perception: A magnetoencephalographic (MEG) investigation.**

## Principal Investigator(s)

**Ms Nicola Jastrzebski, Prof David Crewther**

1. I consent to participate in the project named above. I have been provided a copy of the project consent information statement to which this consent form relates and any questions I have asked have been answered to my satisfaction.

2. ***In relation to this project, please circle your response to the following:***

| | | |
|---|---|---|
| ▪ I agree to undertake MEG recordings of brain activity whilst performing Psychophysical experiments | **Yes** | **No** |
| | **Yes** | **No** |
| ▪ I agree to make myself available for further information if required In relation to this project. | **Yes** | **No** |
| ▪ I agree to undertake tasks that evaluate arithmetic skills | **Yes** | **No** |
| ▪ I agree to undertake tasks that evaluate non-verbal IQ (Ravens matrices) | **Yes** | **No** |

3. I acknowledge that:
   (a) my participation is voluntary and that I am free to withdraw from the project at any time without explanation;
   (b) the Swinburne project is for the purpose of research and not for profit;
   (c) any identifiable information about me which is gathered in the course of and as the result of my participating in this project will be (i) collected and retained for the purpose of this project and (ii) accessed and analysed by the researcher(s) for the purpose of conducting this project;
   (d) my anonymity is preserved and I will not be identified in publications or otherwise without my express written consent.

By signing this document I agree to participate in this project.

**Name of Participant:** ……………………………………………………………………………

**Signature & Date:** ……………………………………………………………

# Appendix C

## Items for the nine sub-scales of the SPQ (Raine, 1991)

**Ideas of Reference**

1. Do you sometimes feel that things you see on the TV or read in the newspaper have a special meaning for you?
10. I am aware that people notice me when I go out for a meal or to see a film.
19. Do some people drop hints about you or say things with a double meaning?
28. Have you ever noticed a common event or object that seemed to be a special sign for you?
37. Do you sometimes see special meanings in advertisements, shop windows, or in the way things are arranged around you?
45. When shopping do you get the feeling that other people are taking notice of you?
53. When you see people talking to each other, do you often wonder if they are talking about you?
60. Do you sometimes feel that other people are watching you?
63. Do you sometimes feel that people are talking about you?

**Excessive Social Anxiety**

2. I sometimes avoid going to places where there will be many people because I will get anxious.
11. I get very nervous when I have to make polite conversation.
20. Do you ever get nervous when someone is walking behind you?
29. I get anxious when meeting people for the first time.
38. Do you often feel nervous when you are in a group of unfamiliar people?
46. I feel very uncomfortable in social situations involving unfamiliar people.
54. I would feel very anxious if I had to give a speech in front of a large group of people.
71. I feel very uneasy talking to people I do not know well.

**Odd Beliefs or Magical Thinking**

3. Have you had experiences with the supernatural?
12. Do you believe in telepathy (mind-reading)?
21. Are you sometimes sure that other people can tell what you are thinking?
30. Do you believe in clairvoyancy (psychic forces, fortune telling)?
39. Can other people feel your feelings when they are not there?
47. Have you had experiences with astrology, seeing the future, UFOs, ESP, or a sixth sense?
55. Have you ever felt that you are communicating with another person telepathically (by mind-reading)?

**Unusual Perceptual Experiences**

4. Have you often mistaken objects or shadows for people, or noises for voices?
13. Have you ever had the sense that some person or force is around you, even though you cannot see anyone?
22. When you look at a person, or yourself in a mirror, have you ever seen the face change right before your eyes?
31. I often hear a voice speaking my thoughts aloud.
40. Have you ever seen things invisible to other people?
48. Do everyday things seem unusually large or small?
56. Does your sense of smell sometimes become unusually strong?
61. Do you ever suddenly feel distracted by distant sounds that you are not normally aware of?
64. Are your thoughts sometimes so strong that you can almost hear them?

**Odd or Eccentric Behavior**

5. Other people see me as slightly eccentric (odd).
14. People sometimes comment on my unusual mannerisms and habits.
23. Sometimes other people think that I am a little strange.
32. Some people think that I am a very bizarre person.
67. I am an odd, unusual person.
70. I have some eccentric (odd) habits.
74. People sometimes stare at me because of my odd appearance.

**No Close Friends**

6. I have little interest in getting to know other people.
15. I prefer to keep myself to myself.
24. I am mostly quiet when with other people.

**No Close Friends—Continued**

33. I find it hard to be emotionally close to other people.
41. Do you feel that there is no one you are really close to outside of your immediate family, or people you can confide in or talk to about personal problems?
49. Writing letters to friends is more trouble than it is worth.
57. I tend to keep in the background on social occasions.
62. I attach little importance to having close friends.
66. Do you feel that you cannot get "close" to people?

**Odd Speech**

7. People sometimes find it hard to understand what I am saying.
16. I sometimes jump quickly from one topic to another when speaking.
25. I sometimes forget what I am trying to say.
34. I often ramble on too much when speaking.
42. Some people find me a bit vague and elusive during a conversation.
50. I sometimes use words in unusual ways.
58. Do you tend to wander off the topic when having a conversation?
69. I find it hard to communicate clearly what I want to say to people.
72. People occasionally comment that my conversation is confusing.

**Constricted Affect**

8. People sometimes find me aloof and distant.
17. I am not good at expressing my true feelings by the way I talk and look.
26. I rarely laugh and smile.
35. My "nonverbal" communication (smiling and nodding during a conversation) is not very good.
43. I am poor at returning social courtesies and gestures.
51. I tend to avoid eye contact when conversing with others.
68. I do not have an expressive and lively way of speaking.
73. I tend to keep my feelings to myself.

**Suspiciousness**

9. I am sure I am being talked about behind my back.
18. Do you often feel that other people have it in for you?
27. Do you sometimes get concerned that friends or co-workers are not really loyal or trustworthy?
36. I feel I have to be on my guard even with friends.
44. Do you often pick up hidden threats or put-downs from what people say or do?
52. Have you found that it is best not to let other people know too much about you?
59. I often feel that others have it in for me.
65. Do you often have to keep an eye out to stop people from taking advantage of you?

# Appendix D

# Items from the AQ (Baron-Cohen, et al., 2001)

1. I prefer to do things with others rather than on my own.
2. I prefer to do things the same way over and over again.
3. If I try to imagine something, I find it very easy to create a picture in my mind.
4. I frequently get so strongly absorbed in one thing that I lose sight of other things.
5. I often notice small sounds when others do not.
6. I usually notice car number plates or similar strings of information.
7. Other people frequently tell me that what I've said is impolite, even though I think it is polite.
8. When I'm reading a story, I can easily imagine what the characters might look like.
9. I am fascinated by dates.
10. In a social group, I can easily keep track of several different people's conversations.
11. I find social situations easy.
12. I tend to notice details that others do not.
13. I would rather go to a library than a party.
14. I find making up stories easy.
15. I find myself drawn more strongly to people than to things.
16. I tend to have very strong interests, which I get upset about if I can't pursue.
17. I enjoy social chit-chat.
18. When I talk, it isn't always easy for others to get a word in edgeways.
19. I am fascinated by numbers.
20. When I'm reading a story, I find it difficult to work out the characters' intentions.
21. I don't particularly enjoy reading fiction.
22. I find it hard to make new friends.
23. I notice patterns in things all the time.
24. I would rather go to the theatre than a museum.
25. It does not upset me if my daily routine is distubed.
26. I frequently find that I don't know how to keep a conversation going.
27. I find it easy to "read between the lines" when someone is talking to me.
28. I usually concentrate more on the whole picture, rather than the small details.
29. I am not very good at remembering phone numbers.
30. I don't usually notice small changes in a situation, or a person's appearance.
31. I know how to tell if someone listening to me is getting bored.
32. I find it easy to do more than one thing at once.
33. When I talk on the phone, I'm not sure when it's my turn to speak.
34. I enjoy doing things spontaneously.
35. I am often the last to understand the point of a joke.
36. I find it easy to work out what someone is thinking or feeling just by looking at their face.
37. If there is an interruption, I can switch back to what I was doing very quickly.
38. I am good at social chit-chat.
39. People often tell me that I keep going on and on about the same thing.
40. When I was young, I used to enjoy playing games involving pretending with other children.
41. I like to collect information about categories of things (e.g. types of car, types of bird, types of train, types of plant, etc.).
42. I find it difficult to imagine what it would be like to be someone else.
43. I like to plan any activities I participate in carefully.
44. I enjoy social occasions.
45. I find it difficult to work out people's intentions.
46. New situations make me anxious.
47. I enjoy meeting new people.
48. I am a good diplomat.
49. I am not very good at remembering people's date of birth.
50. I find it very easy to play games with children that involve pretending.