Selective attention modulates temporal processing

Poppy Sharp

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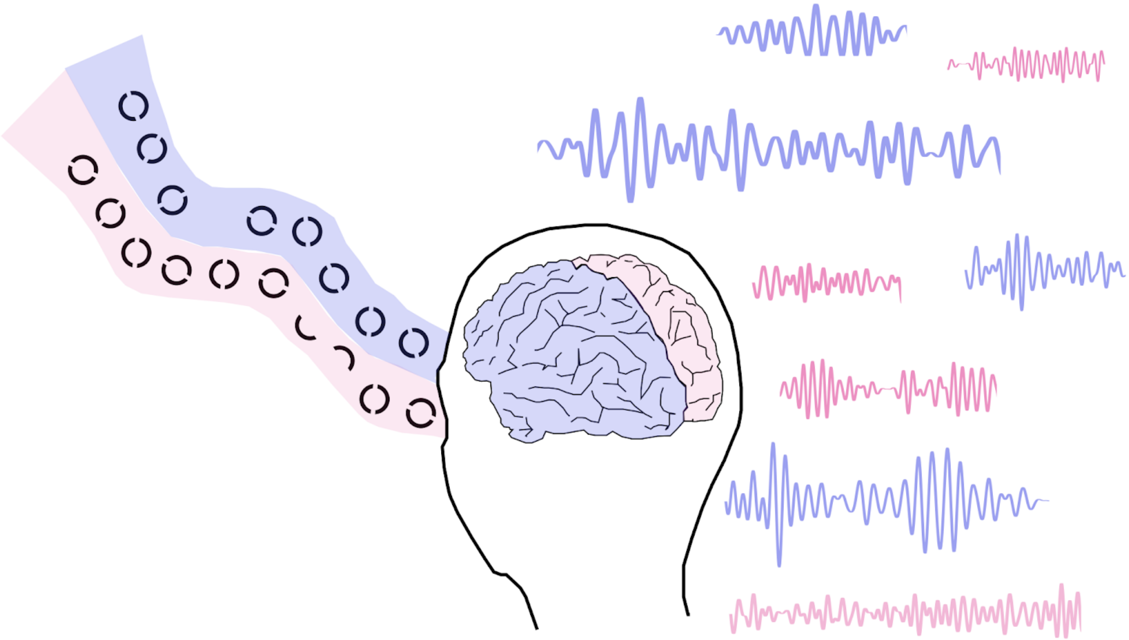
Supervision: Clayton Hickey & David Melcher



Abstract

A near continuous stream of information reaches our eyes and the task of the visual system is to make sense of it. Visual stimuli arrive in quick succession: sometimes it is necessary to integrate stimuli over time, but other times it is necessary to segregate them. These opposing processes of integration and segregation are two forms of temporal processing, a topic which is underrepresented in the literature as compared to spatial processing. In particular, there is limited understanding about how temporal processing is influenced by selective attention. Selective attention refers to a family of mechanisms by which the limited resources of our mental architecture are diverted to preferentially process stimuli more likely to be relevant.

Here, a number of empirical investigations into the effect of endogenous, covert spatial attention on temporal processing are presented. This includes use of a task in which visual stimulation is held constant and only the temporal processing goal (integration versus segregation) and the spatial location of attention are manipulated. There were strong spatial cueing effects: a benefit to performance when validly cued and a cost when invalidly cued. These attentional effects are reliable for both opposing processes of temporal integration and segregation. Furthermore, these spatial cueing effects are robust even when the cues provide no implicit temporal expectations. We used magnetoencephalography and the same task to measure changes in the brain signal associated with these effects, namely shifts in peak alpha frequency for integration as compared to segregation, as well as spatially specific modulations in this metric relative to the locus of attention.

These findings of robust spatial cueing effects on temporal processing and of strategic shifts in oscillatory frequency associated with temporal processing goals and allocation of attention are discussed within a temporal windows framework and in the context of other candidate mechanisms. The empirical evidence reported here can be accounted for by the idea of a flexible adaptation of the size of temporal windows, essentially changing the sampling rate of perception in line with task demands.

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Author’s declaration

I declare that this thesis has not be submitted for any other degree or professional qualification. I confirm that I composed the thesis, and that the work included is my own, with the exception of chapters which are jointly-authored publications. These contributions are indicated indicated at the beginning of the chapters. Where reference has been made to the work of others, appropriate credit has been given.

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List of abbreviations

CRT	Cathode Ray Tube
D1 / D2	First display / Second display
DLP	Digital Light Processing
EEG / MEG	Electroencephalography / Magnetoencephalography
EOG	Electrooculogram
ERF / ERP	Event-Related Potential / Event-Related Field
HPI	Head position indicator
Hz	Hertz
ICA	Independent Component Analysis
ISI	Inter-stimulus interval
LED	Light emitting diode
LGN	Lateral Geniculate Nucleus
NT	Near-threshold
RANOVA / ANOVA	Analysis of Variance (repeated-measures)
SEM	Standard Error of the Mean
SD	Standard Deviation
SOA	Stimulus Onset Asynchrony
SQUID	Superconducting quantum interference device
ST	Supra-threshold

Chapter 1: General Introduction

A rich and changeable stream of visual information flows in through the eyes near-constantly during our waking hours. Limited processing resources mean the visual system must prioritise some information over others, selectively attending to elements in the visual stream that may be more relevant to goals and behaviour. Much work has been done to broaden our understanding of how selective attention modulates spatial processing, from influencing behavioural performance to altering the responses of neurons in the brain. Typically in this previous work, the focus has been on single stimuli or sets of stimuli that are not extended in time. But in real life, stimuli arrive rapidly one after another in the visual stream, and our understanding of how this temporal processing is modulated by selective attention is more limited.

Temporal processing

Rhythmicity in perception

A crucial consideration when discussing temporal processing is that perception is rhythmic: the point in time at which a stimulus reaches the visual system determines the likelihood it will be processed. Moreover, the occurrence of apparent simultaneity - in which rapid sequential stimuli are perceived to occur at the same time (Kristofferson, 1967) - indicates that we can conceive of perception as a rapid sampling of the environment. The base unit of this sampling in this framework is referred to as a ‘temporal window’, where stimuli which fall within the same window are more likely to be integrated into single percept. The idea that perception relies on temporal windows has a long history in psychological research, supported by studies of psychophysics (Allport, 1968; Shallice, 1964; Stroud, 1955), optical illusions (Simpson, Shahani, & Manahilov, 2005; VanRullen & Koch, 2003), somatosensory processing (Baumgarten, Schnitzler, & Lange, 2015), sensorimotor synchronization (Mates, Müller, Radil, & Pöppel, 1994), and human electrophysiology (Samaha & Postle, 2015; VanRullen, 2016). The idea of perception as sampling with base units of temporal windows can thus be a useful framework for driving forward study of temporal processing.

Types of temporal processing

Human perceptual experiences occur across a range of scales. A schematic of the several orders of magnitude across which processing is spread is seen in Figure 1.1, along with some example processes at these various scales. It is vital for the visual system to generate and update estimates of the temporal structure of the environment, just as estimates of spatial structural are important. Indeed, successful perception relies on accurate and efficient estimates of the spatiotemporal structure of the environment. Yet the study of temporal processing has been relatively neglected in psychology and neuroscience until recently.

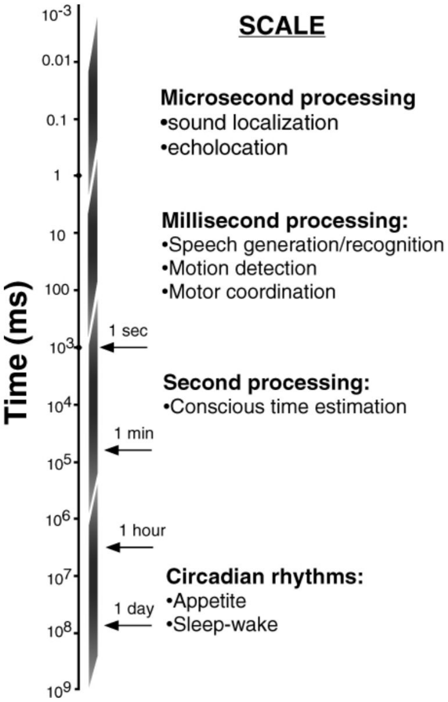

Figure 1.1*: Temporal processing is important across different scales.* *The focus in this thesis is on temporal processing at the millisecond level, within the visual system. Figure adapted from (Mauk & Buonomano, 2004)*

Temporal processing is a term used in different ways to refer to a whole host of phenomena, as can be seen from the variety of example processes in Figure 1.1. Multiple aspects of temporal processing have been investigated, such as judging the duration of (visual) stimuli or the interval of time separating stimuli (Divenyi & Danner, 1977; Grondin, Meilleur-Wells, Ouellette, & Macar, 1998). In the current thesis, I use the term temporal processing to refer to the processing of stimuli presented rapidly one after the other in time. In some situations these rapid sequential stimuli must be parsed into separate percepts, and in others they must be integrated together, and there are different paradigms designed to measure performance at these types of temporal processing.

Temporal integration and segregation

Temporal processing comprises two processes opposite in nature: temporal integration and segregation. We often need to segregate visual input over time so that the visual scene can be parsed into separate features and events, but another common necessity is to integrate strongly related stimuli so that they are perceived as unitary phenomena (Pöppel, 2009; Stroud, 1955). There must be high enough temporal resolution to react to relevant environmental changes, but also integration of related features and objects over time. Perception requires a balance between these opposite temporal processes in line with current goals, akin to the wider tenet of functional organisation that representations must be precise and robust, yet also flexible (Deco, Tononi, Boly, & Kringelbach, 2015).

Any imbalance between temporal integration and segregation (and the resulting inappropriate degree of temporal resolution) could lead to errors in perception in the environment, with potentially serious consequences. An overly fine degree of temporal resolution, with too high a level of segregation of stimuli in time, could lead to an inability to integrate motion signals or other related features of the visual scene reaching the eyes at different times. Furthermore, there could be a higher metabolic cost associated with a very fine grained temporal resolution to processing. The complementary imbalance could pose its own problems. If the degree of temporal resolution is too coarse for a given situation, with too high a level of integration of stimuli over time, this could lead to misinterpretations of motion information (e.g. perceiving a 180 degree direction change as a reduction in speed), or reduced effectiveness of tactile sensations on haptic processing (Ronconi, Busch, & Melcher, 2018).

Paradigms probing temporal processing

The majority of investigations into temporal processing use tasks that probe temporal resolution, where good performance is dependent on the ability to segregate incoming sequential stimuli into separate percepts. These include the two flash fusion paradigm (Purcell & Stewart, 1971): two stimuli - usually Gaussian-enveloped luminance patches - are quickly flashed on screen one after the other in the same location. Participants then report the number of perceived flashes. If the two flashes are inappropriately integrated together this will be detrimental to performance. Performance depends on the ability to segregate for another task: the Temporal Order Judgement (TOJ) paradigm, in which the two stimuli appear in different locations (e.g. to the left and right of fixation) and participants must report which came first (Hirsh, E., & Sherrick, 1961). For both of these tasks other factors could lead to erroneously reporting one stimulus, such as missing either stimulus through inattention. Furthermore, for TOJ it is possible to successfully segregate the stimuli but then fail to identify which came first.

One classical paradigm probes temporal integration rather than segregation: the missing dot task (Hogben & di Lollo, 1974). In this paradigm two displays of stimuli are displayed rapidly one after the other. Each display comprises a grid with some dots and some empty locations, where a location containing a dot in one display is necessarily empty in the other. Crucially, one location is empty in both displays, such that the superimposition of the two displays has one empty space, this ‘missing dot’ is the target for participants to locate. This means performance depends on participants’ ability to integrate two displays into a single percept. Perception of motion requires integration of sequential visual information, and as such temporal integrated is recruited in tasks in which participants must determine the direction of apparent motion of two sequential, spatially displaced stimuli (Braddick, 1974).

More recently, paradigms probing both temporal integration and segregation have been introduced. The colour fusion task features two rapid sequential displays of coloured patches, with patches in the same locations in both displays (Akyürek & van Asselt, 2015). By asking participants to report which colour they perceived at a given location, it can be determined whether they segregated the percepts of the two patches or integrated them into a fused colour patch. Apparent motion paradigms have also been adapted to investigate both sides of temporal processing, where perception of motion is the operationalised outcome for temporal integration and perception of two separate stimuli flashing in different locations (perception of alternation) is the outcome for segregation (Ronconi, Oosterhof, Bonmassar, & Melcher, 2017). A final paradigm allowing investigation of both segregation and integration is an adapted version of the missing dot task in which the dots are replaced by circles comprising two halves (Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 2016). In this version, at one of the locations one half of the circle is in the first display, and its corresponding half is in the second display. Every trial features one location with a missing circle and one with the half circle. When the target is the missing circle, performance depends on integration of the two displays. When the target is the half circle, performance depends on segregation of the two displays. Thus, visual stimulation is held constant while only the temporal processing goal changes. This latter paradigm is therefore well suited to investigations of factors which can influence temporal processing, including top down factors such as attention.

Selective attention

Types of selective attention

Our ability to attend to some things selectively over others is a fundamental aspect of cognition and information processing, and one that has been studied since the earliest forays into psychology and neuroscience. We can pay attention to specific points in space, to different points in time, to specific features of the visual scene, and to specific objects (Carrasco, 2011; Coull & Nobre, 1998; Olson, 2001; Treisman & Gelade, 1980). These different types of selective attention share the commonality that they are the solution to the problem of limited metabolic resources (Treisman, 1969). The visual system must prioritise processing of some pieces information over others, thus more relevant or salient stimuli are preferentially processed while the processing of other stimuli is inhibited (Beck & Kastner, 2009). Here, we focus on spatial attention, which can be further subdivided in terms of whether attention is allocated in an overt or covert fashion.

We can shift the focus of attention by moving our eyes to move our gaze. But as well as these overt shifts of attention, we can covertly shift our attention in space while maintaining fixation with the eyes (Sheliga, Riggio, & Rizzolatti, 1995). Evidence suggests that the mechanisms and neural architecture supporting overt and covert attention overlap to some extent (Hunt & Kingstone, 2003). The experiments presented in this thesis all use paradigms in which participants are maintaining fixation, and thus allocation of spatial attention is covert.

A further taxonomic distinction within the broad umbrella of attention is the difference between endogenous and exogenous attention. The term endogenous refers to the ability to volitionally orient our attention to a particular aspect of the visual environment, whereas exogenous refers to an automatic orienting in response to a stimulus (Carrasco, 2011). These two attentional systems thus differ with respect to the direction of origin in the processing hierarchy: endogenous attention is a top down process, exogenous attention a bottom up process.

Cueing paradigms offer a controlled setting to study an operationalized version of attention. Posner cueing paradigms probe allocation of endogenous spatial attention: typically a predictive, symbolic cue (such as an arrow) is presented at fixation to indicate a position in space where a target will likely appear (Posner, 1980). Equivalent paradigms exist for exogenous attention in which a cue appears peripherally at the same location where a target will likely appear (Carrasco, 2011). These paradigms allow investigation of the effects of attention on behaviour, and elucidation of the underlying mechanisms.

Proposed mechanisms of endogenous spatial attention

A rich body of literature supports the idea that endogenous spatial attention allows flexible adaptation of spatial resolution, including evidence from psychophysics (Montagna, Pestilli, & Carrasco, 2009; Yeshurun & Carrasco, 1999), neuroimaging (Fischer & Whitney, 2009), single-unit recording (Anton-Erxleben, Stephan, & Treue, 2009; Womelsdorf, Anton-Erxleben, & Treue, 2008) and human electrophysiology (Müller & Kleinschmidt, 2007) studies. A number of candidate underlying mechanisms have been proposed.

One mechanism supported by neurophysiology studies is flexible adaptation of spatial receptive field size (Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). Anton-Erxleben and colleagues (2009) mapped the receptive fields of neurons in the macaque visual system, and found a reduction in the area of the receptive field when attention was directed to a location within it. Other putative mechanisms of attentional allocation include gain enhancement, sharpening of neural tuning, and adjusting the weighting of subpopulations preferentially driven by higher spatial frequencies (Carrasco, 2011).

Some of these mechanisms are compatible with one another. One way to inform arbitration between these accounts and understand how they relate to each other is to generate new constraints through new empirical evidence of how attention is allocated during different types of processing. The case of attention and temporal processing is a good example.

Attention and temporal processing

Existing work has largely focussed on exogenous attention and temporal segregation. Results from this work broadly show that exogenous cues degrade the ability to temporally segregate stimuli. In a seminal example, Yeshurun and colleagues conducted a series of experiments using a version of the two flash fusion paradigm with exogenous cues and forward masked stimuli (Yeshurun, 2004; Yeshurun & Levy, 2003). In this paradigm, a small disk is presented either slightly to the left or right of fixation after the presentation of a preceding cue. In many trials, a second disk is presented after a brief delay at the same location, and participants are asked to report the number of disks perceived. Participants' ability to accurately report the number of disks is better following the neutral cue condition than the valid cue, suggesting that the valid exogenous cue degrades the ability to parse two percepts. This idea is consistent with findings from other experiments using various common temporal processing paradigms (Akyürek & van Asselt, 2015; Hein, Rolke, & Ulrich, 2006; Rolke, Dinkelbach, Hein, & Ulrich, 2008; Yeshurun & Hein, 2011). Parallels can be drawn here between these findings and evidence that exogenous attention also increases spatial resolution, which can have detrimental effects for some tasks such as texture segmentation (Yeshurun & Carrasco, 1998). It appears that capture of attention by exogenous factors leads to shifts in the resolution of the system both in time and in space, likely because these resolution increases are useful for many perceptual tasks. This may be especially pertinent when a change has occurred in the visual environment, recruiting exogenous attention. A central question of this thesis is whether in the case of endogenous attention modulation of temporal resolution is instead flexibly and dependent on what is most appropriate in the current situation.

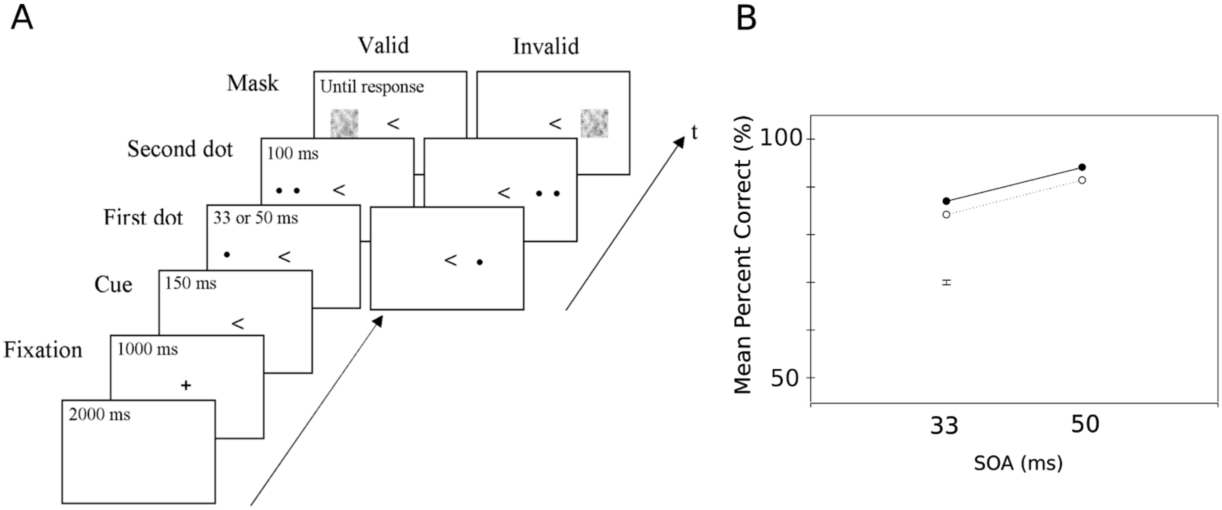

Figure 1.2*: Spatial cueing can increase temporal resolution. A* *Paradigm used to assess effect of spatial cueing on temporal segregation, participants indicated number of dots seen.* ***B*** *Performance at task shown in A, SOA: stimulus onset asynchrony. Black solid line: valid, dotted line: invalid. Both panels adapted from (Hein et al., 2006)*

In the few studies that have directly investigated endogenous cueing effects on temporal processing, results tend to show an improvement of resolution that is in contrast to the degradation caused by exogenous cues. For example, Hein, Rolke, and Ulrich (2006) used a temporal order judgement paradigm in which participants were endogenously cued to a hemifield where they would see two rapid sequential stimuli, finding that valid endogenous cues improved performance at identifying the order in which stimuli had arrived, as shown in Figure 1.2. A gap in our understanding remains as to whether this benefit of endogenous spatial cueing for segregation will replicate and whether endogenous spatial cueing will also benefit integration. It is also unclear how this cueing effect is instantiated in the brain.

Attention to temporal processing: candidate mechanisms

What specialised attentional mechanisms might subserve flexible temporal processing? One account from the literature refers to the differences between magnocellular and parvocellular pathways in visual processing. Spatial attention is thought to act in large part through emphasis and modulation of input from parvocellular neurons, which have small receptive fields (e.g. Schiller & Logothetis, 1990). However, because magnocellular neurons have better temporal resolution, a relative down-weighting of magnocellular input could come at the cost of temporal sensitivity. Evidence for this explanation is mixed, with some support from work in which the relative luminance of stimuli were matched (Yeshurun, 2004), but conflicting results showing survival of the cueing effect under conditions which should have mitigated the magno-parvo difference (Akyürek & van Asselt, 2015; Yeshurun & Levy, 2003).

Another candidate mechanism for flexible temporal processing aided by attention is adjustment of the rate of perceptual sampling. The size of temporal windows, the base unit of sampling, might be adapted to match task requirements. Two stimuli presented rapidly one after the other can lead to a percept of either one or two unique events. In the temporal windows framework, if they fall within the same temporal window, a single stimulus is perceived. There is evidence suggesting the result can be a single integrated percept – as opposed to a preferential processing of the first stimulus over the second – even when there is no benefit of integration, for example in reversal of reported target order in rapid serial visual presentations (Akyürek et al., 2012; Akyürek & Wolff, 2016). In other circumstances, a pair of stimuli separated by the same delay are perceived as two distinct percepts if they fall in different temporal windows, which can occur both on account of the phase of sampling of the visual environment or the size of these windows. Allocation of attention could modulate sampling to use shorter temporal windows when the task required segregation of temporally separate stimuli, but by biasing the system to longer temporal windows when success depended on integration of temporally disparate stimuli (Wutz, Melcher, & Samaha, 2018; Wutz et al., 2016). In this way the temporal window size could influence the perceptual outcome, independent of any effects (such as gain or tuning) on the low-level representation of the stimulus.

Other types of selective attention and temporal processing

Most investigations into attentional influences on temporal processing have used exogenous spatial cueing, but other manipulations have been used to address this question. Goodhew, Shen and Edwards (2015) used a paradigm that implicitly biased participants to use an 'attentional spotlight' that was either spatially focused or spatially diffuse, before subsequently testing spatial and temporal acuity. When biased to employ a focused spotlight, spatial acuity was enhanced, but temporal precision was unaffected. Other results show degraded integration when the availability of attentional resources was reduced by a difficult pre-trial task (Visser &

Enns, 2001) and one unique study shows that accurate temporal processing depends on whether or not participants could see their own hands (Bush & Vecera, 2014).

Another dimension to the topic is that attention can be allocated in time, and there is a rich body of literature on temporal attention to temporal processing. A classical finding on the effects of temporal attention on spatial processing was demonstrated by Los and Van den Heuvel (2001). In this study, a symbolic temporal cue indicated the delay after which a ‘L’ or ‘R’ target appeared, requiring binary choice-response with the spatially congruent hand. Results from this ‘foreperiod task’ led the authors to conclude that symbolic temporal cues can engender strategic temporal orienting. This added to a literature demonstrating that valid temporal expectations impact not only auditory perception, typically using reaction time as a metric (Griffin & Nobre, 2005), but also in the detection of targets in a rapid stream of visual stimuli (Correa, Lupiáñez, Milliken, & Tudela, 2004; Miller & Schröter, 2002). Looking rather at the effect of temporal orienting on temporal processing, Correa and colleagues (2006) employed a temporal order judgement paradigm to probe the influence of endogenous temporal cueing on perception of rapid sequential visual stimuli. Temporal orienting engendered by the cue was found to improve participants’ ability to report which stimulus appeared first. A further consideration in this context is the relationship of temporal cues and hazard rates: stimuli that appear earlier than was indicated by the cue are surprising, whereas those that appear later than was cued are better expected (Correa et al., 2004; Nobre & van Ede, 2018). Temporal orienting paradigms therefore often employ catch trials in which no stimulus appears after the cue, in order to modulate the function describing this increasing probability that a stimulus will appear (Correa et al., 2006; Steinborn, Rolke, Bratzke, & Ulrich, 2008).

Neural correlates

Measuring neural oscillations

Some of the most powerful tools at our disposal to gain insights into neural correlates in humans are noninvasive electrophysiological recordings using electroencephalography (Berger, 1935) and magnetoencephalography (Cohen, 1972), also known as EEG and MEG. These measures exploit the fact that neurons communicate with each other using electrochemical signalling to propagate messages downstream. We can measure electrical potentials at the scalp with EEG electrodes, or measure the small associated magnetic fields with the sensors in an MEG system (called superconducting quantum interference devices or SQUIDS) in a magnetically shielded room. These currents and fields are thought to reflect currents in post-synaptic dendrites, allowing us to characterise brain activity with EEG and MEG. These measures are invaluable in understanding the dynamics of brain activity and their functional relevance, since they provide very high resolution in the time domain (Lopes da Silva, 2013). MEG also offers better spatial resolution than EEG since the signal is less smeared by factors such as conduction differences of electrical potentials through the skull and scalp (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). The signals recorded with EEG and MEG are otherwise broadly similar.

There are two main approaches to analysis of electrophysiological data: analysis in the time domain and analysis in the frequency domain. In the time domain, the most common analysis is to average the signal for many trials, locked to to the onset of a given stimulus. This produces a waveform called an event-related potential (ERP) or event-related field (ERF), for EEG and MEG respectively (Hillyard, Mangun, & Luck, 1990). To provide the relevant background for this thesis I will focus mainly on MEG and analysis in the frequency domain.

One of the main characteristics of the neural signal recorded with MEG is oscillatory activity, reflecting rhythmic fluctuations in the postsynaptic membrane potentials of many neurons (Buzsaki, 2006). An oscillation can be described in terms of its three main features: frequency, power, and phase. The frequency is the speed with which the oscillation is changing, the power is the amplitude of the oscillation, and the phase is the angle or starting point of the oscillation. These interrelated features can be quantified after a mathematical transformation of the MEG signal such as the Hilbert transform (Cohen, 2014) or Fourier transform (Bertrand, Tallon-Baudry, & Pernier, 2000), depending on the purpose of the analysis. Initially dismissed as epiphenomena of human brain activity, neural oscillations have more recently come to be regarded as having a vital functional role in processing cognition throughout multiple areas and systems (Sadaghiani & Kleinschmidt, 2016). Moreover, recent evidence suggests that amplitude fluctuations in prestimulus oscillatory activity can explain the generation of post stimulus ERFs (Mazaheri & Jensen, 2008; Nikulin et al., 2007).

Functional roles of neural oscillations

Oscillatory dynamics are ubiquitous throughout the brain, hence it follows that their functional role is a fundamental dimension of processing. Synchronous activation within and between reciprocally connected groups of neurons in different functionally specialised brain areas is rhythmic in nature, and this organisational principle is thought to support coordination and integration of coherent behaviour on a large scale across disparate brain regions (Varela, Lachaux, Rodriguez, & Martinerie, 2001). A reciprocal causal relationship exists between the firing patterns of neurons which subserve representation in the processing stream and the regulation of synchronised activity in assemblies of neurons by oscillatory dynamics (Buzsaki, 2006). The role of oscillations in supporting this functional organisational principle of the brain means that oscillatory rhythms can be used to index a broad range of functions.

Shorthand labels have developed for categories of oscillations grouped by frequency. The most salient oscillation was first observed by Hans Berger in his clandestine investigations into telepathy: the alpha rhythm (Berger, 1935; Buzsaki, 2006). Alpha stereotypically oscillates at a rate of 10 cycles per second (10 Hz; Hertz); the label alpha is generally applied to oscillations with a frequency in the rough range of 8 to 12 Hz. When the generators are in the somatosensory system this rhythm is also referred to as the mu rhythm (Gastaut, 1952). Other bands have been labelled as follows: the beta band is 15-25 Hz, the theta band 5-8 Hz, and the gamma band 30-150 Hz (Buzsaki, 2006; Fries, 2015; Jensen, Gips, Bergmann, & Bonnefond, 2014). The range of values ascribed to a given category are approximate, owing to some variation in the literature. Although these different bands are associated with multiple cognitive functions in various functional networks, it is important to note that there are considerable interactions between oscillations of different frequency bands through mechanisms such phase-amplitude coupling (Canolty et al., 2006; Cohen et al., 2009; Fries, 2015; Lakatos et al., 2005). To broadly summarise the putative functional associations of different frequency bands: beta rhythms are involved in motor control functions (Engel & Fries, 2010; Murthy & Fetz, 1992), theta is typically associated with episodic and spatial memory encoding (Buzsáki & Moser, 2013; O’Keefe & Recce, 1993), and gamma with sensory integration and top down signals (Fries, 2009; Ray & Maunsell, 2010). The alpha rhythm is of particular relevance for this thesis, on account of empirical evidence of its importance for both spatial attention and temporal processing.

Alpha and spatial attention

Initially dismissed as an ‘idling rhythm’, a growing body of work provides evidence that changes in alpha band oscillations reflect changes in cortical excitability, and that alpha rhythm changes are influenced by top down influences on information flow such as selective spatial attention (Sadaghiani & Kleinschmidt, 2016). Attending to a lateralised location in the visual field results in a reduction in alpha power in the contralateral hemisphere (Gould, Rushworth, & Nobre, 2011; Worden, Foxe, Wang, & Simpson, 2000). An equivalent spatially specific modulation of alpha power by spatial attention is also seen in the somatosensory system (Haegens, Händel, & Jensen, 2011). This desynchronisation is thought to reflect a reduction in inhibitory alpha activity thereby enhancing information processing at the attended location (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007), as illustrated in Figure 3. The complementary alpha power increases in the ipsilateral hemifield are thought to subserve suppression of processing of distractors (Kelly, Lalor, Reilly, & Foxe, 2006; Mazaheri et al., 2014).

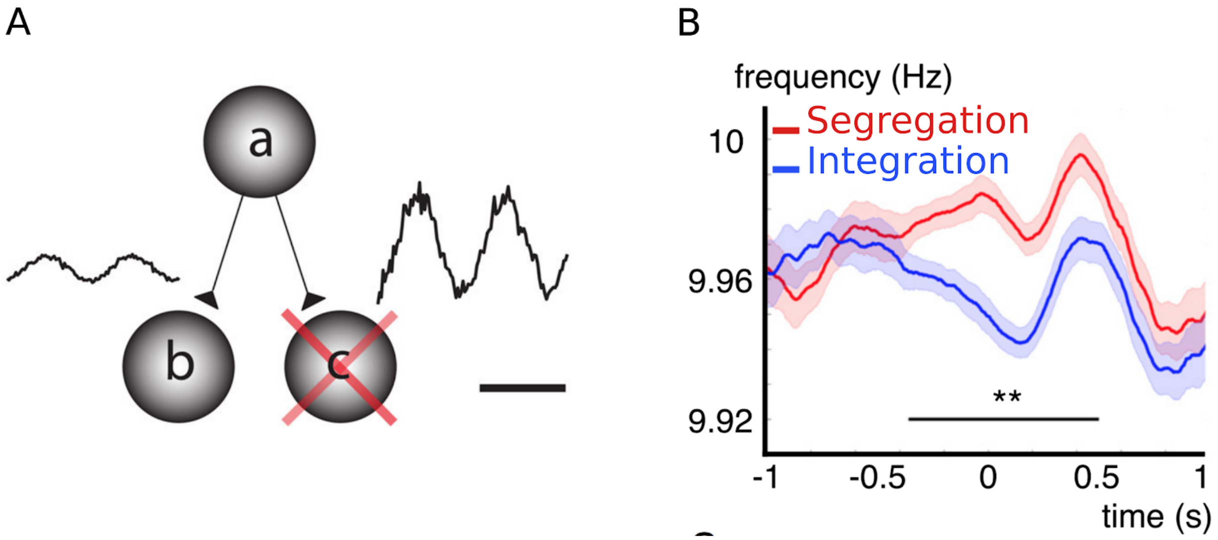

Figure 1.3 ***Alpha oscillations are influenced by endogenous factors such as spatial attention and temporal processing goal. A*** *The gating by inhibition account holds that alpha oscillations allow restriction of information flow from areas not relevant to the current task through pulsed inhibition. Suppression of activity in task irrelevant area 'c' by higher area 'a' is reflected in higher alpha power. Panel adapted from (Jensen & Mazaheri, 2010).* ***B.*** *Prestimulus alpha frequency is higher when the goal is segregation than when the goal is integration. Panel adapted from (Wutz et al., 2018).*

Alpha and temporal processing

Both trait and state dependent differences in alpha frequency have been shown to have important functional implications, particularly for temporal processing (Mierau, Klimesch, & Lefebvre, 2017). Individual differences in peak alpha frequency have been shown to influence perceptual experience of rapid sequential stimuli. Samaha and Postle (2015) measured individual alpha frequency both at rest and during a prestimulus epoch, finding that a higher frequency alpha oscillation correlated with an increased likelihood of segregating two rapid sequential flashes into separate percepts. A lower frequency alpha rhythm correlated with likelihood of perceiving one flash, as would be expected if a lower sampling rate lead to integration of the two stimuli. Minami and Amano (2017) demonstrated perceptual differences linked to alpha frequency differences: the frequency of illusory visual vibrations matched that of the individual alpha rhythm, and furthermore found shifts in perception concomitant with shifts in alpha frequency following electrical stimulation. This finding is supported by other demonstrations of modulation of temporal integration by shifts to the frequency of alpha oscillations, both by sensory entrainment (Ronconi et al., 2018) and electrical stimulation (Cecere, Rees, & Romei, 2015).

Task-dependent fluctuations in frequency within the alpha band have also been found to be functionally relevant, particularly for temporal processing (Babu Henry Samuel, Wang, Hu, & Ding, 2018; Drewes, Zhu, Muschter, & Melcher, 2017). Instantaneous alpha frequency provides a useful time-resolved index of functional changes (Cohen, 2014), which may average out in a related metric such as alpha power (Nelli, Itthipuripat, Srinivasan, & Serences, 2017). Wutz, Melcher and Samaha (2018) tracked prestimulus differences in instantaneous alpha frequency during a task in which the goal was either to integrate or segregate rapid sequential stimuli, as shown in panel C of Figure 3. Instantaneous alpha frequency was higher in the prestimulus period when the goal was to segregate, and lower frequency when the goal was to integrate, as would be expected if this metric was indexing the sampling rate of the visual system. A crucial question remains as to whether these changes to temporal processing and sampling rate can be flexibly modulated by spatial selective attention.

Chapter summary and thesis outline

In this chapter I introduced the broad topic area of the thesis: the influence of covert selective attention on temporal processing in the visual system. Chapter 2 details evidence replicating and extending previous findings showing endogenous spatial attention improves temporal resolution (segregation of rapid sequential stimuli into separate percepts).

I discussed in Chapter 1 the fact that whilst high temporal resolution from successful segregation of rapid sequential stimuli is often crucial, the opposite process of temporal integration can at other times be vital to successful and useful perception. Different accounts of the mechanisms of spatial attention were summarised, and I noted that probing the effects of spatial attention on temporal processing can provide useful constraints for informing arbitration between these accounts. Chapter 3 provides empirical evidence that strong endogenous spatial cueing effects emerge for both opposing temporal processes of integration and segregation, indicating that spatial attention operates in a flexible manner. I present characterizations of these behavioural effects: how performance is influenced by cue validity, and how these cueing effects interact with task difficulty and stimulus eccentricity.

Other types of selective attention are discussed, including the importance of temporal attention in both normal vision and the lab environment. In chapter 4 I provide evidence that these spatial cueing effects on temporal processing occur emerge even in the absence of any implicit temporal expectations about when stimuli will appear. The effects of temporal cueing on temporal integration and segregation are differentiated between.

This chapter also saw introduction of the idea that there is an intuitive parallel between rhythmicity in both brain and behaviour. I discussed the literature highlighting the importance of neural oscillations in the alpha frequency range to temporal processing and spatial attention. I introduced the idea of perception as sampling, and modulation of the sampling rate as a candidate mechanism for how endogenous spatial attention improves both opposing processes of temporal integration and segregation. Chapter 5 concerns an MEG study using the frequency of alpha oscillations over time as a metric of the sampling rate of the visual system. I present evidence that the frequency of alpha oscillations is modulated by whether the current temporal processing goal is integration or segregation, and how this neural correlate is modulated in a spatially specific manner relative to cued location.

I close with general discussion of the results and their relation to the existing literature in chapter 6. Here I also highlight remaining questions beyond the scope of the thesis and potential avenues for future research.

Chapter 2: Endogenous attention improves temporal resolution

Abstract

Selective spatial attention has been demonstrated to improve spatial resolution, yet our understanding of how allocation of attention affects temporal processing remains sparse. We used an adapted version of the two-flash fusion paradigm with endogenous spatial cues, where participants' temporal resolution was measured as their ability to successfully segregate the percepts of the two flashes separated by a varying inter stimulus interval (ISI). There was a significant interaction between cueing and ISI driven by a valid cueing benefit at longer ISIs. This evidence suggests that endogenous spatial cueing boosts temporal resolution.

Introduction

This experiment was conducted to conceptually reproduce and better characterise extant results showing that endogenous spatial cueing benefits temporal segregation. The paradigm was based on the two-flash fusion paradigm (Purcell & Stewart, 1971; Yeshurun & Levy, 2003), but included trials in which the first probe was near threshold (Donchin, Wicke, & Lindsley, 1963). Participants reported whether they perceived one or two flashes, with the target location indicated by a 75% valid spatial cue. Unlike previous work, the inclusion of a neutral cue condition allowed distinction between a benefit to behaviour of valid cueing and a cost of invalid cueing. Our expectation was that validly cued trials would lead to better temporal segregation, and thus that participants would report two-flash stimuli with greater accuracy.

Method

Participants

Thirty-nine healthy participants (11 male; age 22.24 ± 3.32 years, mean ± SD) gave informed consent before completing the experiments. All had normal or corrected-to-normal vision and reported right-handedness. All experiments were carried out in accordance with the Declaration of Helsinki and with the approval of the local ethical committee.

Stimuli and experimental design

The stimuli and task were generated with Psychophysics Toolbox (Brainard, 1997) in MATLAB (MathWorks) and presented on a CRT monitor with a 60Hz refresh rate. The experiment started with a short staircase procedure (Watson & Pelli, 1983) to determine the contrast at which their perception of the experimental stimulus was near threshold (NT). We operationally defined this as the contrast at which they could discern whether the stimulus was presented to the left or right of fixation with 60% accuracy. This threshold was based on piloting of the staircasing procedure: 60% was the lowest threshold at which the staircasing procedure provided a contrast value for which performance remained stable.

The basic trial structure is shown in Figure 2.1. Colour change of a fixation point indicated trial start, then after a random interval of 1500 to 2000ms (rectangular distribution) a left, right, or neutral cue appeared at fixation. The cue was a green ‘T’ measuring approximately 1.5° (visual angle) that pointed toward a hemifield or upright for the neutral condition. We chose to use non-arrow cues here in order to ensure that the cue was truly endogenous; arrow stimuli are known to induce non-strategic shifts of spatial attention (Ristic & Kingstone, 2006) but this does not appear to be the case for spatial indicators that have not acquired social significance. The cue remained onscreen for 300 milliseconds, after which the fixation point appeared again and the first stimulus was presented. The first target was a Gaussian-enveloped luminance patch approximately 1.75° (visual angle) in diameter, at either maximum contrast, or of contrast determined by the adaptive staircase procedure described above. It was presented either to the left or right of fixation at an eccentricity of approximately 11.34° (visual angle), and appeared for only one frame. In approximately 66% of trials, a second target was presented in the same position as the first. There were five visual stimulation conditions: presentation of a single target stimulus at near-threshold contrast (NT), presentation of a single stimulus at suprathreshold (ST), and three 'double pulse' conditions in which one NT stimulus was followed by one ST stimulus after an interstimulus interval (ISI) of 33 milliseconds, 66 milliseconds, or 100 milliseconds. Participants completed five blocks of 100 trials (each comprising 20 neutral trials, 20 invalid trials, and 60 valid trials, with randomized order). Participants were informed that the cue would be valid around 75% of the time.

Task

Participants were instructed to maintain fixation and to respond as quickly and accurately as possible. On each trial, participants made two button presses. First they indicated in which hemifield they had perceived the stimulus by pressing the 'A' key for left hemifield targets (with the left index finger) and the 'L' key for right hemifield targets (with the right index finger). They then indicated whether in that hemifield they had perceived a single or a double flash by pressing the 'A' or 'L' key, respectively.

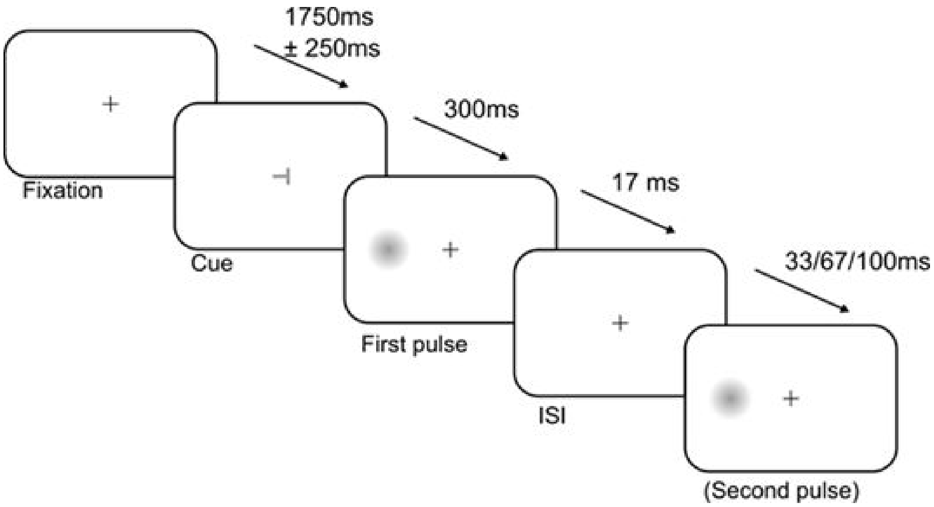

Figure 2.1*: Trial structure.* *On trials with a single pulse, this pulse was either near detection threshold or suprathreshold. On trials with two pulses, the first pulse was always at near-threshold. Stimulus size magnified for illustration. The neutral cue was an upright 'T' providing no information. Participants gave two responses: which hemifield the stimulus/stimuli appeared in, and whether there were one or two stimuli.*

Behavioural data analysis

Behavioural data were analysed using Matlab2013a (Mathworks) and R (R Foundation for Statistical Computing). Prior to the main analyses, the data of participants whose performance did not meet a fixed criterion were excluded. This criterion was set at >45% accuracy in detecting the number of pulses when the two pulses were separated by 100 ms (ie. the easiest condition). This criterion constitutes above-chance performance given that the first pulse was visible in 60% of instances, and chance performance was therefore 30%. Fourteen participants were excluded on this basis (36% exclusion rate). Figure 2.2A illustrates the performance of these excluded participants in the double pulse condition, and demonstrates that these observers were unable to reliably detect the double pulse in even the easiest experimental condition. This is consistent with recent findings demonstrating strong individual differences in integration performance and the possibility of distinct subgroups in the population at large (Drewes et al., 2017).

Accuracy for position (stimulus/stimuli on the left vs right) in NT trials was compared by one-way paired t test, using valid vs. neutral and invalid vs. neutral contrasts. This was repeated on the pooled trials from all other conditions. The main analysis tested accuracy at determining the number of pulses as a function of cue type and ISI. Only double pulse trials were included in this analysis. Percentage accuracy was calculated for each condition and these data were subjected to a two way repeated measures ANOVA with factors for cue validity (valid, neutral, invalid) and ISI (33ms, 67ms, 100ms). Post hoc testing was conducted by Bonferroni-corrected pairwise comparisons.

Results

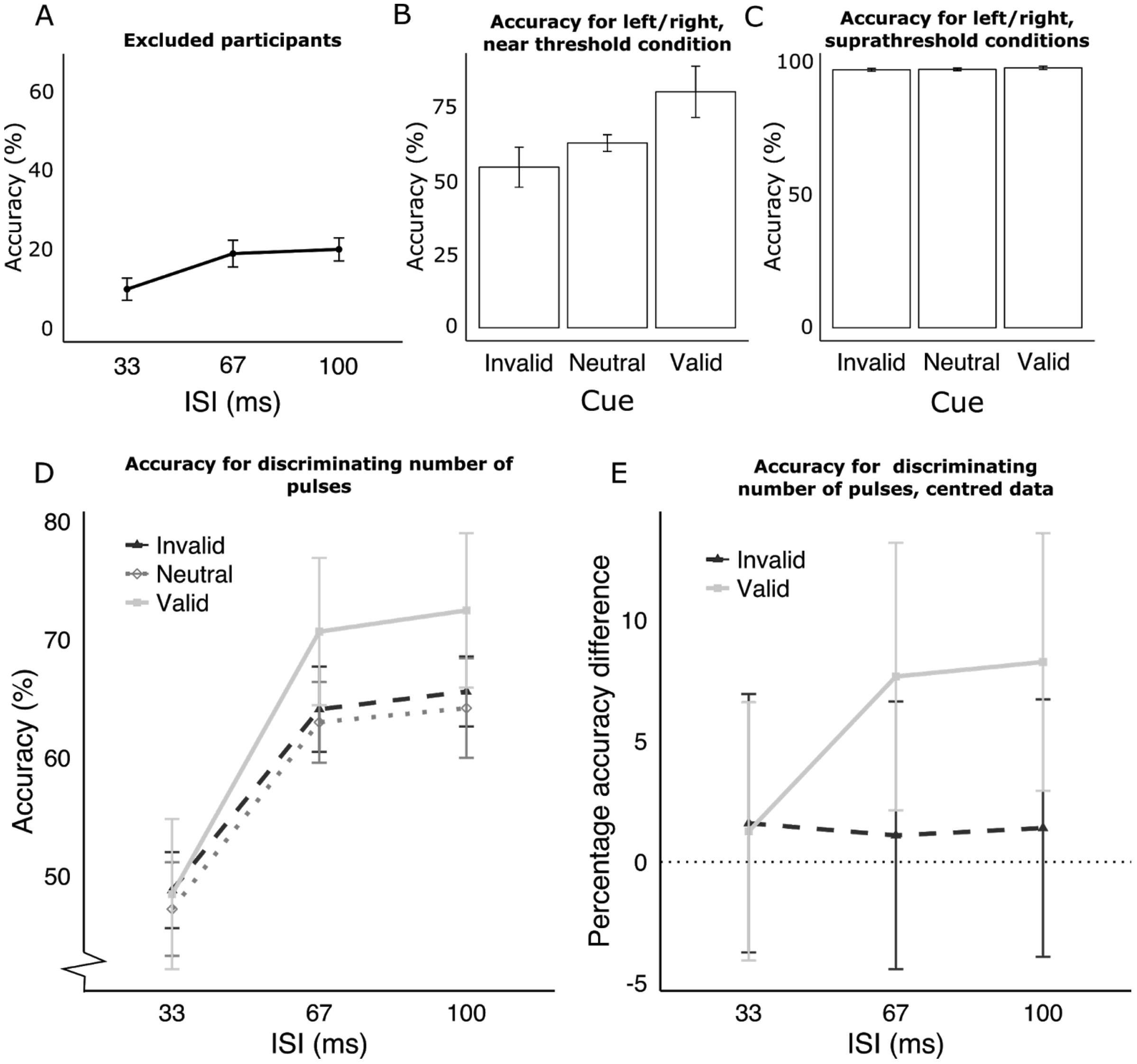

Figure 2.2. ***Results. A.*** *Results from excluded participants. Chance performance is at 30%. Error bars here and in subsequent panels indicate within-subjects 95% confidence interval (Morey, 2008).* ***B.*** *Accuracy for position by cue type for single near-threshold (NT) pulse trials only.* ***C.*** *Accuracy for position (left/right) by cue type. All trials except single NT pulse trials.* ***D.*** *Data after exclusions: accuracy for number of pulses as a function of cue type and ISI.* ***E.*** *Centred data: difference in accuracy from neutral cue case for valid and invalidly cued trials, as a function of ISI. Valid cue: solid line, square markers. Neutral: dotted line, diamond markers. Invalid: dashed line, triangle markers.*

We first tested whether cueing influenced participants' accuracy in determining whether the pulse(s) were on the left or the right. Results are illustrated in Figure 2.2B and C. On trials with a single NT pulse, difference scores were reliably greater in the valid cue condition than the invalid cue condition (*t*(24) = 4.21, *p* <.001). When all other trial types were pooled (single ST pulse and the three double pulse conditions), the difference between the valid and invalid cue conditions was not significant (*t*(24) = 1.76, *p* =.05).

For the main analysis of effect on accuracy, a significant interaction was found between cue and ISI (*F*(2,48) = 5.69, *p* = .006). Figure 2E suggests the interaction was driven by greater accuracy in validly cued trials with longer ISIs (67 and 100ms); however, Bonferroni-corrected post hoc pairwise comparisons did not show a significant difference in mean performance as an effect of cue type at any ISI. No significant main effects were found for cue or ISI (*F*s < 1).

Discussion

The significant interaction suggests that the cue boosted the detectability of the near-threshold pulse at long ISIs. This supports other extant demonstrations of a cueing benefit to temporal segregation. However, one potential criticism of this experiment is that the cue may have increased participant ability to perceive the first near-threshold pulse. If this were the case, the cue should have had a static impact across the ISIs, but the significant interaction in fact demonstrates an effect that is greatest at longer ISIs. But there remains a viable possibility that the cue had an impact on perception of the first NT pulse.

With this in mind, a new experiment was conducted with a different paradigm to a) reproduce and extend results from this experiment using only suprathreshold stimuli, and b) to allow us to investigate the effect of a spatial cue on both integration and segregation within a single task.

Chapter 3: Endogenous attention modulates temporal integration and segregation

A version of this chapter was published in March 2018:

Sharp, P., Melcher, D., & Hickey, C. (2018). Endogenous attention modulates the temporal window of integration. *Attention, Perception, & Psychophysics*, 1-15.

Abstract

Constructing useful representations of our visual environment requires the ability to selectively pay attention to particular locations at specific moments. Whilst there has been much investigation on the influence of selective attention on spatial discrimination, less is known about its influence on temporal discrimination. In particular, little is known about how endogenous attention influences two fundamental and opposing temporal processes: segregation – the parsing of the visual scene over time into separate features, and integration - the binding together of related elements. In four experiments, we tested how endogenous cueing to a location influences each of these opposing processes. Results demonstrate a strong cueing effect on both segregation and integration. These results are consistent with the hypothesis that endogenous attention can influence both of these opposing processes in a flexible manner. The finding has implications for arbitrating between accounts of the multiple modulatory mechanisms comprising selective attention.

Introduction

Goal-directed behaviour requires that visual input be integrated into representations that emphasize task-relevant information. A wealth of evidence demonstrates that this is achieved in part through the deployment of selective attention in space. The spatial deployment of attention strongly impacts visual representations, leading to faster and more accurate target processing (Posner, 1980) and improved perceptual representations at attended locations (Carrasco, Loula, & Ho, 2006; Yeshurun & Carrasco, 1999). However, our understanding of the effect of spatial attention on temporal processing is more limited. Temporal processing has two apparently opposing requirements: we often need to segregate visual input over time so that the visual scene can be parsed into separate features and events, but another common necessity is to integrate strongly-related stimuli so that they are perceived as unitary phenomena (Deco et al., 2015; Pöppel, 2009; Stroud, 1955).

Here, we investigate the possibility that the strategic deployment of spatial attention has a flexible impact on both these temporal processes, depending on task confines. This possibility has not been addressed in extant literature, in large part because existing work has focussed on the effect of attentional capture on temporal segregation. This literature has thus employed exogenous cues that involuntarily draw attention to a location, either by virtue of their raw physical salience or through their correspondence to current attentional control settings. Rather than exhaustively discussing this literature in the body of the manuscript, we summarize representative findings in Table 1. Clearly demonstrated here is the predominant use of exogenous cues and temporal segregation tasks in this literature.

Results from this work broadly show that exogenous cues degrade the ability to temporally segregate stimuli. In a seminal example, Yeshurun and colleagues conducted a series of experiments using a version of the two flash fusion paradigm with exogenous cues and forward masked stimuli (Yeshurun, 2004; Yeshurun & Levy, 2003). In this paradigm, a small disk is presented either slightly to the left or right of fixation after the presentation of a preceding cue. In many trials, a second disk is presented after a brief delay at the same location, and participants are asked to report the number of disks they perceive. Participants' ability to accurately report the number of disks is better following the neutral cue condition than the valid cue, suggesting that the valid cue degrades the ability to parse two percepts. This idea is consistent with findings from other experiments using various common temporal processing paradigms (Akyürek & van Asselt, 2015; Hein et al., 2006; Rolke et al., 2008; Yaffa Yeshurun & Hein, 2011).

One account of this finding is that the degradation stems from the differentiation of magnocellular and parvocellular pathways in visual processing. Spatial attention is thought to act in large part through emphasis and modulation of input from parvocellular neurons, which have small receptive fields (e.g. Schiller & Logothetis, 1990). However, because magnocellular neurons have better temporal resolution, a relative down-weighting of magnocellular input could come at the cost of temporal sensitivity. Evidence for this explanation is mixed, with some support from work in which the relative luminance of stimuli were matched (Yeshurun, 2004), but conflicting results showing survival of the cueing effect under conditions which should have mitigated the magno-parvo difference (Akyürek & van Asselt, 2015; Yaffa Yeshurun & Levy, 2003).

Table 1

Summary of key published findings on attentional manipulation of temporal processing.

Reference	N	Expectation manipulation	Cue Type	Task	Goal	Outcome
Akyürek & van Asselt (2015), *Psychophysiology*	18	Spatial attention	Predictive exogenous cue	Colour fusion	Segregation & integration (both rewarded)	Valid cue biases system towards integration
Yeshurun & Levy (2003), *Psychological Science*	18	Spatial attention	Predictive exogenous cue	Two flash fusion	Segregation	Valid cue hinders segregation
Yeshurun (2004), *Vision Research*	16	Spatial attention	Predictive exogenous cue	Two flash fusion (isoluminant stimuli/ background)	Segregation	Difference between cue conditions not significant
Rolke, Dinkelbach, Hein & Ulrich (2008). *Psychological Research*	20	Spatial attention	Predictive exogenous cue	Two flash fusion	Segregation	Valid cue hinders segregation
Yeshurun & Hein (2011). *Perception* Expts 1,3&4	6, 6, 6	Spatial attention	Predictive exogenous cue	Apparent motion discrimination	Integration (motion perception)	Valid cue hinders motion direction discrimination

Hein, Rolke & Ulrich (2006), *Visual Cognition* Expt 1	22	Spatial attention	Predictive exogenous cue	Temporal Order Judgement	Segregation	“Automatic” allocation of attention hinders segregation
Bush & Vecera (2014), *Cognition*	60	Implicit biasing of attention	Whether or not their hands were visible	Two flash fusion	Segregation	Segregation facilitated when two hands visible (vs not) Opposite pattern for one hand
Visser and Enns (2001), *Perception*	20	Implicit biasing of ‘attentional availability’	No cueing - demanding task at different latencies prior to main task	Missing dot task	Integration	Integration facilitated when more attentional resources available
Goodhew, Shen & Edwards (2015), *Journal of Vision*	41	Spatial attention	Implicit biasing towards ‘focal or diffuse attentional spotlight’	Two flash fusion	Segregation	Difference between focal and diffuse conditions not significant for temporal processing
Yeshurun & Hein (2011), *Perception* Expt 2	6	Spatial attention	Non predictive endogenous cue	Apparent motion discrimination	Integration (motion perception)	Cue hinders motion direction discrimination
Hein, Rolke & Ulrich (2006), *Visual Cognition* Expt 2	25	Spatial attention	Predictive, endogenous cue	Temporal Order Judgement (TOJ)	Segregation	‘Voluntary’ attention facilitates segregation
Hein, Rolke & Ulrich (2006), *Visual Cognition* Expt 3	23	Spatial attention	Non predictive endogenous cue	TOJ	Segregation	‘Automatic’ allocation of attention hinders segregation

Akyürek, Riddell, Toffanin & Hommel (2007), *Psychophysiology*	30	Temporal attention	Implicit manipulation of expectation of ‘fast’ or ‘slow’ events	Parsing and separate identification of two rapidly presented targets	Segregation	Integration facilitated by expectation of slow events (longer integration window)
Correa, Sanabria, Spence, Tudela & Lupiáñez (2006), *Brain Research*	46	Temporal attention	Predictive, endogenous cue for ‘short’ or ‘long’ delay	TOJ	Segregation	Valid cue facilitates segregation

N.B. Typical characteristics of task types: Colour fusion - participants see two rapidly presented colour patches in succession and report individual or fused colours; two flash fusion - participants report seeing either one brief stimulus or two rapidly presented stimuli; apparent motion discrimination - participants report the perceived direction of motion; TOJ - participants report which of two rapid sequential stimuli was presented first (for a review of the related literature on prior entry see (Spence & Parise, 2010); missing dot task - two rapid sequential grid displays with complementary dot elements are presented, participants must identify the grid space with no dot in either of the displays.

Studies of attentional effects on temporal processing using manipulations other than exogenous cues are rarer, and have commonly manipulated aspects of attention other than discrete location. For example, Goodhew, Shen and Edwards (2015) used a paradigm that implicitly biased participants to use an ‘attentional spotlight’ that was either spatially focused or spatially diffuse, before subsequently testing spatial and temporal acuity. When biased to employ a focused spotlight, spatial acuity was enhanced, but temporal precision was unaffected. Other results show degraded integration when the availability of attentional resources was reduced by a difficult pre-trial task (Visser & Enns, 2001) and one unique study shows that accurate temporal processing depends on whether or not participants could see their own hands (Bush & Vecera, 2014).

In the few studies that have directly investigated endogenous cueing effects on temporal processing, results tend to show an improvement of resolution that is in contrast to the degradation caused by exogenous cues, as presented in summary in Table 1. For example, Hein, Rolke, and Ulrich (2006) used a temporal order judgement paradigm in which participants were endogenously cued to a hemifield where they would see two rapid sequential stimuli, finding that valid endogenous cues improved performance at identifying the order in which stimuli had arrived.

A further pattern in this small literature is that the experimental task has nearly exclusively required the segregation of temporal events. The general paucity of investigation into the effect of endogenous cueing on segregation leads to an ambiguity in interpretation: does the cueing effect reflect a reconfiguration of the system that biases temporal acuity specifically? Or is it rather that endogenous attention benefits temporal processing broadly? If the latter, this should become evident in a benefit for temporal integration when task confines require this process.

The current study was thus designed to directly test the possibility that endogenous spatial attention might flexibly benefit both temporal integration and temporal segregation. Importantly, we tested the impact of endogenous spatial cueing on both integration and segregation within a single experimental paradigm, with visual stimulation kept constant across conditions. To this end, we adapted the missing dot paradigm of Hogben and Di Lollo (1974). In the standard version of this task, two grids of dots are presented in quick succession. No location contains a dot in both of the sequential displays, and, importantly, one location contains no dot in either display. Successful temporal integration of the two displays therefore allows the viewer to perceive the location missing a dot. We adapted the design to allow for additional insight on temporal segregation. In our experiment, circles comprising two separated halves were presented in a 4 x 4 grid. In each trial one location in the grid was unfilled, while in another location the complementary halves of the circle were presented across two temporally-separated frames (Wutz et al., 2016). As in the canonical missing dot paradigm, locating the missing circle required integration of the two displays. Locating the ‘half circle’, in contrast, required that the two frames be temporally segregated. In all experiments, we cued target location with a 75% valid cue while participants completed separate integration and segregation versions tasks across blocks.

We approached results with two exclusive hypotheses. If endogenous spatial cueing acts to increase temporal resolution, we expected to find a benefit of cueing when the task required temporal segregation, but a cost when it required integration. If endogenous attention instead is able to flexibly reconfigure temporal processing, cueing benefits should emerge in both integration and segregation conditions.

Experiment 1

Method

Participants

Six healthy participants (2 male; age 22.67 ± 3.39 years, mean ± SD) gave informed consent before completing the experiment. One participant was an author (P.S), with the five remaining participants naïve to the experimental hypotheses. All participants had normal or corrected-to-normal vision and reported right-handedness.

Experimental design and stimuli

The stimuli and task were generated with Psychophysics Toolbox (Brainard, 1997) in MATLAB (MathWorks). Stimuli were presented on an LED backlit monitor specialized for psychophysics experiments (VPixx Technologies, grey-to-grey response time of 7 ms) with a refresh rate of 100Hz.

The basic trial structure is shown in Figure 3.1. A small fixation cross in the form of a red 'X' was present throughout the presentation of stimuli. This cross measured approximately 0.2° (visual angle). At the beginning of each trial, one of the arms of the cross changed from red to green to provide the cue that the target for that trial would likely appear in the indicated quadrant. Participants were instructed that the cue usually indicated the correct quadrant and would help them with the task. In approximately 22% of trials the cue was invalid, in 53% of trials the cue was valid, and in 25% of trials a neutral cue was shown. The neutral cue took the form of a colour change of the tips of all four arms of the cross, such that a similar number of pixels changed from red to green as in the valid/invalid cue condition.

After a fixed interval of 500 milliseconds following the cue, the fixation cross became entirely red again, and the first display appeared on screen for 10 milliseconds. This display comprised a circle at seven locations out of a possible sixteen (on a four by four grid of locations), and each circle was formed from two arc elements. At one position in the display there was a half circle (i.e. a single arc). Each circle was 1.2° (visual angle) in diameter, the grid of possible locations measured 8.4° by 8.4°. Each circle within the display had an irrelevant random orientation selected from the possible orientations of 45°- 315°.

This was followed by an fixed inter-stimulus interval of either 10ms, 30ms, 50ms, 70ms or 100ms. A second display subsequently appeared for ten milliseconds. This display also comprised a circle at seven locations and a half circle at one location. Crucially, the half circle in the second display was the corresponding arc element at the same location as the half circle location from the first display, such that if the two displays were superimposed the two arc elements formed a standard circle stimulus. As illustrated in Figure 3.1, the locations of the seven circles for each display never overlapped, such that if the two displays were superimposed one of the sixteen possible locations remained empty.

After 500 milliseconds, a response probe screen appeared. This comprised a grid of squares where each square identified one of the sixteen possible target locations. Participants indicated, by mouse click, at which location they had perceived the target.

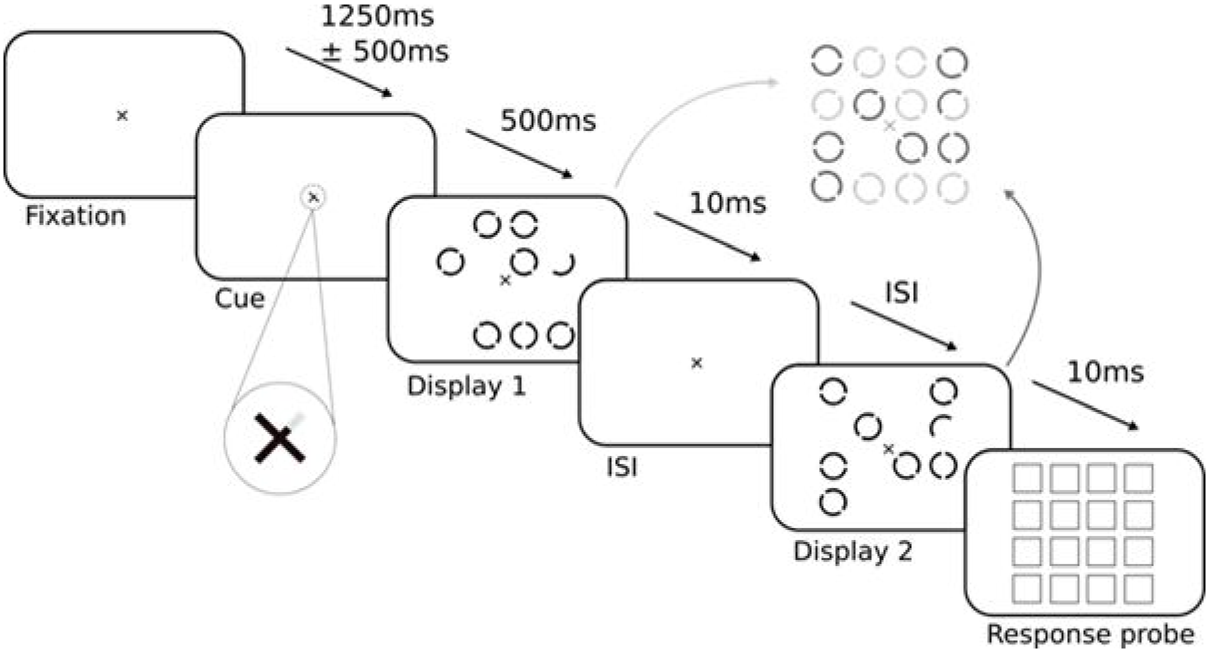

Figure 3.1: Trial structure for all experiments. *In this example the cue indicates the target will likely appear in the top right quadrant of the display. In neutral cue trials all four tips of the cross turned green. If this trial were in a segregation block, the target is the location second-down on the far right (the half-circle). If this trial were in an integration block, the target is the location in the near-left column where no stimuli appeared in either display. in Experiments 1 & 2 the ISI was variable (see Methods), in Experiment 3 the ISI was fixed at 70ms.*

Task

There were two versions of the task: stimulus presentation was the same in both but task instructions were varied across blocks. In one version of the task, the target was the half circle. Successful identification of the half circle requires parsing of the two displays, therefore this is referred to as the segregation task. In the other version, the target was the location in which there was no circle in either display. Successful identification of this location requires a combined percept of the two displays, therefore this is referred to as the integration task. Participants completed 1800 trials total (30 blocks of 60 trials), over two sessions each lasting approximately 90 minutes. Participants were explicitly instructed to fixate the cross in the centre of the screen throughout stimulus presentation.

Behavioural data analysis

Behavioural data were analysed using Matlab2013a (Mathworks) and R (R Foundation for Statistical Computing). Where assumptions of sphericity were not met, reported statistics are Greenhouse-Geisser corrected. As recommended by Lakens (2013), two estimates of effect sizes are provided: partial eta squared and generalised eta squared. The former is better suited for power analyses and comparisons within a study, whereas the latter is a metric more suited to comparisons across experiments (Bakeman, 2005a). Post hoc testing was conducted by Bonferroni-corrected pairwise comparisons.

Results

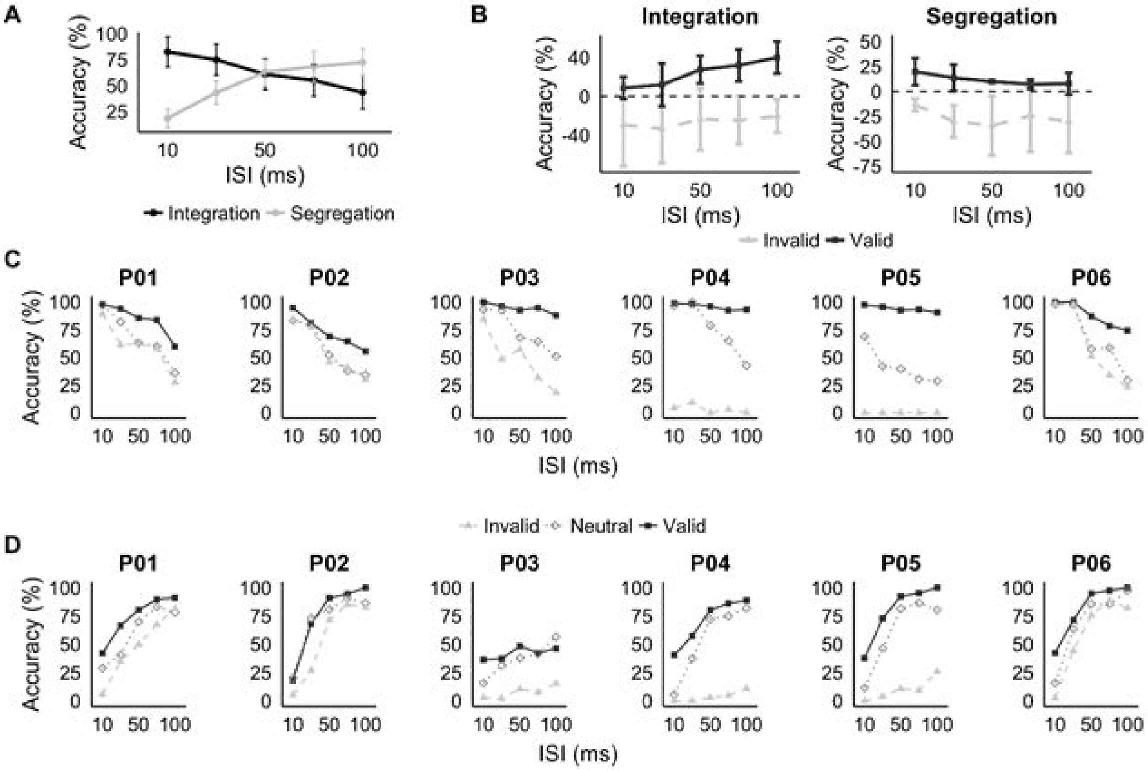

Figure 3.2: Results of Experiment 1. A. *Group average accuracy as a function of task version and ISI. Error bars here and in panel B indicate within-subjects 95% confidence interval (Morey, 2008).* ***B.*** *Group average accuracy by cue type for each task version, difference of (in)valid cue from neutral cue condition.* ***C.*** *Psychophysical curves for each participant as function of cue type and ISI for the integration task and,* ***D.*** *segregation task. Valid cue: solid line, square markers. Neutral: dotted line, diamond markers. Invalid: dashed line, triangle markers.*

As illustrated in Figure 3.2A, mean accuracy was better for longer ISIs in the segregation task but better for shorter ISIs in the integration task. We computed the effect of valid and invalid cues on performance in each of the segregation and integration tasks in reference to the neutral condition; these are plotted for each of the ISIs in Figure 3.2B. Evident here is a performance benefit of the valid cue and performance cost of the invalid cue in both tasks. In addition to this, the results suggest that cues are more effective as a function of task difficulty: valid cues have the greatest benefit on performance when the task is hard and invalid cues have the greatest cost when the task is easy. Thus when integration is required, the valid cue benefits performance at long ISIs and the invalid cue degrades performance at short ISIs, whereas when segregation is required, the valid cue benefits performance at short ISIs and the invalid cue degrades performance at long ISIs.

Results for each of the participants are illustrated in Figure 3.2C and D. Generally, the pattern of cue effect for a participant appears comparable across task versions. For example, one participant (P04) showed a disproportionately large effect of the invalid as compared to the valid and neutral cue condition for both the integration and segregation task versions. Inspection of panels C and D indicates that there is some degree of individual differences in magnitude of the invalid cueing effect as compared to the valid cueing effect.

Statistical analysis began with a repeated measures ANOVA (RANOVA) with factors for cue (valid, neutral, invalid), task (segregation, integration), and ISI (10 ms, 30 ms, 50 ms, 70 ms, 100 ms). Importantly, this identified a main effect of cue (F(2,10) = 13.30, p = .011, η_P^2 = .727, = η_G^2 = .478), reflecting the consistent benefit of valid cues and cost of invalid cues in both tasks. The effect of the cue did not reliably differ across the tasks, as reflected in a non-significant task by cue interaction (F(2, 10) = 3.51, p = .070, η_P^2 = .413, = η_G^2 = .019). Also important is the emergence of an interaction between task and ISI (F(4,20) = 40.02, p < .001, η_P^2 = .889, = η_G^2 = .428), reflecting a pattern in which valid cues most benefited performance when the task was difficult and invalid cues degraded it when the task was easy. Visually, this pattern appears accentuated in the valid cue condition, but the 3-way interaction did not reach significance ($F(8,40) = 2.11$, $p = .058$, $\eta_P^2 = .297$, $= \eta_G^2 = .031$). An effect of ISI ($F(4,20) = 5.33$, $p = .025$, $\eta_P^2 = .516$, $= \eta_G^2 = .044$) also emerged, as did the interaction between cue and ISI ($F(8,40) = 3.23$, $p = .04$, $\eta_P^2 = .393$, $= \eta_G^2 = .015$), but there was no effect of task ($F(1,5) = 1.95$, $p = .226$, $\eta_P^2 = .280$, $= \eta_G^2 = .066$).

Pairwise comparisons between means provided further insight on these results. For the integration task, cue validity (valid, invalid) had an effect at longer ISIs (with corrected alpha of .01; 10ms: $t(5) = 7.79$, $p <.001$; 50ms: $t(5) = 3.68$, $p = .007$; 70ms: $t(5) = 4.53$, $p = .003$; 100ms: $t(5) = 5.17$, $p = .002$), whereas for the segregation task, cue validity had an effect at shorter ISIs ($t(5) = 7.79$, $p <.001$; 30ms: $t(5) = 6.52$, $p = .001$; 50ms: $t(5) = 3.85$, $p = .006$). For completeness, comparisons were also made for valid and invalid cueing as compared to the neutral cueing at each ISI, for each task version. Mean performance in the valid cue condition was better than in the neutral cue condition for the 10ms ISI in the segregation version ($t(5) = 3.72$, $p = .007$). Effects at the longer ISIs did not reach significance (all other p values > .01). The valid cueing effect for the integration task was significant at longer ISIs (50ms: $t(5) = 4.98$, $p= .002$; 70ms: $t(5) = 4.98$, $p= .002$; 100ms: $t(5) = 6.25$, $p= .001$; all other ps > .01). Similarly, the cost of the invalid cue was significant at shorter ISIs in the segregations version (10ms: $t(5) = 5.81$, $p= .001$; 30ms: $t(5) = 4.74$, $p= .003$). Effects at the longer ISIs did not reach significance (all other ps > .01). For the integration task, differences between the invalid and neutral results were not significant at corrected alpha.

Results from Experiment 1 demonstrate a benefit of the endogenous deployment of spatial attention on both integration and segregation tasks, though these required opposing mechanisms of temporal processing. In addition, Experiment 1 identified a pattern wherein spatial attention has the greatest impact on temporal perception when the task is more difficult, consistent with broader theoretical understanding of the role and function of spatial attention (Luck, Girelli, McDermott & Ford, 1997).

Though participants in Experiment 1 were explicitly instructed to maintain fixation, eye movements were not monitored and so it is theoretically possible that participants may have moved their eyes in response to cue stimuli. To address this possibility and to reproduce the pattern of results observed in Experiment 1 we conducted an expanded replication in which gaze position was monitored.

Experiment 2

Method

Power analysis

Sample size choice for the experiment was informed by power analyses conducted with G*Power 3 (Faul, Erdfelder, Lang, & Buchner, 2007). Using the effect size (partial eta squared) for the interaction effect of cue by ISI in Experiment 1, we estimated that a minimum sample size of six participants would be required for 95% power at the 5% alpha level for this effect. As noted above, we included eyetracking to exclude any trials containing eye movements. Thus, there were two possible sources of reduced power in this design: losing trials and, potentially, weaker effects for covert compared to overt attention shifts. To ensure sufficient power we recruited more participants than the minimum suggested by this power analysis.

Participants

Twelve healthy participants (3 female; age 25.17 ± 5.95 years, mean ± SD; 2 left-handed) gave informed consent before completing the experiment. All participants had normal or corrected-to-normal vision and none had taken part in Experiment 1.

Experimental design, stimuli & task

The design and stimuli were as in Experiment 1. In addition, gaze position was recorded in order to exclude from analysis those trials where participants inappropriately broke fixation. One participant completed 27 rather than 30 blocks due to time constraints.

Eye tracking apparatus

A tower-mounted Eyelink 2000 eye tracker (SR Research, Ontario, Canada) was used to record the gaze position of the left eye at a sampling rate of 1000Hz.

Behavioural data analysis

Behavioural data were analysed using Matlab2014a (Mathworks) and R (R Foundation for Statistical Computing). Prior the the main analysis, trials with unwanted eye movements were removed, with the following criteria: saccades larger than 1° (visual angle) during the cue interval, presentation of the displays & ISI, blinks during presentation of the displays. This resulted in a grand average rejection rate for fixation broken of 13.10% ± 11.22% (mean ± SD), and for blinks a rejection rate of 1.02% ± 1.41% (mean ± SD) of trials.

Results

As illustrated in Figure 3, Experiment 2 replicated the results from Experiment 1. The valid cue benefitted performance in both the segregation and integration tasks and the invalid cue degraded performance in both tasks. The valid cue once again appeared to have the greatest benefit when the task was difficult (i.e. at shorter ISIs for segregation, longer ISIs for integration).

In a RANOVA with factors for cue (valid, neutral, invalid), task (segregation, integration) and ISI (10 ms, 30 ms, 50 ms, 70 ms, 100 ms) these patterns emerged in a main effect of cue ($F(2,22) = 28.53$, $p < .001$, $\eta_P^2 = .722$, $= \eta_G^2 = .274$) and an interaction of task and ISI ($F(4,44) = 40.71$, $p < .001$, $\eta_P^2 = .787$, $= \eta_G^2 = .201$). A three-way interaction emerged reliably in Experiment 2 ($F(8,88) = 5.63$, $p = .007$, $\eta_P^2 = .338$, $= \eta_G^2 = .011$), driven by a pattern in the segregation task in which the valid cue had a larger effect at short ISIs but the invalid cue had a larger effect at long ISIs. A significant interaction of task and cue ($F(2,22) = 3.48$, $p = .048$, $\eta_P^2 = .240$, $= \eta_G^2 = .005$) reflected a slightly larger cueing effect in the integration task. An additional main effect of ISI ($F(4,44) = 10.38$, $p < .001$, $\eta_P^2 = .486$, $= \eta_G^2 = .024$) appeared, as did a significant interaction of cue and ISI ($F(8,88) = 3.21$, $p = .003$, $\eta_P^2 = .226$, $= \eta_G^2 = .003$), but no effect of task was detected ($F<1$, $\eta_P^2 = .0003$, $= \eta_G^2 = .0001$).

For the integration task, cue validity (valid, invalid) had a significant effect at all ISIs (with corrected alpha of .01, 10ms: $t(11)=4.19$, $p < .001$; 30ms: $t(11)=4.55$, $p < .001$; 50ms: $t(11)=5.92$, $p < .001$; 70ms: $t(11)=7.35$, $p < .001$; 100ms: $t(11)=5.51$, $p < .001$). The invalid cueing effect was also significant for all ISIs (10ms: $t(11)=3.24$, $p = .004$; 30ms: $t(11)=3.95$, $p = .001$; 50ms: $t(11)=3.67$, $p = .002$; 70ms: $t(11)=3.35$, $p = .003$; 100ms: $t(11)=4.55$, $p < .001$). Similarly, for the segregation task, the valid cueing effect was significant for the four shortest of the five ISIs (10ms: t(11)=5.10, p < .001; 30ms: t(11)=5.57, p < .001; 50ms: t(11)=3.05, p = .005; 70ms: t(11)=2.88, p = .008; 100 ms: t(11) = 2.20, p = .025). Invalid cueing effects were significant for all ISIs (10ms: t(11)=3.40, p = .003; 30ms: t(11)=4.25, p = .001; 50ms: t(11)=4.55, p < .001; 70ms: t(11)=3.46, p = .003; 100ms: t(11)=4.75, p < .001).

Experiment 2 confirms the observations drawn from Experiment 1. Firstly, the valid endogenous cue benefitted task performance and the invalid cue degraded performance in both segregation and integration tasks, despite these tasks involving opposing temporal operations. Secondly, the benefit of the valid cue was greatest when the task was hard and the cost of the invalid cue was greatest when the task was easy.

As noted in the introduction, studies of exogenous cueing have found that the capture of attention can result in degraded ability to temporally segregate stimuli at that location. One account is that the deployment of spatial attention acts in part by emphasizing parvocellular visual input, resulting in a relative down-weighting of the temporally-precise input from magnocellular neurons (Yaffa Yeshurun & Levy, 2003). As a result, visual perception becomes less sensitive to temporal asynchrony.

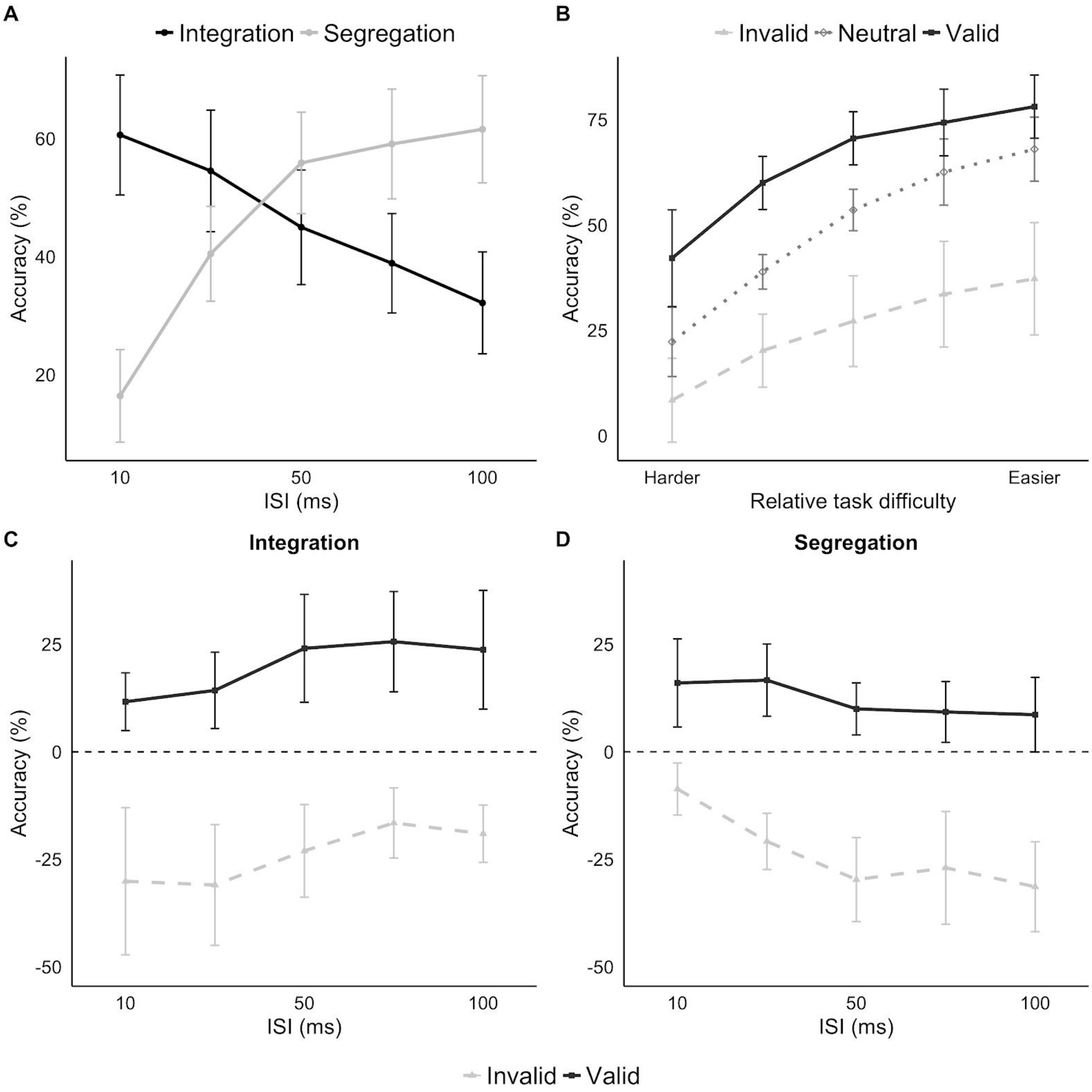

Figure 3.3: Results of Experiment 2. A. *Accuracy as a function of task version and ISI. Error bars here and in all panels indicate within-subjects 95% confidence interval (Morey, 2008).* ***B.*** *Accuracy as a function of cue type and relative task difficulty collapsed across segregation and integration tasks: for the segregation version the 'hardest' ISI is the shortest, for integration the 'hardest' ISI is the longest.* ***C.*** *Accuracy for integration as a function of cue type and ISI. Values reflect the difference of (in)valid from neutral cue conditions (centred data).* ***D.*** *Accuracy for segregation as a function of cue type and ISI, difference of (in)valid cue from neutral cue condition (centred data). Valid cue: solid line, square markers. Neutral: dotted line, diamond markers. Invalid: dashed line, triangle markers.*

The current results suggest that endogenous spatial attention must differ fundamentally from exogenous spatial attention because the endogenous deployment of attention benefits temporal segregation, whereas the exogenous deployment of attention degrades it (Yeshurun & Levy, 2003). However, the idea that effects of spatial attention on temporal processing are instantiated through a bias toward parvocellular or magnocellular input remains compelling. It may be that exogenous spatial attention necessarily biases perception toward parvocellular input, but that endogenous attention is able to flexibly emphasize either stream as a function of task requirements. In order to gain some perspective on this issue, we conducted a third experiment examining the impact of target eccentricity.

The parvocellular and magnocellular visual systems are defined by a split in the visual pathway beginning in the retinal ganglion cells that propagates through the lateral geniculate nucleus to cortex. The two streams subserve distinct functionality: parvocellular neurons are selective for colour and have high spatial resolution, whereas magnocellular neurons are fast and have high contrast sensitivity (Livingstone & Hubel, 1987). Importantly for our present purpose, there is evidence that the ratio of parvocellular to magnocellular neurons in a given area decreases with retinal eccentricity (Azzopardi, Jones & Cowey, 1999; Connolly & Van Essen, 1984). As a result, if endogenous spatial attention is able to flexibly bias perception towards either parvocellular or magnocellular input, this should express in different ways for stimuli located near fovea or at the periphery. On the one hand, when the goal is to integrate and target location near fovea, the predominance of slow parvocellular cells at this retinotopic location may lead to relatively good performance. Sparse parvocellular representation of peripheral stimuli may lead to comparatively worse performance. There would therefore be greater opportunity for endogenous spatial cueing effects at peripheral than at foveal locations. On the other hand, when the goal is to segregate, performance may be comparatively better at periphery than near-foveal locations on account of the proportion of fast magnocellular cells at these retinotopic locations. This would therefore lead to greater opportunity for spatial cueing effects at near foveal locations as compared to peripheral ones.

To test these hypotheses, Experiment 3 was identical to preceding experiments with one exception: sequential stimulus displays were separated by a consistent ISI of 70 ms. This reduced the dimensionality of the design and resulted in an increased number of trials per condition, which allowed us to introduce a new analytic factor representing retinal eccentricity.

Experiment 3

Method

Participants

Twenty healthy participants (4 male; age 21.53 ± 3.64 years, mean ± SD) gave informed consent before completing the experiment. All had normal or corrected-to-normal vision and reported right-handedness.

Experimental design, stimuli & task

Prior to the main experimental blocks of this experiment, participants completed a short version of the paradigm with no cueing and multiple ISIs. In this pre-experiment version, participants completed five practice trials for each of the two versions of the task, followed by two blocks of 80 trials (one block for each task version, each block comprised ten trials for each of the eight ISIs). This data was used to provide context as the relative difficulty of each task version at the fixed ISI used in the main experiment. Participants then completed 15 practice trials with cueing for each task version (30 total) before subsequently completing 10 blocks of the main experiment where each block comprised 60 trials (mixed design, except for task version which varied blockwise). Experimental design was otherwise as described for Experiments 1 and 2, with the exception that the ISI was fixed at 70ms.

Results

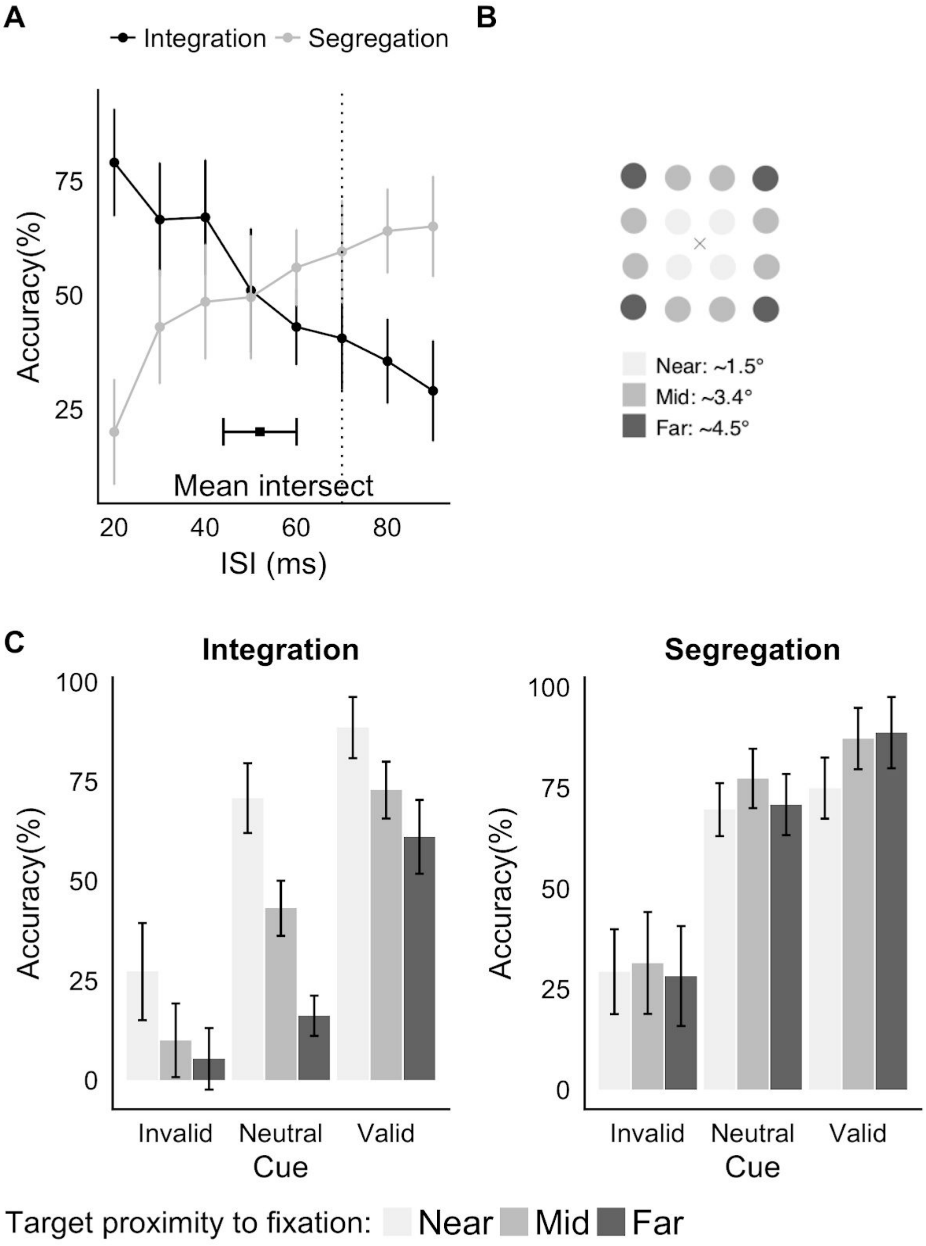

Figure 3.4: Results of Experiment 3. A. *Results of pre-experiment task. Dotted vertical line indicates fixed ISI used for the main blocks. Error bars here and in panel C indicate within-subjects 95% confidence interval* (Morey, 2008)*. Intersect error bars indicate SEM.* ***B.*** *Illustration of stimulus locations comprising each of the three proximity conditions.* ***C.*** *Results of main experiment. Accuracy for each task as a function of cue type and target eccentricity.*

As can be seen in Figure 3.4A, mean accuracy in the pre-experiment was better for longer ISIs for the segregation task but better for shorter ISIs for the integration task, as expected. The mean intersect was 52ms ± 36ms (mean ± SD) – slightly shorter than the fixed ISI of 70ms used in the primary experiment.

Figure 3.4C illustrates how Experiment 3 again replicates the core finding from Experiment 1: valid cues benefited performance in both the integration and segregation task and invalid cues degraded it. The results suggest that performance in the integration task was strongly impacted by the eccentricity of the target, but that this was not the case in the segregation task. In the integration task the efficacy of the valid cue appears to be accentuated for targets in the periphery.

In line with these impressions, a RANOVA with factors for task (segregation, integration), cue (valid, neutral, invalid) and target proximity to fixation (near, mid, far: see Figure 3.4B) identified a main effect of cue ($F(2,38) = 78.33$, $p < .001$, $\eta_P^2 = .805$, = $\eta_G^2 = .485$) and a cue by proximity interaction ($F(4,76)= 8.47$, $p < .001$, $\eta_P^2 = .308$, $\eta_G^2 = .022$). Variance in cue efficacy across levels of proximity was further modulated by task, as reflected in a significant three-way interaction ($F(4,76)= 6.176$, $p < .001$, $\eta_P^2 = .245$, $\eta_G^2 = .015$). A reliable cue by task interaction ($F(2,38)= 8.72$, $p < .001$, $\eta_P^2 = .315$, $\eta_G^2 = .028$) reflects an accentuated cueing effect in the integration task (alongside a shift in accuracy in the neutral cue condition across the tasks), and a reliable proximity by task interaction ($F(2,38)= 47.85$, $p < .001$, $\eta_P^2 = .716$, $\eta_G^2 = .104$) reflects an increased impact of target eccentricity in the integration task. A main effect of task ($F(1,19) = 14.31$, $p = .001$, $\eta_P^2 = .430$, = $\eta_G^2 = .122$) was driven by better performance in the segregation task, reflecting our use of a fixed ISI that favoured segregation, and a main effect of target proximity ($F(2,38) = 24.848$, $p < .001$, $\eta_P^2 = .594$, = $\eta_G^2 = .060$) was driven by performance on the integration task, where accuracy was greatest for central targets.

We conducted two additional RANOVAs with with factors for cue and proximity on results from the integration and segregation tasks in isolation. Analysis of the integration task revealed significant main effects of cue (F(2,38)= 78.44, $p < .001$, $\eta_P^2 = .805$, $\eta_G^2 = .543$) and proximity (F(2,38)= 55.78, $p < .001$, $\eta_P^2 = .746$, $\eta_G^2 = .286$) and a significant interaction (F(4,76)= 11.15, $p < .001$, $\eta_P^2 = .370$, $\eta_G^2 = .066$). Analysis of the segregation task revealed a robust main effect of cue (F(2,38)= 52.06, $p < .001$, $\eta_P^2 = .733$, $\eta_G^2 = .446$). In the segregation task, the main effect of proximity was not significant at the corrected alpha level of .025 (F(2,38)= 4.83, $p = .027$, $\eta_P^2 = .203$, $\eta_G^2 = .014$), and nor was the interaction (F(4,76)= 2.91, $p = .027$, $\eta_P^2 = .133$, $\eta_G^2 = .012$).

Though participants in Experiment 3 were explicitly instructed to maintain fixation, eye movements were not monitored and so, again, it is possible that participants may have moved their eyes in response to cue stimuli. To address this possibility and to reproduce the pattern of results observed in Experiment 3 we conducted an expanded replication in which gaze position was monitored.

Experiment 4

Method

Power analysis

Sample size choice for the experiment was informed by power analyses conducted with G*Power 3 (Faul et al., 2007). Using the effect size (partial eta squared) for the three way interaction effect in Experiment 3, we estimated that a sample size of ten participants would be required for 95% power at the 5% alpha level for this effect.

Participants

Ten healthy participants (2 male; age 22.40 ± 1.71 years, mean ± SD) gave informed consent before completing the experiment. All had normal or corrected-to-normal vision and reported right-handedness.

Experimental design, stimuli & task

As described for Experiment 3. In addition gaze position was monitored in order to reject trials in which participants inappropriately broke fixation.

Eye tracking apparatus

A tower-mounted Eyelink 2000 eye tracker (SR Research, Ontario, Canada) was used to record the gaze position of the left eye at a sampling rate of 1000Hz.

Behavioural data analysis

Behavioural data were analysed using Matlab2014a (Mathworks) and R (R Foundation for Statistical Computing). Prior the the main analysis, trials with unwanted eye movements were removed, with the following criteria: saccades larger than 1° (visual angle) during the cue interval or presentation of the displays & ISI, blinks during presentation of the displays. This resulted in a grand average rejection rate for fixation broken of 3.90% ± 4.75% (mean ± SD), and for blinks a rejection rate of 0.30% ± 0.48% (mean ± SD) of trials.

Results

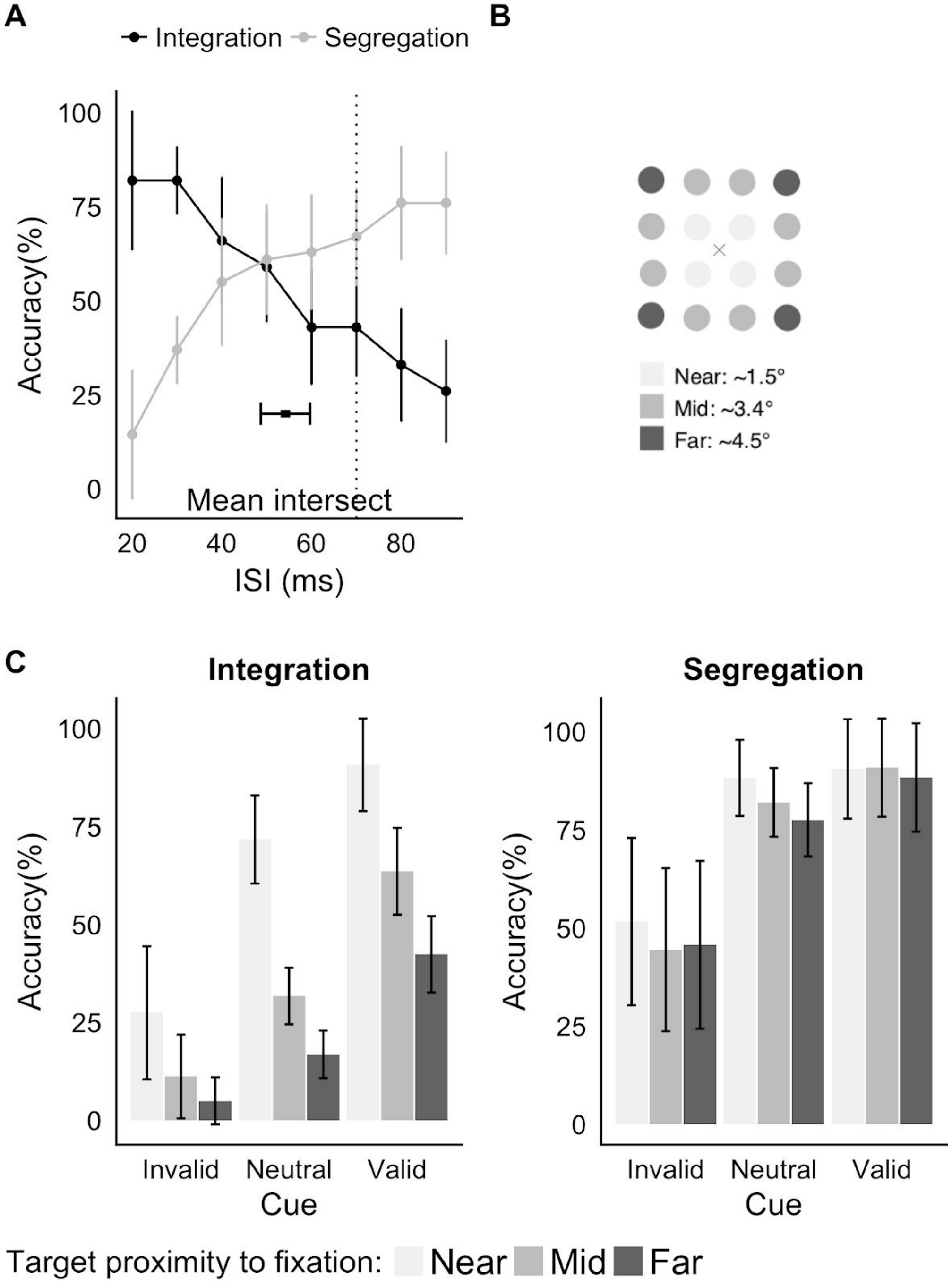

Figure 3.5: Results of Experiment 4. A. *Results of pre-experiment task. Dotted vertical line indicates fixed ISI used for the main blocks. Error bars here and in panel C indicate within-subjects 95% confidence interval* (Morey, 2008)*. Intersect error bars indicate SEM.* ***B.***

Illustration of stimulus locations comprising each of the three proximity conditions. ***C.*** *Results of main experiment. Accuracy for each task as a function of cue type and target eccentricity.*

Figure 3.5A shows that the results of the pre-experiment were comparable to those in Experiment 3, with a similar intersect at the group level: 52ms ± 18ms (mean ± SD), again indicating that the fixed ISI of 70ms in the main blocks was slightly greater than the mean intersect.

As can be seen from Figures 3.5C and D, Experiment 4 broadly replicated Experiment 3. As in Experiment 3, A RANOVA with factors for task (segregation, integration), cue (valid, neutral, invalid) and target proximity to fixation (near, mid, far: see Figure 3.5B) identified a main effect of cue (F(2,18) = 29.26, p < .001, η_P^2 = .765*,* = η_G^2 = .452), an interaction between cue and proximity (F(4,36)= 4.22, p = .006, η_P^2 = .319, η_G^2 = .024), and a three-way interaction between cue, proximity and task (F(4,36)= 4.71, p = .004, η_P^2 = .344, η_G^2 = .018). Also commensurate with Experiment 3 was a significant main effect of task (F(1,9) = 48.68, p < .001, η_P^2 = .844*,* = η_G^2 = .376), a main effect of target proximity (F(2,18) = 38.70, p < .001, η_P^2 = .811*,* = η_G^2 = .180), and an interaction between proximity and task (F(2,18)= 21.37, p < .001, η_P^2 = .704, η_G^2 = .107). In Experiment 4 the cue by task interaction was not significant, though it had similar directionality and effect size estimates (F(2,18)= 2.63, p = .1, η_P^2 = .226, η_G^2 = .029).

This consistency with results from Experiment 3 continued in further analysis of each task separately. Analysis of the integration task revealed significant main effects of cue (F(2,18)= 58.28, p < .001, η_P^2 = .866, η_G^2 = .581) and proximity (F(2,18)= 48.38, p < .001, η_P^2 = .843, η_G^2 = .492) and a significant interaction (F(4,36)= 5.05, p = .002, η_P^2 = .360, η_G^2 = .104). Analysis of the segregation task revealed a robust main effect of cue (F(2,18)= 12.04, p < .001, η_P^2 = .572, η_G^2 = .366). In the segregation task, the main effect of proximity was not significant at the corrected alpha level of .025 ($F(2,18) = 1.70$, $p = .21$, $\eta_P^2 = .203$, $\eta_G^2 = .013$), and nor was the interaction ($F(4,36) = 1.84$, $p = .14$, $\eta_P^2 = .169$, $\eta_G^2 = .005$).

Discussion

In all four experiments, spatial cueing impacted temporal processing regardless of whether the current goal was segregation or integration. This supports the notion that strategic attentional allocation engendered by endogenous cueing modulates temporal processing in a flexible manner. When the task requires that discrete events be integrated to allow for the detection of a target stimulus, endogenous spatial cueing aids this process. But when the task requires that discrete events be segregated, endogenous spatial cueing continues to have a positive impact. Critically, our experimental design allows us to demonstrate this consistent benefit on orthogonal temporal processes when visual stimulation was the same and only task goals differed.

Our experiments replicate existing results show that endogenous cues facilitate temporal segregation (Hein, Rolke, & Ulrich, 2006), extending this finding by demonstrating that a.) there is a cost to segregation when attention is invalidly cued and, b.) endogenous cues have a commensurate benefit to temporal integration. The benefit of endogenous cues contrasts with findings from studies of exogenous cueing, where the capture of attention has been found to degrade temporal segregation (eg. Yeshurun & Levy, 2003). This is in line with a broad notion that endogenous and exogenous attention fundamentally differ in terms of neurophysiological basis, phylogenetic origins, and behavioural impact (see Chica et al., 2013, for discussion), and additionally supports the notion that exogenous attention may operate at a lower level of the visual hierarchy than endogenous attention (Hein et al., 2006; Klein, 1994).

One account for the negative impact of exogenous attention on temporal processing is based on the idea that exogenous cues accentuate parvocellular input, resulting in a relative downweighting of magnocellular input (Yeshurun & Levy, 2003). Because magnocellular neurons have better temporal resolution than parvocellular neurons, this could cause a decrease in sensitivity for temporal asynchrony. In line with the general idea that deployment of spatial attention impacts the relative weighting of parvocellular and magnocellular visual input, in Experiments 3 and 4 we find that the eccentricity of a target has an impact on temporal integration that varies as a function of cue validity. Stimuli at central locations are strongly represented in the parvocellular system by default, but stimuli in the periphery are not. Our results show that valid cues have the greatest benefit for targets at peripheral locations, thus where parvocellular representation is sparse and a bias toward this input stream would have the greatest benefit.

However, we do not see a corresponding relationship between cueing and target eccentricity in results from our segregation task. Though cueing strongly impacts performance in the segregation task, there is no reliable impact of target eccentricity on cueing. This suggests that endogenous cueing effects on temporal integration and segregation are unlikely to act solely through a weighting of parvocellular and magnocellular input.

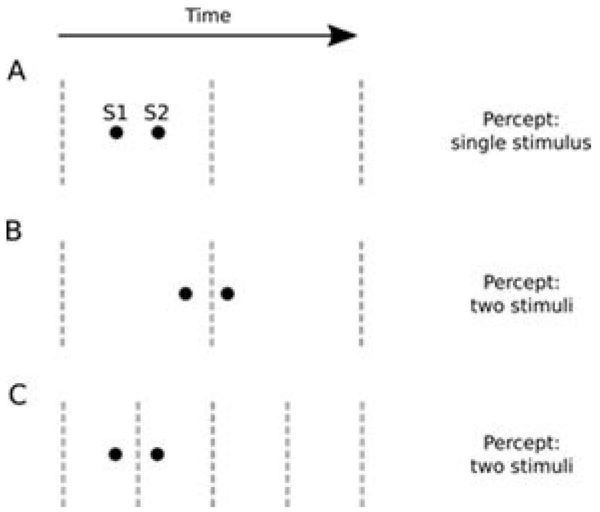

Figure* 3.*5. Theoretical schematic of perceptual result with different temporal integration windows. *Grey dashed lines indicate boundaries of temporal integration windows. Black dots indicate separate, sequentially appearing stimuli: S1 – stimulus one, S2 – stimulus two. Stimuli which fall within the same window are more likely to be integrated into a single percept.*

How else might endogenous spatial attention benefit apparently-opposing temporal processes of segregation and integration? One possibility is that endogenous spatial attention might flexibly adapt the size of rapidly sampled perceptual moments. The idea that perception relies on ‘temporal windows’ has a long history in psychological research, supported by studies of psychophysics (Allport, 1968; Shallice, 1964; Stroud, 1955), optical illusions (Simpson et al., 2005; VanRullen & Koch, 2003), somatosensory processing (Baumgarten et al., 2015), sensorimotor synchronization (Mates et al., 1994), and human electrophysiology (Samaha & Postle, 2015; VanRullen, 2016). Previous studies using this variant of the missing dot task suggest that integration windows usefully describe the temporal processing in the integration and segregation task. First, performance alternates over time between better integration versus better segregation: when segregation is better than average, integration is worse, and vice-versa (Wutz et al., 2016). Second, participants strategically increase the instantaneous frequency of their alpha oscillations shortly before segregation trials, compared to integration trials (Wutz et al., 2018). Third, the phase of particular neural oscillations, when the stimulus appears, predicts whether two stimuli are integrated or segregated (Ronconi et al., 2017; Wutz et al., 2016). Together, these studies suggest that temporal integration depends on whether or not two sequential stimuli fall within the same temporal window in sensory processing (Cecere et al., 2015; Samaha & Postle, 2015).

Figure 3.5 illustrates how the size of temporal windows might be adapted to match task requirements. Two stimuli presented rapidly one after the other can lead to a percept of either one or two unique events. If they fall within the same temporal window (Figure 3.5A), a single stimulus is perceived. There is evidence suggesting the result can be a single integrated percept – as opposed to a preferential processing of the first stimulus over the second – even when there is no benefit of integration, for example in reversal of reported target order in rapid serial visual presentations (Akyürek et al., 2012; Akyürek & Wolff, 2016). In other circumstances, a pair of stimuli separated by the same delay are perceived as two distinct percepts if they fall in different temporal windows, which can occur both on account of the phase of sampling of the visual environment (Figure 3.5B) or the size of these windows (Figure 3.5C). Applying this concept to the present findings, attentional processing may have operated by biasing the system to sample the visual environment with shorter temporal windows when the task required segregation of temporally separate stimuli, but by biasing the system to longer temporal windows when success depended on integration of temporally disparate stimuli (Wutz et al., 2016; Wutz et al., 2018). In this way the temporal window size could influence the perceptual outcome, independent of any effects (such as gain or tuning) on the low-level representation of the stimulus. However, it is important to note that while our results are consistent with this model, they do not demonstrate its necessity: other accounts are equally possible.

In the experimental paradigm employed in the current study, spatial cues provided temporal information as well as spatial information, and this temporal cueing may have impacted task performance independently of the spatial cueing effect. Consistent with this possibility, Correa and colleagues (2006) reported a benefit to temporal resolution from temporal cueing using a version of the temporal order judgement paradigm, which requires participants to segregate rapid sequential stimuli in order to report their order of presentation. One possibility is that valid cues in our design may have caused the "phase" of the temporal windows to be adapted to current task goals (Wutz et al., 2016; Ronconi et al., 2017a,b). For example, when performance required integration, alignment of the onset of a temporal window to the onset of the stimulus could have increased the likelihood of sequential stimuli falling within the same window, boosting the magnitude of the cueing effect through the synergistic allocation of spatiotemporal attention. This concept fits with the wealth of literature indicating that the ongoing phase of neural oscillations – particularly of those at lower frequencies such as alpha band – is important in many aspects of visual perception, from detection and selection (Milton & Pleydell-Pearce, 2016; Varela, Toro, John, & Schwartz, 1981), to causality judgements and conscious updating (Chakravarthi & Vanrullen, 2012; Cravo, Santos, Reyes, Caetano, & Claessens, 2015). In future experiments it will be important to separate these influences on temporal processing.

Given that our experiments involve the detection of rapidly presented stimuli with varying duration, it is important that we consider the possible role of luminance-duration reciprocity in generating our results. Bloch's law of temporal summation suggests that within a range of short stimulus durations, perceived stimulus energy will be defined by the combination of luminance and duration (Bloch, 1885). This raises the possibility that participants may have completed our integration task by monitoring for circles that were perceived as being completed, but with lower stimulus intensity (because of the temporal gap in presentation of the two circle halves). However, we do not think this is likely. First, each independent circle segment was presented for an equal duration: two segments could appear together for 10 ms, or each circle half could appear in a separate 10 ms interval. For this difference to impact the perceived luminance of the completed circle, the two circle halves would have to be integrated into a single circle object before summated stimulus energy was computed by the visual system. To our knowledge, there is no evidence that this occurs in the visual system, and results suggests that the integration of form across spatially separated stimuli occurs later than the integration of luminance and duration (Kahneman, Norman, & Kubovy, 1967). Second, the circle segments employed in our work were relatively large, high-contrast stimuli that, in Experiments 3 and 4, were consistently separated by an ISI of 70 ms. This is beyond the critical interval in which luminance-duration reciprocity occurs for supra-threshold stimuli (Davy, 1952; Gorea & Tyler, 1986).

To conclude, the current study provides evidence that endogenously cued spatial attention has much the same benefit to integration and segregation, two opposing temporal processes. This distinguishes endogenous attention from the exogenous capture of attention, which has been found to degrade temporal processing. Our results constrain theoretical models of selective attention and are broadly in line with the developing idea that attention in time may act through the adaptation of temporal windows.

Chapter 4: Different effects of spatial and temporal attention on temporal processing

A version of this chapter was published in November 2018:

Sharp, P., Melcher, D., & Hickey, C. (2018). Different effects of spatial and temporal attention on the integration and segregation of stimuli in time. *Attention, Perception, & Psychophysics,* 1-9.

Abstract

Having expectations about when and where relevant stimuli will appear engenders endogenous temporal and spatial orienting, and can provide vital benefits to visual processing. Whilst more is known about how each of these forms of orienting affect spatial processing, comparatively little is understood about their influence on temporal integration and segregation of rapid sequential stimuli. A critical question is whether the influence of spatial cueing on temporal processing involves independent spatial and temporal orienting effects or a synergistic spatiotemporal impact. Here, we delineate between temporal and spatial orienting engendered by endogenous cues by using a paradigm with identical visual stimulation when the goal is to integrate or segregate stimuli in separate blocks of trials. We find strong effects of spatial orienting on both integration and segregation performance. In contrast, temporal orienting engendered only an invalid cueing cost, for integration trials only. This clear differentiation between spatial and temporal cueing effects provides constraints to inform arbitration between theories of how

attention biases the visual processing stream and influences the organization of visual perception in time.

Introduction

In complex and dynamic visual environments, processing can be optimized by attending to where and when relevant information will appear. Endogenous cues can prompt spatial or temporal orienting independently, but often elicit both at the same time. Research has generally focused on how these different types of orienting affect spatial processing. However, an additional, critical challenge for the visual system is to parse the incoming sensory input into coherent objects and events over time, binding together disparate sensory signals together (integration) as well as distinguishing between subsequent sensory inputs that reflect two unique objects/events (segregation). Our understanding of the influence of spatial and temporal cues on such temporal processing remains sparse.

In studies of spatial processing, there are similarities between how spatial and temporal orienting affect vision. For example, Coull and Nobre (1998) demonstrated that valid endogenous cues indicating either when or where a target would appear had a qualitatively similar benefit on target detection. Spatial orienting to a particular location after a valid cue provided a larger performance benefit than temporal orienting to a particular interval, but both had a benefit. Further investigations also using endogenous cues confirmed this pattern of valid cueing effects on spatial discrimination for both spatial and temporal orienting (Griffin, Miniussi, & Nobre, 2002; Olk, 2014). Similarly, in a oddball detection task using auditory stimuli, both spatial and temporal orienting were found to benefit spatial processing performance (Lange, Krämer, & Röder, 2006). Whilst there is evidence of dissociations between the effects on performance of spatial and temporal orienting following exogenous cueing (Ahrens, Veniero, Gross, Harvey, & Thut, 2015; Jones, 2014), when attentional shifts are endogenously driven the evidence points to similarities and even interacting performance benefits from spatial and temporal orienting. Rohenkohl and colleagues (2014) reported benefits to spatial discrimination performance afforded by both spatial and temporal orienting, as well as characterising the interaction between these two types of orienting. Whereas spatial orienting benefits were further boosted by valid temporal expectations, for the case of temporal orienting performance benefits were extinguished if spatial expectations were misleading. There is also evidence that temporal expectations can combine synergistically with other forms of expectations, for example with event-specific information about stimulus identity (Langner, Steinborn, Eickhoff, & Huestegge, 2018).

Shifting focus from studies of different types of orienting on spatial processing to those pertaining to temporal processing, we note that these studies have typically featured paradigms in which stimuli appear after a fixed interval from onset of endogenous spatial cues. Because these cues implicitly provide temporal information, this introduces some ambiguity of interpretation: is performance impacted purely by information about the location of the target, or is it important that the cue provide information about timing? For example, Hein and colleagues (2006) demonstrated that a valid cue indicating the spatial location of two rapid sequential stimuli facilitates segregation of the stimuli, such that participants were able to discriminate which of them appeared first. However, the onset of the cue employed in this work also provided information about when the stimuli would appear, opening the possibility that temporal orienting mechanisms might also have been recruited to facilitate performance. Similarly, we have demonstrated that spatial cueing affects both segregation and integration of rapid sequential stimuli, depending on which of these opposing temporal processes is required for successful target detection. This was achieved using a paradigm with two forms whereby visual stimulation remains the same while task goals are manipulated (Sharp, Melcher, & Hickey, 2018b). Again, the spatial cues in that paradigm could have engendered temporal orienting since the interval between cue and stimulus onset was of fixed duration. It therefore remains unclear if spatial cueing effects on temporal processing are driven by spatial orienting alone, or via a combined, synergistic influence of spatial and temporal orienting combined.

Under normal circumstances, spatial and temporal orienting often co-occur, since we often have access to combined spatiotemporal expectations about the visual environment. Indeed, unique objects or events are defined by their spatio-temporal conjunction. Perception of an object in motion is an obvious example of this maxim. Doherty and colleagues (2005) tested whether implicit spatiotemporal expectations about the trajectory of a moving object which disappeared behind an occluder influenced participants' speed in detecting a dot on the object when it reappeared. Both spatial and temporal expectations improved performance as compared to the control condition. Crucially, combined spatiotemporal expectations had a synergistic effect, leading to faster reaction times than in either the purely spatial or purely temporal orienting condition. It is important to note that perception of motion is a salient feature which by definition relies on combined spatiotemporal information, raising a question about the generality of this finding for other forms of temporal processing and leaving open the question of whether the facilitatory effect of valid spatial cues on temporal integration and segregation is in part due to the combined influence of spatial and temporal orienting.

A secondary focus of the current study is on remaining uncertainty regarding how purely temporal orienting impacts segregation and integration processes. A classical finding on the effects of temporal orienting on spatial processing was demonstrated by Los and Van den Heuvel (2001). In this study, a symbolic temporal cue indicated the delay after which a 'L' or 'R' target appeared, requiring binary choice-response with the spatially congruent hand. Results from this ‘foreperiod task’ led the authors to conclude that symbolic temporal cues can engender strategic temporal orienting. This added to a literature demonstrating that valid temporal expectations impact not only auditory perception, typically using reaction time as a metric (Griffin & Nobre, 2005), but also in the detection of targets in a rapid stream of visual stimuli (Correa et al., 2004; Miller & Schröter, 2002). Looking rather at the effect of temporal orienting on temporal processing, Correa and colleagues (2006) employed a temporal order judgement paradigm to probe the influence of endogenous temporal cueing on perception of rapid sequential visual stimuli. Temporal orienting engendered by the cue was found to improve participants’ ability to report which stimulus appeared first. A further consideration in this context is the relationship of temporal cues and hazard rates: stimuli that appear earlier than was indicated by the cue are surprising, whereas those that appear later than was cued are better expected (Correa et al., 2004; Nobre & van Ede, 2018). Temporal orienting paradigms therefore often employ catch trials in which no stimulus appears after the cue, in order to modulate the function describing this increasing probability that a stimulus will appear (Correa et al., 2006; Steinborn et al., 2008).

Here we test whether spatial cues impact temporal integration and segregation independent of any temporal expectations, and whether temporal cues impact temporal integration and segregation when no spatial expectations are provided by cueing. The paradigm features manipulation of the task goal - either integration or segregation of visual events - across blocks of experimental trials. Importantly, visual stimulation remains constant, with endogenous cues predicting either where or when the upcoming target will likely arrive. For purely spatial orienting, we expected a performance benefit of valid spatial cueing and performance cost of invalid cueing for both integration and segregation, consistent with our earlier work (Sharp et al., 2018b). In the case of temporal orienting, the prediction is less clear and we did not have strong predictions. One possible outcome is temporal orienting effects similar to those found with spatial orienting. Alternatively, temporal orienting might be particularly useful for rapid temporal segregation, allowing greater precision in time. A third possibility is that any temporal integration might be more demanding in terms of temporal coding and thus be more influenced by the temporal cue, given the requirement to encode both stimuli across time.

Method

Participants

Twenty-one healthy participants (4 male; age 22.14 ± 2.94 years, mean ± SD) gave informed consent before completing the experiment. All reported normal or corrected-to-normal vision and right-handedness. Participants provided informed consent in accordance with the Declaration of Helsinki and approval for the study was granted by the ethics committee of the University of Trento.

Experimental design and stimuli

The stimuli and task were generated with Psychophysics Toolbox (Brainard, 1997) in MATLAB (MathWorks). Stimuli were presented on an LED backlit monitor designed for psychophysics stimulus presentation (VPixx Technologies) with a 100Hz refresh rate.

The experiment used a 3x2x2 fully within-subjects design: 3 levels of cue validity (valid/neutral/invalid) x 2 task versions (segregation/integration) x 2 types of orienting (spatial/temporal). An overview of the design is shown of panel B of Figure 4.1. The experimental task was varied by block (alternating between segregation and integration); cue validity was varied fully randomly by trial and the type of orienting indicated by the cue varied across the two separate sessions (counterbalanced such that half of participants completed the temporal orienting session first).

The basic trial structure is shown in Figure 4.1. A small fixation cross in the form of a red 'X' was present throughout the presentation of stimuli, this cross measured approximately 0.2° (visual angle). For the spatial orienting session, at the beginning of each trial, one of the arms of the cross changed from red to green to provide the cue that the target for that trial would likely appear in the indicated quadrant. For the temporal orienting session, the cue indicated whether the displays featuring the target would likely appear after a short or a long delay (350 or 850 ms). The form of the cue was a green cross with two sections filled in, resembling a sand timer either upright or on its side (see Figure 4.1), with the pairing between cue and delay counterbalanced across participants. Participants were instructed that the cue was valid around 75% of the time, thus in approximately 22% of total trials the cue was invalid, in 53% of trials the cue was valid, and in 25% of trials a neutral cue was shown. The neutral cue took the form of a colour change of the tips of all four arms of the cross, such that a similar number of pixels changed from red to green in the neutral condition as in the valid/invalid cueing conditions. In 10% of trials the cross turned blue after the maximum cue interval of 850 ms and no target or displays were presented. These catch trials were included to mitigate the influence of a rising hazard rate as time elapsed during the cue interval (Janssen & Shadlen, 2005; Steinborn et al., 2008).

In the spatial orienting session, the duration of the cue interval had a jitter from a square distribution between 350 and 850 ms, meaning that the cue did not give any information about the timing of the stimulus onset. In the temporal cueing session, the cue interval was either 350 or 850 ms and gave no information about the spatial location of the target. After the cue interval, the fixation cross became entirely red again, and the first display appeared on screen for 10 milliseconds. The two frames comprised an odd-element (OE) or missing-dot (MD) task, as used previously to measure both temporal integration and segregation using the same stimulus (Sharp et al., 2018b; Wutz et al., 2016). This display comprised a circle at seven locations out of a possible sixteen (on a four by four grid of locations), and each circle was formed from two arc elements (see Figure 4.1: ‘Display 1’). At one position in the display there was a half circle (i.e. a single arc). Each circle was 1.2° (visual angle) in diameter, the grid of possible locations measured 8.4° by 8.4°. Each circle within the display had an irrelevant random orientation selected from the possible orientations of 45°- 315°.

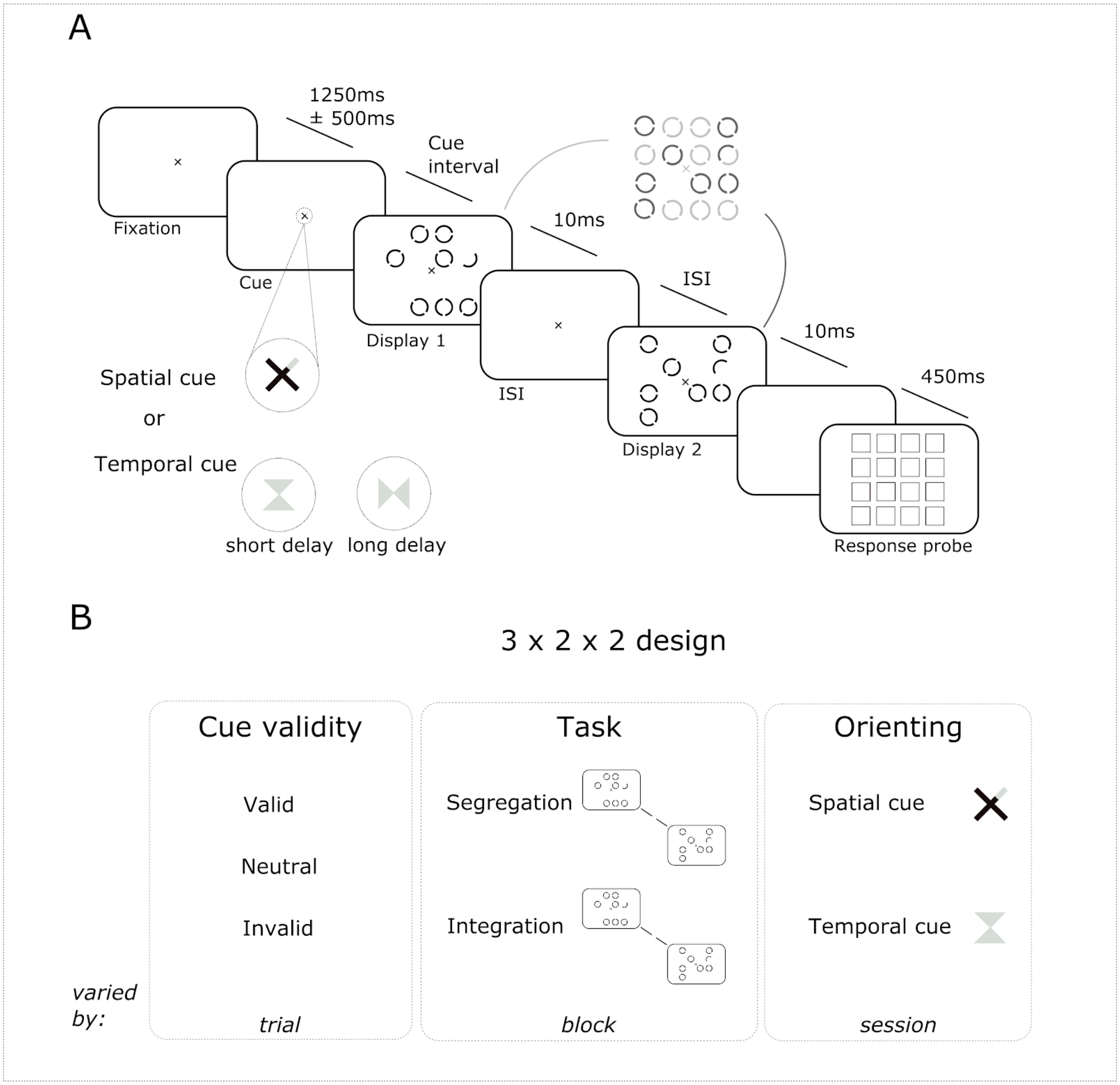

Figure 4.1 ***Paradigm and design. A.*** *Trial structure. In the spatial orienting session the cue indicated where the target would likely appear. In this example the spatial cue indicates the target will likely appear in the top right quadrant of the display. In the temporal orienting session the cue indicated when the target would likely appear, either after a short or long delay. In neutral cue trials all four tips of the cross turned green. If this trial were in a segregation block, the target would be the location second-down on the far right (the half-circle). If this trial were in*

an integration block, the target would be the location in the near-left column where no stimulus appeared in either display. In the spatial orientation session, the cue interval was jittered between 350 and 850 ms, in the temporal orienting session this interval was either 350 or 850 ms. In the pre-experiment the ISI varied (see Methods), while in the main experimental blocks it was fixed at 50 ms. ***B.*** *Overview of the full within-subjects design (see Methods). The segregation target was the half circle, the integration target was the missing circle.*

Following a fixed inter-stimulus interval (ISI) of 50 ms, a second display appeared for ten milliseconds (see Figure 4.1: ‘Display 2’). This display also comprised a circle at seven locations and a half circle at one location. Crucially, the half circle in display two was the corresponding arc element at the same location as the half circle location from display one, such that if the two displays were superimposed the two arc elements formed a standard circle stimulus. The locations of the seven circles for each display never overlapped, such that if the two displays were superimposed one of the sixteen possible locations remained empty. This hypothetical superimposition is illustrated in Figure 4.1 (top right image). After 500 milliseconds, a response probe screen appeared. This comprised a grid of squares where each square identified one of the sixteen possible target locations. Participants indicated, by mouse click, at which location they had perceived the target.

Task

Participants completed two sessions for the experiment (separated by a minimum of one day and a maximum of ten days). On separate days, the cue provided information either about the location of the target in one session (spatial session), or about when the displays featuring the target would appear in the other session (temporal session). The order of sessions was counterbalanced across subjects. There were two versions of the task goal, such that the stimulus presentation was the same and only the task instruction differed blockwise. In one version of the task, the target was the half circle. Successful identification of the half circle requires temporal parsing of the two displays, therefore this is referred to as the segregation task. Integration of the two displays would result in a combined percept (see Figure 4.1) in which the half circle location is indistinguishable from the other locations.

In the other version, the target was the location in which there was no circle in either display. Successful identification of this location requires a combined percept of the two displays, therefore this is referred to as the integration task. Participants were explicitly instructed to fixate the cross in the centre of the screen throughout stimulus presentation.

In the first session, prior the main experimental blocks, participants completed a version of the paradigm with no cueing and multiple ISIs to identify baseline performance. In this screening task, participants completed five practice trials for each of the two versions of the task, followed by two blocks of 80 trials for analysis (one block for each task version, each block comprised ten trials for each of the eight ISIs). Screening results were used to exclude participants whose difference in performance for the different versions of the uncued task constituted an outlier (described below).

Each experimental session began with 25 practice trials with cueing for each task version (50 total), which were repeated if accuracy on either task version was low (<25%); one participant was excluded as they could not attain this level of performance for the segregation task after four attempts. For each of the two sessions, participants completed ten blocks of the main experiment where each block comprised sixty full trials plus seven catch trials. Practice trials and catch trials were excluded from the main analysis.

Behavioural data analysis

Behavioural data were analysed using Matlab2013a (Mathworks) and R (R Foundation for Statistical Computing). To identify outliers we used data from the screening task which featured multiple ISIs and no cueing. We calculated a least square fit for results from the screening task for each participant, estimating the intersect between tasks (i.e. the ISI at which performance on the segregation and integration of the tasks was equal). We excluded participants when this intersect was more than two standard deviations from the group mean. This, along with the exclusion of a participant who could not achieve reasonably performance on the practice for the segregation version, resulted in the exclusion of two participants (10% exclusion rate).

For data of the main blocks of the spatial orienting session, the trials were binned by duration of the cue interval, and only data from the short interval (350 to 500 ms) and long interval (600 to 850 ms) bins were used for the main analysis (in the temporal orienting session the cue interval was always either 350 or 850 ms).

As recommended by Lakens (2013), two estimates of effect sizes are provided: partial eta squared and generalised eta squared. The former is better suited for power analyses and comparisons within a study, whereas the latter is a metric more suited to comparisons across experiments (Bakeman, 2005b). Post hoc testing was conducted by Bonferroni-corrected pairwise comparisons. For these tests, we report Cohen's d_z which is a measure of effect size for repeated measures tests.

Results

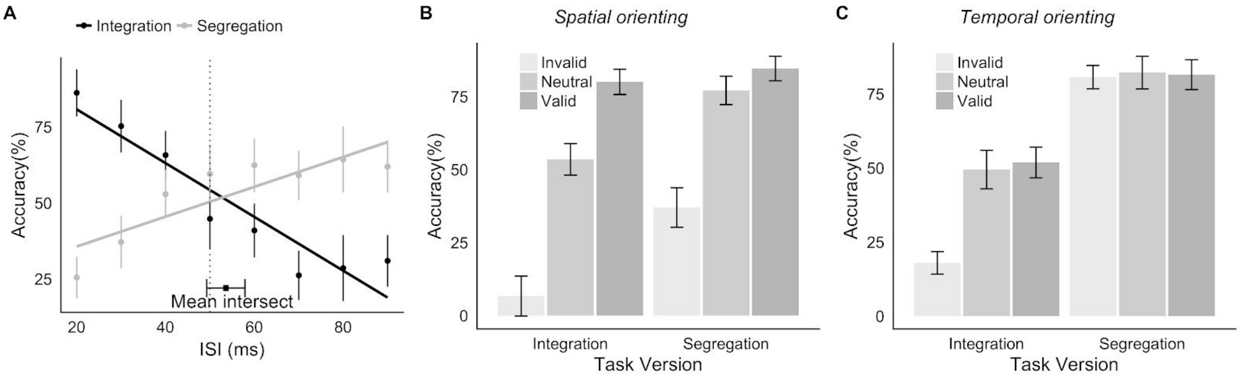

Figure 4.2 ***Main findings. A.*** *Results of pre-experiment task. Dotted vertical line indicates fixed ISI used for the main blocks. Error bars here and in all panels indicate within-subjects 95% confidence interval (Morey, 2008). Intersect error bars indicate SEM.* ***B.*** *Results of main experiment for spatial orienting. Accuracy as a function of task and validity of cue.* ***C.*** *Results of main experiment for temporal orienting. Accuracy as a function of task and validity of cue.*

Figure 4.2A shows that in the pre-experiment with no cueing, participants performed better at integration when the ISI was shorter and better at segregation when the ISI was longer, as expected (Sharp et al., 2018; Wutz et al., 2016). The mean intersect at which performance was matched for integration and segregation was close to the fixed ISI of 50 ms used for the main experimental blocks.

For the data of the main experiment a repeated measures ANOVA was conducted, with factors of task (segregation/integration), cue validity (valid/invalid) and type of orienting (spatial/temporal). As in previous experiments, significant main effects were found for task ($F(1,18)= 57.12$, $p < .001$, $\eta_P^2 = .760$, $\eta_G^2 = .502$) and cue validity ($F(2,36)= 137.25$, $p < .001$, $\eta_P^2 = .884$, $\eta_G^2 = .547$), and a significant interaction was found between task and cue validity

($F(2,36)= 61.17$, $p < .001$, $\eta_P^2 = .773$, $\eta_G^2 = .137$). The type of orienting (spatial vs temporal) had a significant main effect on performance ($F(1,18)= 7.17$, $p = .015$, $\eta_P^2 = .285$, $\eta_G^2= .018$) and interactions of task and type of orienting ($F(1,18)= 50.67$, $p < .001$, $\eta_P^2 = .738$, $\eta_G^2 = .116$) and cue validity and type of orienting were observed ($F(2,36)= 48.23$, $p < .001$, $\eta_P^2 = .728$, $\eta_G^2 = .255$), as well as a significant three-way interaction ($F(2,36)= 11.30$, $p = .001$, $\eta_P^2 = .386$, $\eta_G^2 = .024$).

As can be seen in Figure 4.2B, strong spatial cueing effects emerged in both tasks, as confirmed by the results of a follow up RANOVA constrained to results from spatial cueing conditions which revealed significant main effects of task ($F(1,18)= 18.88$, $p < .001$, $\eta_P^2 = .512$, $\eta_G^2 = .244$) and cue validity ($F(2,36)= 97.27$, $p < .001$, $\eta_P^2 = .844$, $\eta_G^2 = .688$), and a significant interaction ($F(2,36)= 18.84$, $p < .001$, $\eta_P^2 = .511$, $\eta_G^2 = .091$). Post hoc testing revealed that spatial cueing effects were driven both by a benefit of valid cueing for both segregation ($t(18) = 4.17$, $p < .001$, $d_z = .93$) and integration ($t(18) = 9.06$, $p < .001$, $d_z = 2.03$), as well as a cost to invalid cueing for both segregation ($t(18) = 5.76$, $p < .001$, $d_z = 1.29$) and integration ($t(18) = 12.41$, $p < .001$, $d_z = 2.78$).

The pattern of effects for temporal cueing was remarkably different. A follow up RANOVA constrained to results from temporal cueing conditions revealed main effects of task ($F(1,18)= 100.32$, $p < .001$, $\eta_P^2 = .848$, $\eta_G^2 = .722$) and cue validity ($F(2,36)= 100.40$, $p < .001$, $\eta_P^2 = .848$, $\eta_G^2 = .83$), and a significant interaction ($F(2,36)= 85.71$, $p < .001$, $\eta_P^2 = .826$, $\eta_G^2 = .251$). However, as can be seen from Figure 4.2C, the pattern of results in the temporal cueing condition was quite different from that observed in the spatial cueing condition. Post hoc testing revealed a significant cost to performance of invalid cueing in the integration task only ($t(18) = 11.49$, $p < .001$, $d_z = 2.57$), with no effect of invalid cueing for segregation ($t(18) = 1.13$, $p = .14$,

d_z = 0.25), and no valid cueing effects for segregation (t(18) = .61, p = .73, d_z = .14) or integration (t(18) = 1.35, p = .10, d_z = .30).

Given the primary research question of the study was whether the effects of spatial cueing on temporal processing are found not only when spatiotemporal cues are used (as in previous work), but also when purely spatial cues are used (as in the present study), we compared present results with previous findings. Following Verhagen and Wagenmakers (2014), we conducted a Bayes Factor Replication Test, taking as the input *t* and *n* values, to quantify the evidence in favour of a successful replication of the spatial cueing effects from our earlier study (Sharp et al., 2018b). Comparing cueing effects between two experiments with near-identical methodology that differed in terms of whether the cues were spatiotemporal or purely spatial in nature, we found extreme evidence in favour of a successful replication of cueing effects on temporal processing for all comparisons: valid cueing on segregation (BF > 100), invalid cueing on segregation (BF > 100), valid cueing on integration (BF > 100) and invalid cueing on segregation (BF > 100).

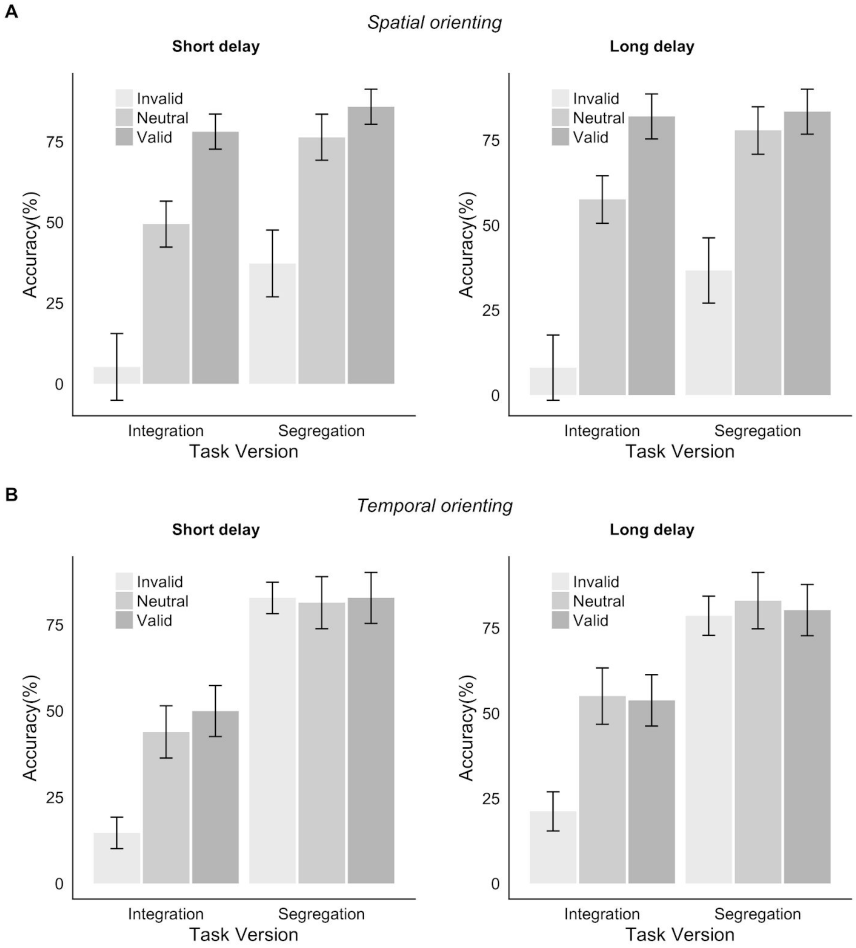

Figure 4.3 *Results of main experiment split by delay between cue and stimulus onset.* ***A.*** *Spatial orienting. Left: short delay, right: long delay. Error bars here and in panel B indicate within-subjects 95% confidence interval (Morey, 2008).* ***B.*** *Temporal orienting. Left: short delay, right: long delay.*

To investigate more closely the nature of the temporal cueing effect, we analyzed the data as a function of the delay between cue and stimulus onset (Figure 4.3). To test whether the main findings showed any interaction with the delay between cue and stimulus onset, an additional ANOVA was conducted with factors of task (segregation/integration), cue (valid/neutral/invalid), orienting (spatial/temporal), and delay between cue and stimulus onset (short/long). In addition to the effects identified above, this analysis revealed a main effect of delay ($F(1,18)= 19.90$, $p < .001$, $\eta_P^2 = .525$, $\eta_G^2 = .006$), with a small but reliable benefit to performance at longer cue intervals. An interaction between task and delay ($F(1,18)= 28.98$, $p < .001$, $\eta_P^2 = .726$, $\eta_G^2 = .013$) was driven by better integration performance at the long delay, and an interaction between cue validity and delay ($F(2,36)= 6.64$, $p = .003$, $\eta_P^2 = .014$, $\eta_G^2 = .005$) reflected slightly stronger cueing effects at short delay (see Figure 4.3). Importantly, however, the four-way interaction was not significant ($F(2,36) = 1.00$, $p = .3$, $\eta_P^2 < .0001$, $\eta_G^2 = .0006$), indicating that the critical three-way interaction observed in the main analysis was not influenced by delay. No other effects emerged (task by orienting by delay: $F(1,18) = 3.12$, $p = .1$, $\eta_P^2 = .020$, $\eta_G^2 = .0007$; all other F values < 1).

Discussion

The present results provide evidence for a strong dissociation between spatial and temporal cueing effects in a task that involves combining or segmenting stimuli over time. Consistent with our prior work, endogenous cues providing spatial information benefited performance when valid, and created a cost when invalid, for both integration and segregation tasks (Sharp et al., 2018b). In sharp contrast, temporal cueing provided a quite different and specific effect. Invalid temporal cues created a performance cost in the integration task, but not in segregation, and valid temporal cueing had no impact on either task (relative to neutral cues).

This study provides support for the idea that performance benefits following valid spatial cueing were driven by the action of spatial orienting mechanisms, rather than confounded effects of temporal cueing or synergistic effects of combined spatiotemporal cues (Hein et al., 2006; Sharp et al., 2018b). This finding provides an important clarification, since in previous work on the effect of spatial orienting on temporal processing, spatial cues often also implicitly provided temporal expectations about stimulus onset. Even in the absence of this temporal expectations about stimulus onset, spatial cueing benefits to both temporal integration and segregation performance were quite large and of similar effect sizes to our previous work (Sharp et al., 2018b). These results provide further evidence that allocation of endogenous attention is able to act in a flexible, spatially-specific manner to aid both of these opposing temporal processes.

Striking differences emerged here between the influence of spatial and temporal orienting on temporal processing, ostensibly in contrast to evidence of cueing benefits for both spatial and temporal orienting in the case of spatial processing (Coull & Nobre, 1998; Griffin et al., 2002). Whereas spatial and temporal orienting have both been shown to aid spatial processing, leading to better and faster target detection (Griffin et al., 2002; Lange et al., 2006), here performance benefits were only found for spatial orienting. One possibility is that spatially specific gain modulations facilitate target detection, for example whereas evidence suggests spatial attention can enhance the spiking responses of cells with relevant receptive fields (Bosman & Womelsdorf, 2009), attending to a point in time would not allow this selective gain modulation of a specific group of cells. Another interpretation would be that any benefits of temporal orienting may principally act on decision and motor related processing (Vangkilde, Coull, & Bundesen, 2012; Volberg & Thomaschke, 2017), particularly benefiting speeded responses through a temporal alignment of readiness allowing efficient and attentive information process at the expected time point (Steinborn, Langner, & Huestegge, 2017).

The pattern of behavioural results for temporal orienting demonstrated here is novel, and initially appears inconsistent with previous findings on temporal cueing. Correa and colleagues (2006) showed a small cueing benefit to performance when participants reported the order in which two rapid sequential stimuli were presented. Here we find no corresponding benefit of valid temporal cues. One interpretation is that this apparent disparity arises due to task differences: making a judgement about the temporal order of stimuli arguably relies more heavily on higher level decision processes than the target-search task employed here. Since temporal orienting effects usually emerge when the primary measure is a metric, like reaction time, that reflects differences in processing stages further up the hierarchy like decision or motor processing (Langner et al., 2018; Thomaschke & Dreisbach, 2015; Vangkilde et al., 2012; Volberg & Thomaschke, 2017), this is a pertinent difference between the current study and previous work. Reaction time data in the current study were unsuitable for analysis due to the response collection method: unspeeded mouse click on a probe grid of sixteen locations after a fixed delay from stimulus offset.

Consideration of details of the paradigm may also provide an explanation for the cost to integration performance an invalidly cued in the temporal orienting condition. Missing one of the rapidly presented displays is more detrimental to performance when the goal is integration than when the goal is segregation, since locating the integration target (missing circle) requires perception of both displays. Invalid temporal cues may have caused participants to sometimes miss one of the displays. Indeed, when comparing the types of errors participants made, we saw that in the segregation task participants clicked roughly equally as often on an element of the first display as of the second, whereas in the integration task their responses indicated a bias to click on missing elements from one display. Crucially, the pattern of whether their bias was towards the first or second display was reversed for invalid as compared to the neutral and valid temporal cueing conditions.

Despite inclusion of catch trials to in an attempt to mitigate the influence of a growing urgency rate or hazard signal to act (Janssen & Shadlen, 2005), performance was found to improve at longer delays between cue and stimulus onset. This is consistent with work indicating that inclusion of catch trials does not obviate the need to consider results in terms of a rising urgency to act (Steinborn et al., 2008). The small but reliable effect of delay was slightly more evident for integration than segregation, indicating that the readiness of the system is of particular importance for temporal integration. This delay effect was slightly more pronounced in neutral cue trials than valid cue trials, indicating that likely the allocation of selective attention compensated for the delay effect at shorter cue intervals. Critically, the three-way interaction between orienting, cue validity and task was not influenced by these delay effects.

The current findings were not consistent with our hypothesis that temporal cueing would be particularly helpful for the ability to rapidly segment the two stimuli in time. The odd-element task (finding the half circle) requires the ability to isolate the two sequential displays, such that a lack of temporal precision might be expected to reduce performance. Instead, performance in that task was particularly good for all temporal cueing conditions. One possibility is that the mere presence of a temporal cue helped participants to be diligent. Alternatively, the fact that targets appeared at only two discrete times may have provided the opportunity for participants to effectively focus their temporal attention to both of these times. Consistent with this idea, previous studies demonstrating an effect of temporal cueing have also tended to employ two temporal delays (Coull & Nobre, 1998; Griffin et al., 2002). However, our results demonstrated an invalid cue cost for integration trials. This is difficult to reconcile with a general diligence or split-attention interpretation. Thus, an ability of participants to focus attention at both temporal delays seems unlikely, but it cannot be completely ruled out. Future work is needed to differentiate between these possibilities, for example using an adapted version of the paradigm with speeded responses (e.g. whether the target was on the left or the right), so as to be better suited to detecting temporal orienting effects.

To conclude, the pattern of results from the current study cuts a clear distinction between the effects of spatial and temporal orienting in a task involving the parsing of rapidly presented stimuli over time. Parsing the incoming sensory flow into meaningful objects and events is a key challenge for visual perception. The current findings suggest that spatial attention may increase the efficiency of this process in a task-relevant way, while temporal attention has, surprisingly, a comparably weaker influence on the temporal organization of visual processing.

Chapter 5: Changes is brain oscillation frequency subserve temporal processing at attended visual locations

This chapter is a version of an article in preparation for publication, co-authored with David Melcher and Clayton Hickey.

Abstract

Perception requires two opponent processes: rapid sequential stimuli must often be integrated to form unitary percepts, but at other times be segregated or parsed into separate events. Using magnetoencephalography, we characterize the changes in ongoing oscillatory brain activity associated with spatial attention to temporal integration and segregation. We did so by cueing participants to the spatial location where a target would likely occur and requiring them, blockwise, to either integrate or segregate temporal events that occurred at that location. Behavioural results revealed strong spatial cueing effects for both integration and segregation. Neuroimaging results indicated shifts in peak alpha frequency for integration as compared to segregation, as well as spatially specific modulations in this metric relative the cued location. Together, these results provide evidence of strategic shifts in oscillatory frequency in line with task demands, which may reflect a flexible modulation of the sampling rate of vision.

Introduction

Voluntary spatial attention is linked to many neural changes subserving enhanced spatial processing, yet evidence remains sparse regarding instantiation of attentional influences on temporal processing. In particular, strategic deployment of spatial attention improves both temporal integration and segregation of sequential stimuli, but our understanding of underlying neural mechanisms is limited.

Behavioural measures of temporal processing reveal robust endogenous spatial attention effects. Hein and colleagues (2006) reported better temporal resolution following spatial cueing, as measured by performance at segregating sequential stimuli into separate percepts. Extending these findings, we used a paradigm where task was manipulated while stimulation was held constant: target detection required either temporal integration or segregation of sequential displays. Endogenous spatial attention not only influenced temporal segregation, but also integration (Sharp et al., 2018b), even when cues provided no implicit temporal expectations (Sharp, Melcher, & Hickey, 2018a). Voluntary spatial attention can flexibly adapt temporal resolution, much like it can adapt spatial resolution (Carrasco, 2011; Müller & Kleinschmidt, 2007). One mechanism subserving modulation of spatial resolution is modification of the spatial receptive fields: a shrinking of receptive field size by spatial attention (Womelsdorf et al., 2008).

Unlike prior work, here we focus on identification of neural mechanisms underlying modulation of temporal processing by spatial attention. One candidate is flexible modulation of temporal window size by top-down factors, akin to adaptation of spatial receptive field size. This has been demonstrated for top-down factors like temporal expectations (Akyürek, Riddell, Toffanin, & Hommel, 2007; Akyürek, Toffanin, & Hommel, 2008). This adaptation of the visual sampling rate could be indexed by neural oscillations changes (Ronconi & Melcher, 2017; Ronconi et al., 2017).

Alpha oscillations are influenced by spatial attention (Sadaghiani & Kleinschmidt, 2016). Attending to a lateralised location in the visual field reduces alpha power in the contralateral hemisphere (Gould et al., 2011), facilitating processing at the attended location (Jensen & Mazaheri, 2010). Furthermore, trait- and state- dependent differences in alpha frequency have important functional implications (Mierau et al., 2017).

Individual differences in alpha frequency influence perception of rapid sequential stimuli. Samaha and Postle (2015) measured individuals’ resting alpha, finding that those with a higher alpha were more likely to segregate the stimuli and those with a lower alpha more likely to integrate them. Minami and Amano (2017) demonstrated that the frequency of illusory visual vibrations matched an individual’s alpha, and furthermore found perceptual shifts concomitant with alpha frequency shifts following electrical stimulation. This fits with evidence of modulated temporal integration following shifts to the alpha frequency, both by sensory entrainment (Ronconi et al., 2018) and electrical stimulation (Cecere et al., 2015).

Task-dependent alpha frequency fluctuations are also functionally relevant, particularly for temporal processing (Babu Henry Samuel et al., 2018; Drewes et al., 2017). Instantaneous frequency provides a time-resolved index of functional changes (Cohen, 2014), which may average out in a related metric such as power (Nelli et al., 2017). Wutz and colleages (2018) tracked prestimulus alpha frequency during a task where the goal was either to integrate or segregate rapid sequential stimuli. Prestimulus alpha frequency was higher when segregating, and lower when integrating, as would be expected if this metric was indexing the sampling rate of the system. A crucial question remains regarding whether these changes to alpha frequency are modulated by spatial attention.

We tested the idea that spatially-specific changes in alpha frequency would emerge in line with task demands. We hypothesized that prestimulus alpha frequency would be higher when segregating than when integrating (Wutz et al., 2018), and that when spatial information was provided this effect would be spatially specific. When segregating, alpha frequency would show a relative upshift contralateral to the cued hemifield as compared to ipsilateral. Conversely when integrating, alpha frequency would show a relative downshift contralateral to the cued hemifield as compared to ipsilateral.

Method

Participants

Twenty nine healthy participants (11 male; age 24 ± 2.7 years, mean ± SD) gave informed consent before completing the experiment. All had normal or corrected-to-normal vision. Participants provided informed consent in accordance with the Declaration of Helsinki and approval for the study was granted by the ethics committee of the University of Trento.

Stimuli

The stimuli and task were generated with Psychophysics Toolbox (Brainard, 1997) in MATLAB (MathWorks). Using a DLP projector (PROPixx, VPixx Technologies Inc., Saint-Bruno, QC, Canada), stimuli were projected onto a translucent screen (projected screen size 510mm x 380mm) in a dimly lit, magnetically shielded room at a viewing distance of 1000mm. Timing of stimulus presentation was recorded with a photo diode placed on the lower right corner of the projection screen and used to correct the delay between trigger and stimulation onset.

The basic trial structure is shown in Figure 5.1. A small fixation cross in the form of a red 'X' was present throughout the presentation of stimuli, this cross measured approximately 0.2° (visual angle). At the beginning of 75% of trials, one of the arms of the cross changed from red to green to cue the quadrant where the target was likely to appear. In the remaining 25% of trials a neutral cue was presented. This took the form of a colour change of the tips of all four arms of the cross, such that a similar number of pixels changed from red to green as in the valid/invalid cue condition. The directional cue was valid 75% of the time, thus in 22% of total trials cue was invalid and in 53% of total trials the cue was valid. Participants were explicitly informed of the 75% cue validity.

After a jittered cue interval of 850 - 1450 ms (randomly selected from rectangular distribution), the fixation cross became entirely red and the first display appeared on screen for 16.67 ms. This display had circles at seven locations on a four by four grid (see #fig_stimfig). Each circle was formed from two arc elements. At one position in the display there was a half circle (i.e. a single arc). Each circle was 1.2° (visual angle) in diameter, the grid of possible locations measured 8.4° by 8.4°, and each circle within the display had an irrelevant random orientation selected from the possible orientations of 45°- 315°.

Following a fixed inter-stimulus interval (ISI) of 48.3ms, a second display appeared for 16.67ms. This display also had circles at seven locations and a half circle at one location. Crucially, the half circle in display 2 was the corresponding arc element at the same location as the half circle location from display 1, such that if the two displays were superimposed the two arc elements formed a standard circle stimulus. The locations of the seven circles for each display never overlapped, such that if the two displays were superimposed one of the sixteen possible locations remained empty. This hypothetical superimposition is illustrated in Figure 5.1. To mitigate the influence of an increasing hazard rate over the cue interval (Janssen & Shadlen, 2005), 10% of trials were catch trials in which a blue cross appeared instead of any displays. No response was required and these catch trials were excluded from analysis of the post-stimulus interval.

After 400ms, a response probe screen appeared. This comprised a grid of squares where each square identified one of the sixteen possible target locations. Participants indicated the which location where they had perceived the target using two button boxes (DataPixx, VPixx Technologies Inc, Saint-Bruno, QC, Canada). With their left hand they moved a highlighted square around the response probe (one button for horizontal movement, one for vertical), and with their right hand they pressed a button to indicate that the highlighted square was where they perceived the target.

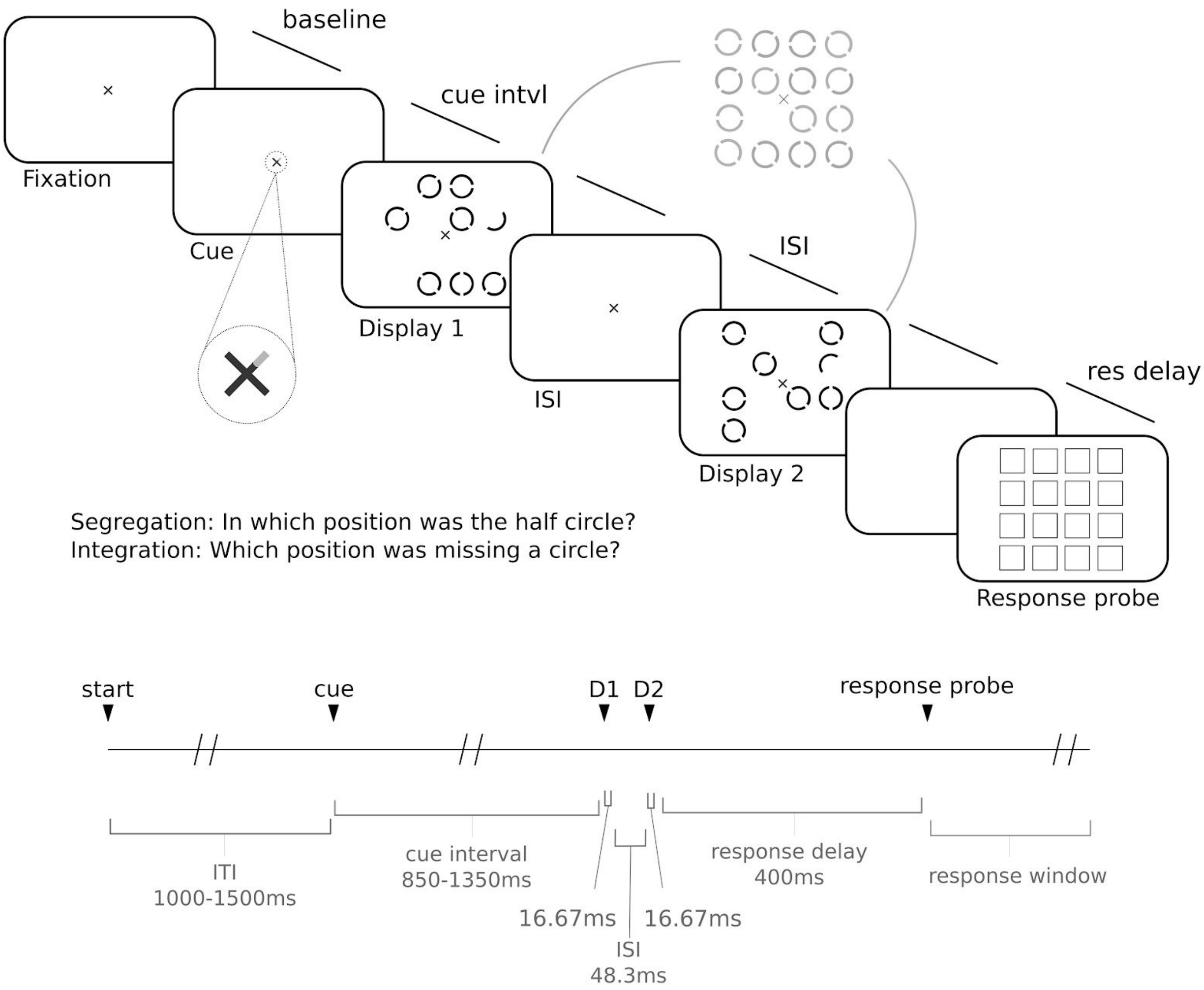

Figure 5.1 Trial structure. *In this example the cue indicates the target will likely appear in the top right quadrant of the display. In neutral cue trials all four tips of the cross turned green. If this trial were in a segregation block, the target is the location second-down on the far right (the half-circle). If this trial were in an integration block, the target is the location in the near-left column where no stimuli appeared in either display.*

Task

There were two versions of the task (see Figure 5.1). The stimulus presentation was the same in each, but task instructions were varied across blocks.

In one version of the task, the target was the half circle. Successful identification of the half circle requires parsing of the two displays, therefore this is referred to as the segregation task. In the other version, the target was the location in which there was no circle in either display. Successful identification of this location requires a combined percept of the two displays, therefore this is referred to as the integration task. Participants were explicitly instructed to fixate the cross in the centre of the screen throughout stimulus presentation and eye movements were monitored (details below).

Prior the main experimental blocks, participants completed 30 practice trials with cueing for each task version (60 total) in a room adjacent to the scanner. Participants repeated these two practice blocks until they were able to perform better than 25% accuracy in both task version (chance level in this task is 6.25%). Participants then completed ten blocks of the main experiment in the MEG scanner, where each block comprised 67 trials (mixed design, except for task version which varied blockwise).

MEG apparatus

Brain activity was recorded in a magnetically shielded room with a whole head MEG system comprising 102 magnetometers and 204 planar gradiometers at an online sampling rate of 1000Hz (Neuromag306 system; Elekta, Stockholm, Sweden). Prior to the experimental blocks, a subject-specific head frame was digitized (3Space Fastrack; Polhemus, Colchester, VT). Each head frame featured the three cardinal landmarks (nasion and left and right preauricular points), the position of five head position indicator (HPI) coils, and between 200-300 other head shape sample points. The head frame was used in localizing the position of the participant’s head in relation the the sensors at the beginning of each block.

Eye tracking apparatus

An Eyelink 1000 Desktop Mount eye tracker (SR Research, Ontario, Canada) was fixed to the stimulus presentation screen at a distance of 1000mm from the MEG helmet. The position of the right eye was recorded at a sampling rate of 1000Hz.

EOG and Eyetracker preprocessing and data analysis

The vertical and horizontal electrooculogram (EOG) was recorded and low pass filtered offline with a 25Hz cutoff. This and eyetracking data was used to mark trials with suspected eye movements for removal from analysis. This resulted in removal of 3% ± 4% of trials per participant (mean ± SD) for blinks and 7% ± 7% of trials per participant for saccades.

MEG data preprocessing and analysis

The data were preprocessed using MNE-Python (Gramfort, Luessi, Larson, Engemann, Strohmeier, Brodbeck, Parkkonen & Hämäläinen, 2014)and the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) for MATLAB (Mathworks).

MEG channels with non-biological noise were identified by visual inspection of the raw data, leading to the removal and interpolation of 10 ± 1 channels per participant (mean ± SD). The data was then Maxfiltered (Elekta Neuromag) to remove noise originating from outside the helmet and to align head position across runs. The data was then epoched with trigger timings corrected to match data from a photodiode that monitored real, absolute onset of stimuli on the projector screen.

A semi automatic artefact rejection procedure was implemented. An independent component analysis (ICA) decomposed the data into independent source components. Heartbeat and eyeblink components were identified and removed (2 ± 1 components rejected, mean ± SD). Prior to the ICA, the dimensionality of the data was reduced in line with rank after Maxfiltering (median rank 70, range 66.71). Trials with suspected blinks or saccades in the time window of cue or stimulus presentation were removed. Finally, outlier trials (in terms of global variance) were identified by visual inspection and removed.

Instantaneous frequency estimation

A time series of instantaneous alpha frequency was estimated using an established analysis pipeline (Cohen, 2014; Samaha & Postle, 2015; Wutz et al., 2018). The data were bandpass filtered with a FIR filter with passband of 7-14 Hz and transition bandwidth of 15%. An estimate of instantaneous phase angle was subsequently obtained by Hilbert transform. From this, an estimate of instantaneous frequency was calculated as the first temporal derivative. The resulting signal was subsequently median filtered to remove nonphysiological artefacts (Cohen, 2014). This involved calculation of the median for each sample 10 times, where each median was calculated across a window of different size varying between 10 and 400 ms. The median of the 10 resulting values was taken as an estimate of the instantaneous frequency at each timepoint.

Experimental design and Statistical Analysis

Behavioural data were analysed using Matlab2013a (Mathworks) and R (R Foundation for Statistical Computing). Prior to statistical analysis, trials marked for removal during MEG preprocessing and artefact rejection were removed from the behavioural data. To test the effect of the experimental manipulations on accuracy, we performed a two way repeated measures ANOVA with factors of task version (segregation, integration) and cue type (valid, neutral, invalid). Where assumptions of sphericity were not met, reported statistics are Greenhouse-Geisser corrected. Post hoc testing was conducted by Bonferroni-corrected pairwise comparisons.

MEG data were analysed using the FieldTrip toolbox (Oostenveld et al., 2011) for MATLAB (Mathworks), and R (R Foundation for Statistical Computing). All analysis was conducted at the sensor level on magnetometer data, unless otherwise specified. Instantaneous frequency data for neutral cue trials were averaged per channel per subject and then entered into a nonparametric cluster based permutation test (Maris & Oostenveld, 2007) to compare differences between segregation and integration in the prestimulus period. To rule out that instantaneous frequency changes reflect conditional differences in power in the alpha band, a cluster based permutation test with the same parameters was conducted on traditional time frequency data.

Prestimulus instantaneous frequency data was averaged over the epoch of -300 ms to onset of the first display (D1). These data were centred on the neutral cue condition in order to provide a baseline against which to compare the effect of spatial cueing. Virtual conditions were generated by selecting all lateralised sensors behind the central midline and selecting sensors contralateral and ipsilateral to the locus of attention. These data were subjected to a 2x2

RANOVA (repeated-measures analysis of variance) with factors of task (segregation, integration) and hemisphere (contralateral to attended location, ipsilateral to attended location).

Results

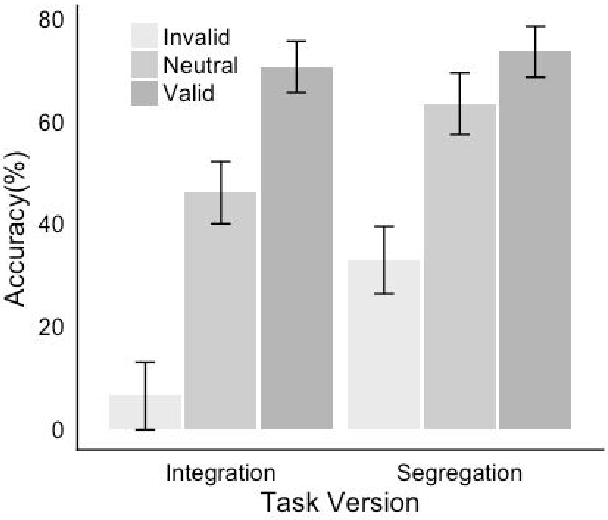

Figure 5.2 Behavioural results. *Accuracy as a function of task and validity of cue. Error bars indicate within-subjects 95% confidence interval (Morey, 2008)*.

As can be seen from Figure 5.2, there were robust spatial cueing effects for both temporal integration and segregation. This was supported by the results of a 2x3 RANOVA (repeated-measures analysis of variance) with factors of task (segregation, integration) and task (valid, invalid): there was a significant main effect of cue ($F(2,56)= 127.47$, $p < .001$, $\eta_P^2 = .820$, $\eta_G^2 = .604$). Performance was slightly better for segregation that integration (significant main of task; $F(1,28)= 19.62$, $p < .001$, $\eta_P^2 = .412$, $\eta_G^2 = .163$) and cueing effects were larger for the harder task (significant interaction between task and cue validity; $F(2,56)= 21.83$, $p < .001$, $\eta_P^2 = .438$, $\eta_G^2 = .070$). Post hoc testing with a corrected alpha level revealed that when segregating there was a significant benefit of valid cueing ($t(28) = 4.77$, $p < .001$), and a significant cost for invalid cueing ($t(28) = 6.40$, $p < .001$); similarly when integrating there was a significant benefit of valid cueing ($t(28) = 10.72$, $p < .001$) and cost for invalid cueing ($t(28) = 13.79$, $p < .001$).

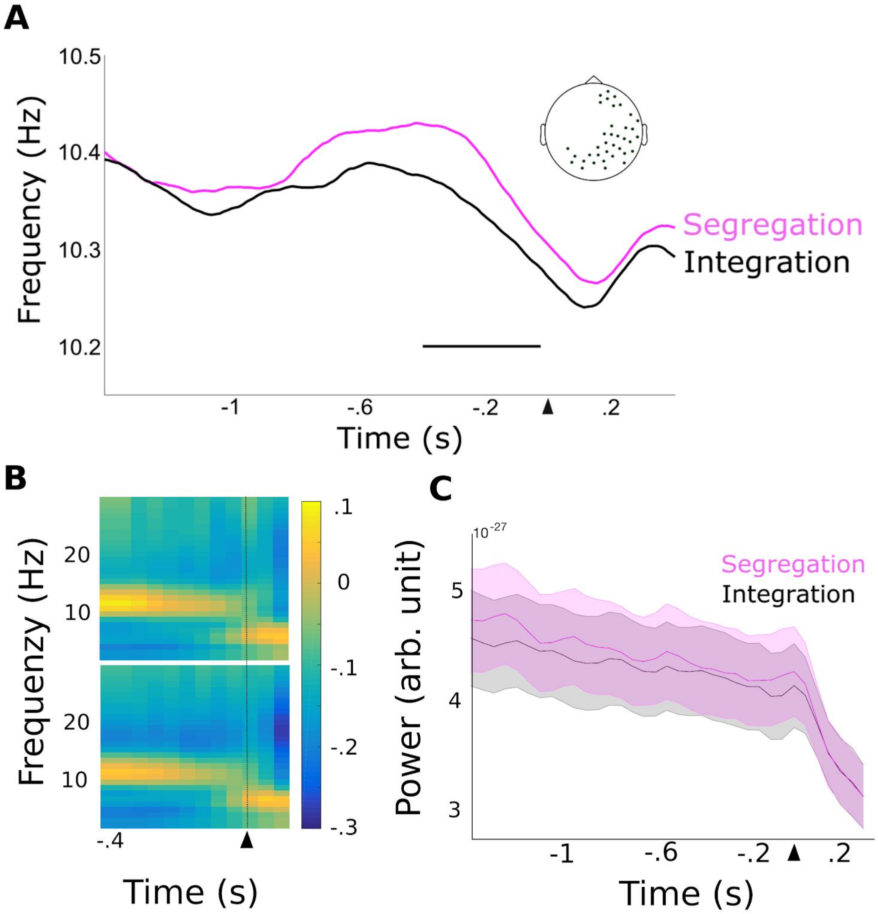

Figure 5.3 Modulation in alpha band by task. A. *Modulation of alpha frequency. Inlaid topoplot shows sensors for which a cluster permutation revealed a significant difference between conditions; the epoch in which this significant difference emerged is indicated by the black bar. Here in and in all panels black triangle indicates stimulus onset (display 1). Neutral cue trials only.* ***B.*** *Time frequency representation for the highlighted epoch and channels in panel A. Upper: segregation, lower: integration.* ***C.*** *Mean power in the alpha band.*

A significant difference in prestimulus instantaneous frequency between segregation and integration was revealed by a cluster based permutation test in the epoch from 396 to 20 ms prior to onset of the first display. This effect was most pronounced over a large cluster of sensors in occipito-parietal cortex and was lateralized to the right hemisphere. Alpha frequency was higher prior to stimulus onset when segregating as compared to integrating in this cluster, as shown in Figure 5.3*.* This reproduces results from Wutz and colleagues (Wutz et al., 2018). A further cluster test on time frequency data showed no conditional differences in alpha power.

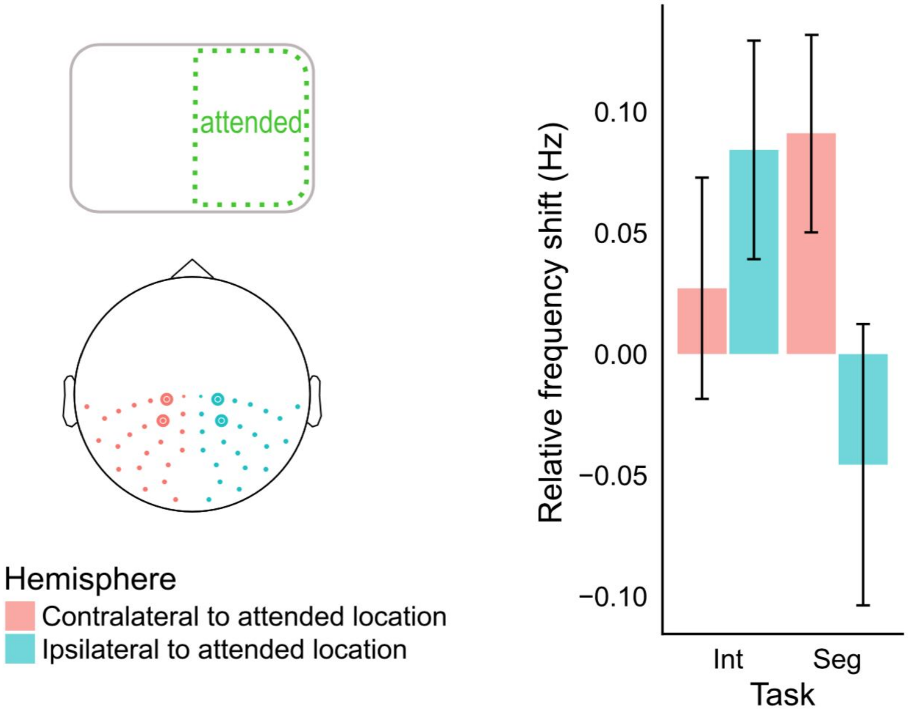

Figure 5.4 Modulation of alpha frequency as a function of task and location of attention. *Relative frequency shift against baseline of neutral cue case. Topographical plot shows sensors of interest, epoch of interest was -300ms to stimulus onset (display 1). Bar plot of effect in highlighted sensors (those which survived multiple comparison correction). Error bars indicate within-subjects 95% confidence interval (Morey, 2008)*.

The relative shift in prestimulus instantaneous frequency was compared for sensors ipsilateral and contralateral to the cued location in each of the segregation and integration conditions separately. A RANOVA with factors of task (segregation, integration) and hemisphere (contralateral, ipsilateral to attended location) revealed a significant main effect of task ($F(1,28)= 5.14$, $p = .031$, $\eta_P^2 = .155$, $\eta_G^2 = .031$) and a significant interaction between task and hemisphere ($F(1,28)= 4.59$, $p = .041$, $\eta_P^2 = .141$, $\eta_G^2 = .199$). This was a driven by a significant increase in instantaneous frequency contralateral to cued location as compared to ipsilateral for segregation ($t(57) = 3.04$, $p = .002$).

In order the further localise this effect, this analysis was run for pairs of sensors at ipislateral and contralateral locations over occipitoparietal cortex, as shown in Figure 5.4. The highlighted pairs were those for which the task by hemisphere interaction survived false discovery rate (FDR) correction for multiple comparisons (Benjamini & Hochberg, 1995). From this figure we see that contralateral to the cued location, instantaneous frequency is higher during segregation, whereas for integration this pattern is reversed.

Discussion

We found shifts in prestimulus alpha frequency in line with temporal processing goal: an increase in frequency when segregating stimuli in time as compared to when integrating stimuli in time. An interaction was found between this frequency shift effect and spatial cueing: when segregating there was relative shift to a higher frequency in visual cortex contralateral to the attended location. In the parietal sensors where the effect was most pronounced, a trend was seen for integration where the pattern was reversed: there was a relative shift to a lower frequency contralateral to the attended location than ipsilateral. These spatially-dependent changes in alpha frequency were most robust in occipito-parietal cortex, as would be expected of an attentional modulation.

The replication of the modulation of alpha frequency by task (Wutz et al., 2018) here lends support to the notion that the speed of perceptual sampling can be flexibly and endogenously adapted in line with task goals. This is extended by novel evidence here of flexible and strategic modulation of alpha frequency by endogenous spatial attention: the upshift in sampling frequency to support segregation performance is greater in the hemisphere contralateral to the attended location. This suggests that spatial attention can act to bias local processing towards a mode optimised for segregating through the mechanism of speeding up the sampling rate of the system, adaptively modulating the size of the temporal window of integration. This adds a new dimension to the existing literature on adaptive modulation of the size of temporal windows in an endogenous manner (Akyürek et al., 2007; Mierau et al., 2017; Wutz et al., 2018, 2016).

The direction of the alpha frequency shift effect was in the predicted direction for integration and segregation: a relative downshift contralateral as compared to ipsilateral for integration, and an upshift contralateral as compared to ipsilateral for segregation. The effect in this instantaneous frequency metric was only statistically robust for the segregation task, which could be the case for a number of reasons. Across conditions we see that a general effect of having spatial expectations engendered by cueing is an increase in instantaneous frequency, this is consistent with characterisation of alpha frequency as an indicator of cortical excitability (Babu Henry Samuel et al., 2018). Here the current findings intersect with indications that alpha frequency increases are linked to arousal or cognitive preparedness (Angelakis, Lubar, Stathopoulou, & Kounios, 2004; Kovrov, Merkulova, Posokhov, & Garakh, 2018). A relative downshifting of alpha frequency contralateral to the locus of attention when integrating could therefore have been dampened by this general arousal effect reflected in the same signal. It is worth noting that alpha frequency shifts, like other electrophysiological metrics, are likely indexing multiple aspects of processing and cognition (Mierau et al., 2017). This is one of a number of possibilities for the difference in the lateralized effect for segregation versus integration.

The difference in the lateralized alpha shift effect between segregation and integration might instead provide context for interpretation for the segregation versus integration effect when there are no spatial expectations. This effect - of a relative downshift in alpha frequency for integration as compared to segregation - is necessarily ambiguous: since there is no baseline between these opposing processes the difference could either reflect a downshift for integration, an upshift for segregation, or both a downshift for integration and an upshift for segregation. That the magnitude of the effect size is similar for the lateralized downshift in alpha frequency as for the generalized downshift lends support to this interpretation of the effects reported here and in previous literature (Wutz et al., 2018).

Ostensibly, the findings here of lateralized alpha frequency shifts may seem hard to relate with the literature of lateralized alpha power decreases associated with spatial attention, but they are easily reconciled. Alpha power decreases contralateral to the locus of attention (Haegens et al., 2011) have been accounted for in a number of theoretical frameworks in which alpha oscillations provide rhythmic inhibition so as to gate the propagation of representations along the visual processing stream (Jensen & Mazaheri, 2010; Mathewson et al., 2011). With a slower alpha oscillation, this down-ramping part of the oscillation would be larger, and thus the temporal window within which multiple inputs could be integrated and propagated would also be larger. Similarly, for the opposing case of segregation, the down-ramping portion of the cycle would be shorter, supporting propagation of a series of percepts with finer temporal resolution. In analytic terms, power and frequency are linked - frequency changes can predict power differences (Nelli et al., 2017). It is likely that modulations of alpha frequency and power by spatial attention are functionally linked too. This prospect is highlighted by recent evidence that canonical lateralized power decreases occur mainly in the lower alpha band (6-9 Hz) and can be distinguished from changes in the high alpha band (10-14 Hz) with a difference profile functional profile (Lobier, Palva, & Palva, 2018).

Similarly, findings here are easily reconciled with evidence regarding the role of oscillatory activity in other frequency bands in visuospatial attention. Lateralized alpha desynchronisation has been linked to gamma band activity (Bonnefond & Jensen, 2013; Poch, Campo, & Barnes, 2014), and recent evidence suggests has indicated that attention in some situations be characterised as a sampling process at the theta frequency (Fiebelkorn, Pinsk, & Kastner, 2018; Helfrich et al., 2018; Landau & Fries, 2012). Cross frequency coupling can manifest in a number of ways, including phase to power, phase to frequency, power to power and phase to phase (Jensen & Colgin, 2007). This cross frequency coupling is proposed as a mechanism by which processing is modulated between regions and across different timeframes and spatial scales (Canolty & Knight, 2010). This suggests that different sampling processes (such as perceptual sampling and attentional sampling) could be nested hierarchically, influencing each other in line with task goals and allocation of attention.

In conclusion, we present novel evidence of spatial specificity to alpha frequency shifts in line with temporal processing goals. These findings are in keeping with the idea that spatial attention and current goals can flexibly adapt the sampling rate of perception through a modulation of the size of temporal windows.

Chapter 6: General Discussion

The central aim of this thesis is to elucidate the role of selective attention in temporal processing. To this end, a number of empirical studies were conducted. In chapter 2, I presented behavioural evidence that endogenous spatial attention can increase temporal resolution, improving the segregation of rapid sequential stimuli in time. In chapter 3, I showed empirical evidence that endogenous spatial attention is able to flexibly adapt temporal resolution in line with task goals: robust spatial cueing effects were seen for both temporal integration and segregation of rapid sequential stimuli. A further behavioural experiment detailed in chapter 4 provided evidence that these spatial cueing effects are reliable even when the spatial cues do not provide any implicit temporal expectation about stimulus onset. In this chapter I also reported an interesting dissociation between the effects of spatial and temporal cueing on temporal integration and segregation. The neural correlates of the endogenous spatial attention effects on temporal processing were investigated in an MEG experiment, detailed in chapter 5. Here, I reported shifts in peak alpha frequency for integration as compared to segregation, as well as spatially specific modulations in this metric relative the cued location. These findings provide evidence of strategic shifts in oscillatory frequency in line with task demands, which may reflect a flexible modulation of the sampling rate of vision.

In this chapter I will seek to contextualize these results within the body of literature introduced in chapter 1 and beyond, as well as discussing what conclusions can be drawn. I will address the theoretical implications of the results and their wider relevance to the world. Finally, I will outline outstanding questions relating to the thesis topic, and propose some avenues for future research.

Discussion of findings

In many ways, the notion of flexible adaptation of the sampling rate of vision is an intuitive concept. Selective attention is an umbrella term we use to refer to a family of processes by which some stimuli are preferentially boosted along the visual stream, at the expense of others. It could therefore be argued that it is unsurprising that endogenous spatial attention aids both temporal integration and segregation. However, since these processes are opposite in nature, any account of a unitary mechanism is ill-suited to account for these behavioural effects. Instead, the mechanism must be flexible enough to support both integration and segregation of rapid sequential stimuli. One candidate is modulation of the sampling rate such that temporal windows are longer when the goal is integration and shorter when the goal is to segregate, as indexed by changes in frequency of neural oscillations (in this case alpha). Questions remain as as to how this may be implemented neurally, and in a spatially specific way. Furthermore it is worth discussing how these findings relate to previous literature on spatial attention.

As previously introduced, similar mechanisms likely underlie spatial attention to temporal processing as those underlying spatial attention to spatial processing. However, at a certain point these comparisons and analogies become stretched. For this reason the current findings are useful in informing arbitration between theories of selective attention. For example, a putative mechanism of spatial attention is gain modulation of cell responses (Ling, Liu, & Carrasco, 2009), yet this is a unitary mechanism which struggles to account for the findings reported here of spatial processing benefits to both opposing processes of temporal integration and segregation. Another aspect to consider regarding differences between spatial attention to spatial processing versus to temporal processing is the role of oscillatory activity in the alpha band.

Evidence from electrophysiological studies with non-human primates suggests that the alpha rhythms so prominent in the visual system are generated in cortical and thalamocortical loops (Bollimunta, Mo, Schroeder, & Ding, 2011). Other findings, including those reported in this thesis, support the notion of strategic shifts in the frequency of the alpha rhythm in line with task goals. This likely requires the involvement of brain regions higher up the visual hierarchy, analogous to how top down controlled changes to alpha power in visual regions subserves allocation of spatial attention to spatial processing (Haegens et al., 2011). Further study is required to tease apart the interplay between putative cognitive control brain regions, visual regions and subcortical structures in the modulation of alpha frequency in line with task goals and allocation of spatial attention. One point worth noting is that although the results here focus on hemisphere differences, the spatial specific of alpha frequency modulation by allocation of attention in space could be more fine grained than is possible to measure with the tools currently available to cognitive neuroscience, which tend to have low signal to noise ratio.

Given the emphasis in the literature on the importance of suppression of alpha oscillations for visuospatial processing and selective attention, it might ostensibly seem strange to discuss alpha oscillation frequency shifts as a mechanism for strategic modulation of temporal processing. However, the two concepts are easily reconciled. In analytic terms there is no conflict between the power (or amplitude) of an oscillation decreasing while the frequency shifts either up or down. In theoretical terms the two ideas are also compatible. The current consensus on the role of alpha is one of gating by inhibition or pulsed inhibition (Jensen & Mazaheri, 2010; Mathewson et al., 2011), whereby alpha activity has an inhibitory role and thus inputs which arrive during the ramping down of a cycle are more likely to be propagated to the next stage of processing. With a slower alpha oscillation, this down-ramping part of the oscillation would be slower, and thus the temporal window within which multiple inputs could be integrated and propagated would also be larger. Similarly, for the opposing case of segregation, the down-ramping portion of the cycle would be faster, supporting propagation of a series of percepts with finer temporal resolution.

A further crucial consideration is that neural oscillations are ubiquitous within the brain and modulated by many factors, and thus likely index a number of features of processing. Mounting evidence points to oscillatory activity as a fundamental organisational characteristic of neural processing (Buzsaki, 2006), and as such it is unsurprising if oscillations within a given frequency band are found to be a useful metric for tracking changes in a wide range of seemingly disparate functions. Whilst a large body of evidence speaks to the idea of a functional role for neural oscillations in cognition and processing, it is important to make the bear in mind that oscillations do not determine function per se. Rather, there is a reciprocal causal relationship between firing rates of pools of neurons and the (oscillatory) temporal dynamics of these firing rates at the population level (Buzsaki, 2006). Future investigations both in vitro and in vivo are needed to address the question of how shifts in alpha frequency precipitated by top down factors can be implemented at the level of single unit and population activity. Here, consideration of the reciprocal causal relationship between spiking and oscillations would again be vital. This avenue of research will require understanding of how the properties of neural circuits give rise to attentional modulation of alpha oscillations. For oscillations in another band - theta - attentional modulation of this rhythm has been proposed to arise from interactions between inhibitory-excitatory centre-surround cells, and other factors such as the structure of inhibitory connections within neuronal populations (Kienitz et al., 2018; Moldakarimov, Rollenhagen, Olson, & Chow, 2005; Rollenhagen & Olson, 2005).

This brings us to another consideration: how shifts to alpha frequency relate to putative roles of oscillatory activity in other frequency bands. This links to discussion of how shifts to alpha frequency fit with the literature on changes to alpha power that were addressed above, since lateralized alpha desynchronisation has been linked to gamma band activity (Bonnefond & Jensen, 2013; Poch et al., 2014). Recent evidence suggests that as well as perception being a rhythmic sampling process, selective endogenous attention also manifests as a rhythmic sampling process (Landau & Fries, 2012). This has been linked to oscillatory activity in the theta band in human behaviour and electrophysiological evidence, as well as in non-human primates (Fiebelkorn et al., 2018; Fiebelkorn, Saalmann, & Kastner, 2013; Helfrich et al., 2018). These findings come from studies which are broadly different from those reported in the previous chapters, typically probing sustained attention and simple spatial processing such as detection tasks. However, they do raise questions as to what the relationships and interaction are between these multiple sampling processes. Further, related questions are raised as to the how and why interactions between activity in the alpha band and activity in the theta and gamma band emerge. Cross frequency coupling can manifest in a number of ways, including phase to power, phase to frequency, power to power and phase to phase (Jensen & Colgin, 2007). This cross frequency coupling is proposed as a mechanism by which processing is modulated between regions and across different timeframes and spatial scales (Canolty & Knight, 2010). This suggests that different sampling processes (such as perceptual sampling and attentional sampling) could be nested hierarchically, influencing each other in line with task goals and allocation of attention.

What can we learn from the detailed characterisation of the robust behavioural effects reported in this thesis? The inclusion of a neutral cueing condition allows clear demonstration of both valid cueing benefits to performance and invalid cueing costs, building on previous work in which a lack of neutral cue condition meant there was no baseline against which to compare. The effect sizes of the valid cueing benefit and invalid cueing cost are of similar magnitude, which is unusual. This suggests that the mechanisms engendered to direct attention to temporal processing in space may bias processing to one temporal processing mode at attended locations while at unattended locations processing is, relatively speaking, biased towards the other. This fits with the idea of spatially specific shifts to the sampling rate of perception.

The behavioural and electrophysiological results reported here can be accounted for well by the idea of flexible adaptation of the size of temporal windows used for perceptual sampling. However, further research is needed to establish more direct evidence for this theory. What other explanations have been posited for the mechanisms of spatial attention on temporal processing, and how well do they account for the findings reported here? Previous literature and characterisation of behavioural effects are informative in answering this question. In chapter 3 the finding that cueing effects interacted with proximity of the target to fixation is in keeping with the notion of attention biasing processing to rely on more on either high temporal resolution magnocellular inputs or lower temporal resolution parvocellular inputs. Results of attempts to directly test this theory have been inconclusive, with some support (Yeshurun, 2004) and some contrasting results (Akyürek & van Asselt, 2015; Yeshurun & Levy, 2003). Interestingly, the proximity-cueing interaction seen in chapter 3 only emerged for the integration task version, whereas the spatially specific shifts to alpha frequency effects were clearer and more robust for the segregation task version only. Future work in animal models is needed to elucidate the relative involvement of magnocellular and parvocellular pathways from the retina, to the lateral geniculate nucleus (LGN) and beyond in spatial attention to temporal processing. Given evidence of correlation between alpha rhythms in the LGN and visual cortex (Bollimunta et al., 2011), there is also some potential for this line of investigation to reconcile and integrate the two accounts discussed here (magnocellular-parvocellular and temporal window size adaptation).

Wider relevance

The empirical investigations reported here have been conducted with a specific focus on covert spatial attention to temporal processing in the visual system, specifically using endogenous spatial cues and rapid sequential stimuli. To what extent might the findings and conclusions here generalise to other types of integration and segregation? The benefits of spatial attention on temporal processing may also arise in different modalities, and at different timescales. The adaptation of temporal window size framework is easily applied at different timescales and modalities, since much like the hierarchy of increasing spatial receptive field size (Van Essen & Maunsell, 1983), the size of temporal windows increases up the hierarchy (Hasson, Yang, Vallines, Heeger, & Rubin, 2008; Van Essen & Maunsell, 1983). Flexible adaptation of the size of temporal windows by spatial attention at a given level could provide a means to improve performance in a given task if the window size at that level is slightly suboptimal.

Multisensory integration is a form of temporal processing in the sense that inputs from different sensory systems arrive with difference temporal dynamics, for example differences in visual and auditory inputs arriving and being processing (Freeman et al., 2013). Much like the results reported here, spatial attention has been shown to influence multimodal perceptual experiences (Talsma & Woldorff, 2005), and has been linked to oscillatory activity changes (Cecere et al., 2015; Senkowski, Talsma, Herrmann, & Woldorff, 2005). The role of spatial attention in biasing processing towards an integration or segregation mode also has relevance to topics such as perceptuomotor processes and motor control, where the balance between finer temporal resolution and a more coarse grained integrated percept could have significant impact on the success of responsive actions.

Differences in multisensory integration and abnormal temporal processing have been related to inappropriately sized temporal windows in a number of patient populations, such as people with schizophrenia, autism spectrum disorders, reading disorders and attention deficit hyperactivity disorder (Hahn, Foxe, & Molholm, 2014; Toplak, Dockstader, & Tannock, 2006; Zhou et al., 2018). These differences are typically characterised as a deficit to temporal resolution i.e. use of an inappropriately large temporal window (Goswami, 2011; Kawakami, Uono, Otsuka, Zhao, & Toichi, 2018; Stevenson et al., 2014). Some evidence suggests that perceptual training can mitigate these differences (Wallace & Stevenson, 2014), with the potential for impact on symptoms and development of the disorder. A potentially fruitful avenue of research would be to test for differences in the effect of spatial attention on temporal processing in these patient populations, and to probe whether spatial attention manipulations could play a role in improving therapeutic perceptual training efforts.

Future directions

In the preceding sections some avenues for further study have already been indicated. These include the need for better understanding of how spatial cueing modulated alpha frequency shifts relate to changes in alpha power, and quantifying the relative reliance on magnocellular versus parvocellular inputs in humans.

The proposed candidate mechanism discussed here - of a strategic modulation of the sampling rate of the visual system in line with task goals and spatial expectations - presents some interesting predictions. We report that when the goal is segregation, there is a relative upshift in alpha frequency in the hemisphere contralateral to the attended location, and a relative downshift ipsilaterally. Interpreting these changes as strategic shifts in the sampling rate in line with task demands leads to testable predictions. Perceptual experiences in the attended hemifield should be more likely to be successfully segregated, whereas those in the unattended hemifield more likely to be inappropriately integrated. This could be tested in a number of ways, such as using the colour fusion paradigm comprising two rapid sequential displays of colour patches and collection of responses about a primary target and also perceptual experience in the unattended hemifield.

Given the existing evidence indicating dissociations between endogenous and exogenous attention on spatial and and temporal processing, it would be interesting to employ the main paradigm used in this research to probe the effects of exogenous cueing on the opposing temporal processes of integration and segregation while holding visual stimulation constant. Based on previous findings (Hein et al., 2006), we would expect to see an exogenous cueing benefit for segregation but a cost for integration. In this way we could further characterize differences between exogenous and endogenous attention.

Other avenues of future research could be fruitful in testing the extent to which the effects and mechanisms discussed here generalize to other situations. It would be interesting to probe the effects of spatial cueing in other modalities, such as the auditory domain. Here too a flexible adaptation of the sampling rate of perception could be useful. Efforts to investigate these spatial cueing effects in other integration processes such as multisensory integration would contribute to wider understanding of how selective attention adaptively biases perceptual systems towards a more useful mode of processing stimuli over time.

La ricerca in breve / The research in brief

I'm a firm believer that if you can explain something in simple terms then you probably don't really understand it. So I've summarised the main ideas of the thesis using the minimum amount of jargon I can manage. English version follows the Italian one.

Quasi in ogni momento mentre siamo coscienti un flusso di informazioni visive raggiunge i nostri occhi. Anche se sembra che la nostra percezione sia continua, in realtà ha un andamento ritmico: il momento in cui ogni piccolo pezzo di informazione visiva raggiunge i nostri occhi determina la probabilità con cui sarà percepito. Per capire questo concetto si può pensare a un film che sembra continuo, ma è composto da tanti fotogrammi. Ciò porta ad alcune illusioni ottiche ed esperienze visive inaspettate: per esempio, guardando una piccola luce che sta cambiando intensità rapidamente con andamento casuale, la percezione sarà di una luce che sta cambiando intensità in modo ritmico.

Grazie alle macchine per osservare l'attività cerebrale, sono emerse prove del fatto che il ritmo sia anche una caratteristica fondamentale del cervello. Le cellule cerebrali (o neuroni) comunicano tra di loro attraverso la trasmissione di impulsi elettrici. Quando un alto numero di neuroni manda impulsi elettrici in modo sincronizzato, possiamo usare una tecnica chiamata magnetoencefalografia (o MEG) per registrare i piccoli campi magnetici associati all'attività elettrica dei neuroni. Possiamo quindi descrivere quest'attività in termini di caratteristiche delle onde del cervello come la frequenza o l'ampiezza delle onde (ovvero quanti neuroni sono coinvolti nell'attività sincronizzata). Il parallelo intuitivo tra l'andamento ritmico del cervello e l’andamento ritmico della percezione ha prodotto nuove interessanti indagini scientifiche e nuovi modi di studiare la percezione.

Questa ricerca si è basata sull’idea della percezione visiva come campionamento d’informazioni visive, e sull’idea che possiamo cambiare la frequenza di campionamento (ovvero la velocità dell’andamento ritmico della percezione). La nostra ricerca si è concentrata sull’elaborazione di stimoli consecutivi. Abbiamo testato la capacità dei partecipanti sia di integrare gli stimoli in un’esperienza combinata sia di tenerli distinti. Inoltre abbiamo testato gli effetti sulla percezione e sull’attività cerebrale quando in presenza di un indizio che indica in che punto dello spazio è probabile che gli stimoli appariranno.

Le nostre scoperte comportamentali dimostrano che avere un indizio che indica il punto in cui gli stimoli appariranno aiuta nel caso in cui si stia cercando di integrarli in un’esperienza combinata. Curiosamente, lo stesso tipo di indizio aiuta se anche quando si sta cercando di fare l’esatto contrario, ovvero tenerli distinti. Questo indica che il fatto di fare attenzione ad una posizione aiuta la percezione visiva in modo flessibile. Per quanto riguarda l’attività cerebrale, i risultati mostrano che la frequenza dei ritmi cerebrali è influenzata da ciò che stiamo cercando di fare e dalle nostre aspettative. Ciò suggerisce che cambiamenti della frequenza dei ritmi cerebrali riflettano cambiamenti strategici della frequenza di campionamento della percezione.

Nearly every waking moment a stream of visual information reaches our eyes. Even though it seems that our perception of the world is continuous, it is actually rhythmic: the moment at which each small piece of visual information reaches our eyes determines the probability that it will be perceived. You can think of this a bit like how a movie seems continuous but is made up of lots of individual frames. This leads to some surprising illusions and visual experiences: for example, if you look at a small light changing brightness rapidly and at random, your perception will be of a light changing brightness rhythmically.

Neuroimaging machines allow us insight into ongoing human brain activity, and here too we find that rhythmicity is a fundamental characteristic. Brain cells (or neurons) communicate with one another using electrical signals. When a large number of neurons send electrical signals in sync, we can use a technique called magnetoencephalography (or MEG) to record the small magnetic fields associated with the electrical activity of the brain. The recorded signal can be compared in terms of features of neural oscillations, such as their frequency (how often the cells are firing) and power (how many cells are firing together). The intuitive parallel between rhythmicity in both brain and behaviour has generated exciting new investigations and ways of thinking about perception.

This research is based on the idea of visual perception as a sampling of information about the environment, where we are able to flexibly change the rate of sampling (the speed of the rhythmicity in perception). Our research focuses on the processing of stimuli that follow each other rapidly in time. We tested people's ability to either integrate sequential stimuli into a combined perceptual experience or to keep them separate, and furthermore their ability to use information about where in space stimuli will likely appear.

Our behavioural findings show that having an expectation about where in space stimuli will appear helps you when trying to integrate them into a single perceptual experience. Interestingly, this expectation also helps when you are trying to do the exact opposite and keep them separate. This indicates that paying attention to a location in space enhances visual processing in a flexible way. Neural evidence shows that the frequency of neural oscillations is changed by what you’re trying to do and your expectations. This supports the idea that these neuronal changes may reflect strategic shifts of the sampling rate of perception.

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