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Top-down and exogenous effects on covert and overt orienting

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Top-down and exogenous effects on covert and overt orienting

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Abstract

Due to numerous bottlenecks, the human brain is unable to consciously process all data available at the retina. To overcome these constraints, evolution has developed a system that breaks down retinal information into fragments and subsequently analyses them according to current goals and expectations. This biasing system is frequently referred to as attention. Yet despite a long history of itself having been the focus of analysis, there are a number of questions about attention that are clearly unanswered by the literature. Therefore, we wanted to address three problems highlighted by our **literature review**. Specifically, we wanted learn, **(I)** Are the effects of probabilistic expectations, when instructed either by spatial blocking of the target location or through a central cue, on response latencies the product of a ballistic, attentional process, or the product of an information theoretical decision-making process? **(II)** Can the inhibitory aspects of spatial attention be pre-deployed by using a central cue to manipulate prior expectations of where a task-irrelevant distractor is likely to appear? **(III)** What is the relationship between attention and eye movements?

We investigated this last question by way of testing healthy participants on covert and overt versions of the behavioural paradigms designed to address questions I and II, and then in a neuropsychology patient who presented with hypometric saccades, we investigated if eye movements and attention can be dissociated. **Experiments 1-4,** showed that the effects of target probability - when either spatially manipulated or instructed through a central cue - can neither be fully accounted for by attentional accounts or information theoretical accounts. Additionally, the outcome of target probability is context dependent. That is, outcomes depend on how target probability was instructed. **Experiment 5** showed that spatial inhibition cannot be endogenously deployed using central cues. Although we found that distractor suppression takes place when targets are invalidly cued, suggesting distractor suppression takes place during reorienting. **Experiments 6-7** showed that attentional orienting can be preserved in the presence of oculomotor impairment, indicating eye movements and attention can be structurally dissociated. Whereas the results of **experiments 1-5** are consistent with claims that covert and overt orienting are similarly affected by expectations due to a common attentional process. We conclude that expectations influence a mechanism common to overt and covert responses, but ultimately, both processes are distinct.

In the **discussion chapter**, we discuss a number of future avenues of research,

including how electrophysiology could be used to further understand the phenomena presented here. Overall, the contribution of this body of research is to illustrate that the relationship between top-down expectations and exogenous effects is extremely complicated, and are, currently, inadequately captured by present models of attention.

Chapter I

Introduction

A fundamental behaviour of biological organisms is to orient in response to a sensory stimulus. This behaviour has been empirically observed in bacteria (Chen, Ma, Jiang, & Song, 2011), plants (Adams, Volk, Hoehn, & Demmigadams, 1992), and humans (Posner, 1980). Unsurprisingly, orienting towards a sensory stimulus has long been a subject of scholarly interest. As far back as the Age of Enlightenment, Descartes claimed that humans oriented towards salient objects by tilting the pineal gland in the direction of the stimulus (1649). William James noted that that attentional orienting could be reflexively captured by suddenly appearing stimuli (1890). An early introspective report from Helmholtz (1896) concluded that attention could be covertly and willingly orientated independently of gaze. In the early 20th century, orienting was of interest to Soviet scientists. Pavlov (1927) famously reported that when there were changes in the environment, such as a door opening or a light switch being activated, that the dogs kept within his laboratory would orientate their gaze and/or ears towards the estimated location of the stimulus. Later, Sokolov (1960) reported a number of cortical and subcortical areas that were active during orienting, suggesting that orienting is represented at various levels within the central nervous system. An important methodological advance was provided by Michael Posner (1980), in the way of a simple but elegant cueing paradigm for manipulating and measuring the effect of expectations on covert attentional orienting. Later, and somewhat ironically, data obtained using this paradigm was used to make the claim that attention is simply the by product of cortical activation of the oculomotor circuitry (Rizzolatti, Riggio, Dascola, & Umiltá, 1987). More recent efforts have attempted to capture the nature of attentional orienting using computational models, ranging from the simple (e.g. Carpenter & Williams, 1995) to the complex (Itti & Koch, 2001).

Therefore the question of how animals orientate towards a sensory stimulus has not only historically been of interest but is still an important, interesting, and challenging topic**.** The purpose of this present body of work is to investigate the nature of top-down expectations on covert and overt attentional orienting. Specifically, our goals were to learn: **A)** How do top-down, probabilistic expectations influence attentional orienting to an imperative stimulus? **B)** Can top-down expectations prevent orienting towards a spatial location where distractors are expected to appear? **C)** Is it possible to dissociate covert and overt attention behaviourally and neuropsychologically? Therefore, the remainder of this chapter will describe the current state of the visual attention literature, as relevant to these topics.

Visual Attention

Visual environments are rich in information and due to various processing bottlenecks within the brain, biological systems are unable to consciously access all sensory data available at the retina (e.g. Levin, 1997). To counter these limitations, evolution has developed a biasing system for the purpose of maximizing the use of limited computational resources by breaking down retinal information into sections, which are then selectively processed according to system priorities. This system is referred to as visual attention.

Attention is a crucial process for biological systems, enabling them to identify dangers within the environment, or resources required for survival and reproduction. For example, sustained attention allows a snake to focus on its prey for prolonged periods, until the right moment to strike; alternatively, attention can be involuntarily orientated towards a predator detected in peripheral vision. Attention may also required for processing and bringing awareness of internal events, such as thirst, hunger or fear. Failures of attention are often features of many pathologies such as Alzheimer's disease, schizophrenia, or attention deficit disorder, and therefore attention may be the focus of medical intervention – even though a clinicians notion of attention will be different to that of scientists. When considering these examples, they highlight that the term *attention* describes a multitude of different processes for laymen, clinicians, and scientists. For the purpose of this thesis, when discussing attention we shall use the classical view that has driven much of contemporary attention research, given by Williams James in the principles of Psychology:

> "*Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others.*".

This quote has become something of a cliché within attention research, however it is so often used precisely because it provides an excellent description of attention, in it is a selective process that allows a selected stimulus to receive priority processing whilst simultaneously deprioritizing other stimuli. Although somewhat ironically, despite the long history of research and many experiments, Sutherland claimed that only slightly more is known about attention than the contents of a black hole (Sutherland, 1998).

Whilst there are indeed a number of unresolved debates, there are several principles that are accepted by contemporary attention researchers.

Attention is selective and other principles

How selection of a stimulus is specifically achieved has received a number of hypothetical solutions. Some accounts have claimed that attention operates as a spotlight (e.g. Posner, 1980) or a zoom lens (e.g. Eriksen & James, 1986; Laberge, 1983). The core tenant of such descriptions is that within the visual environment, attention acts as a beam, which prioritizes whatever falls within it loci for processing. Whilst there are criticisms of this account (see review by Cave & Bichot, 1999), for example; the observation that multiple locations may be attended simultaneously (e.g. McMains & Somers, 2004), such metaphors provide a useful shorthand description of how attention is controlled, independent of gaze. Another characteristic of focal attention is the manner in which it may be summoned. Attention can be summoned *exogenously* by the sudden appearance of a new stimulus, or it can be deployed *endogenously*, through top-down processes. Finally, attention can be deployed *overtly*, through shifting body, head or eye position, or *covertly* by adjusting the focus of attention without adjusting bodily position.

Models of attention

Models of attention have played an important role in designing experiments and interpreting their results. Early selection models have generally described attention as a mechanism for preferentially allocating limited resources to visual stimuli, in accordance with either overwhelming exogenous contingencies or current behavioural goals (Broadbent, 1958; Treisman & Gelade, 1980; Bundesen 1990; Carrasaco, 2011). One influential conception of attention, which has strongly influenced the literature, was formulated by Posner (1980) and later associated with specific neural circuits (Posner & Peterson, 1990; Petersen & Posner, 2012). According to this perspective, attention is comprised of several functionally and anatomically distinct systems - the alerting system, the orienting system, and the detection system - designed to facilitate the binding of sensory representations to action and cognition. These systems are described in greater detail below.

Alerting system

The first system described by this model is alerting, which promotes a state of readiness, to facilitate prompt and accurate responses to stimuli. For example, a warning signal prior to an event causes a change in alertness, which can facilitate the response to subsequent targets (Petersen & Posner, 2012). Alertness is sensitive to a number of physiological and circadian factors (Posner, 1975) and is considered lateralized to the right hemisphere (Posner & Peterson, 1990). Neurochemically, alerting has been associated with the noradrenergic brainstem nuclei. Since warning signals are known to increase metabolic activity in the locus coeruleus (Aston-Jones & Cohen, 2005) a brainstem nucleus whose noradrenergic neurons project diffusely to cerebral cortex. Whilst separate processes, it is considered that alerting and orienting operate closely together (Fan et al., 2009).

Orienting

Orienting refers to the process of directing attention to spatially localized signals (Posner, 1980). More specifically, overt orienting refers to the alignment of sensory signals away from irrelevant stimuli, and towards relevant stimuli to for the purposing of improving the quality of the sensory data concerning targets of potential interest. Generally, orienting can take place also covertly and allows the observer to respond to the attended stimulus. It has been suggested that orienting may also take place in non-spatial dimensions (Corbetta & Shulman 2002). In other words, when attending to colour or shape, observes may use the same neural processes employed when orienting to a location.

Orienting is clearly a dynamic process since attention is deployed at different locations. A crucial aspect of the orienting response, as conceptualized by Posner, is that this response depends on distinct processes; which (i) disengage attention from a location; (ii) shift attention to a new location; (iii) before finally engaging attention to the new location. These separate operations are carried out by different brain structures, so that brain lesions can disrupt different subcomponents of the orienting response with separate effects on attention. Posner proposed that attention could be summoned exogenously by a suddenly appearing stimulus, or endogenously through internal, cognitive processes (Posner, 1978). The idea that attention can be summoned both voluntary or reflexively is now well established (Berger, Henik, & Rafal, 2005).

According to neurological models of attention, there are separate neural systems for endogenous and exogenous orienting (Corbetta & Shulman, 2002). There is a dorsal attentional network that is distributed hemispherically and includes mainly areas along the Intra-Parietal Sulcus (IPS) and in the Frontal Eye Fields (FEF) and a right hemisphere lateralized ventral attention network, which includes the Temporal-Parietal Junction (TPJ) and Ventro-Lateral Prefrontal (VPF) cortex. Evidence for the dorsal system includes increased activity in the IPS and FEFs following the presentation of a central arrow cue, used to guide endogenous spatial attention (Corbetta & Shulmen, 2002). Additionally, activity in the IPS shows sustained increases in the hemisphere contralateral to the attended visual stimulus (Shomtsein & Yantis 2004). When the target appears in a location other than that indicated by the central cue, then the ventral system is activated, suggesting a specific susceptibility to exogenous targets and possibly reorienting of attention. The ventral system has been described as responsible for interrupting current attentional processes when a salient, but unexpected stimulus requires reorienting of attention. The function of the ventral attentional system has been compared to that of a circuit breaker (Corbetta & Shulman, 2002). Recent evidence has called into question this highly popular interpretation of the function of the ventral attentional system. A number of investigators have suggested that the ventral attentional system may be more concerned with evaluative processes that follow the detection of the target, rather than processes that precede it (Doricchi et al., 2010; Hiang & Marois, 2014). One distinct feature of the activity of the ventral attentional system is that it is modulated by the probability of a target (Corbetta & Shulman, 2002).

Detection/executive system

In the original Posner and Peterson (1990) review, the third system was described in terms of processes engaged following target detection. In a recent elaboration (Petersen & Posner, 2012) this was renamed the executive system. This third system describes the moment when a target enters into conscious awareness, which according to the authors encompasses two main systems. The first system relates to a global system or state, that is maintained across the block of a task and signals may be related to participant instructions provided at the start of a block (Peterson & Posner, 2012). Cortical regions that have been proposed to be involved in this maintenance signal include the medial frontal/cingulate cortex and bilateral anterior insula (Dosenback et al., 2006). Whereas activity of the second system is allied to single trials within a task, and appears to be more concerned with adapting performance to the current required demands. Cortical regions associated with the more reactive signals include the parietal and lateral frontal regions (Dosenback et al., 2006). With the main advantage of duel networks being a system that can be adaptive to transient, trial events, whilst also stable across the block of a task (Doesnbach, Fair, Cohen, Schlaggar, Petersen, 2008).

Effects of top-down expectations on attentional orienting

Expectations in the context of this thesis refers to brain states that reflect an internal estimate of the prior about some probable, future event (Summerfield & Egner, 2009). Much of the empirical support for selective models of attention are provided in the way of experimental paradigms where attentional orienting is manipulated through biasing observer expectations through a centrally presented cue. The cue is thought to be symbolic, because it provides indirect information regarding where the target is likely to appear. This paradigm is generally referred to as the Posner paradigm (Posner, 1980), although it was first employed by Leonard (1953) to investigate the time required for an observer to process a single bit of information.

The general format of the Posner paradigm is as follows (see figure 1): Observers fixate on a centrally located fixation point at the center of a display. After a period of time delay, a cue will appear, either centrally or peripherally located for a fixed amount of time. After another brief period of time, known as a foreperiod, the target will appear either at the location indicated by the cue (validly cued) or at one of the other locations (invalidly cued).

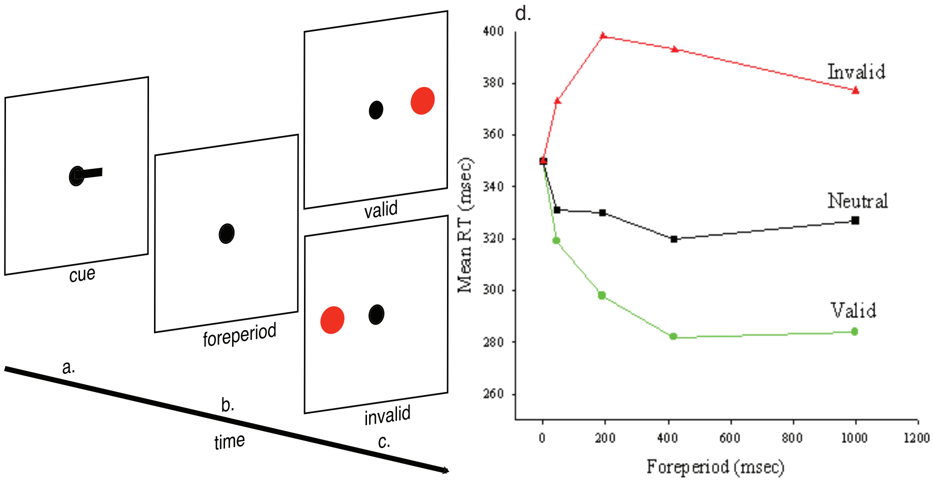

Figure 1. Prototypical Posner paradigm. **A**. Observers are first presented with a cue for a period of time, which is then followed by a **(B.)** foreperiod, before (**C**.), the target appears. If the target appears at the previously cued location it is validly cued, if it appears at a location other than the cued one, it is invalidly cued. **D.** Results presented here are from Posner, Nissen, and Ogden (1978) demonstrating that reaction-times are faster for validly cued targets than invalidly cued targets.

The consistent findings in such experiments are that reaction times are faster on valid trials compared to invalid trials, and that validly cued trials are only marginally faster than uncued trials in which the target is preceded by an uninformative cue (Green & Woldorff, 2012; Hommel, Pratt, Colzato, & Godijn, 2001; Jonides, 1983; Posner, 1980). Furthermore, it is possible to calculate a *validity effect* by subtracting the difference between response times for invalid trials from valid trials, to provide an estimate of the measurable benefit from using the cue. The canonical explanation for faster responses to valid than invalid targets (e.g**.** Posner, 2014) is that during validly cued trials when the target appears at the cued location, attention is not required to orientate as it is already at the location containing the target. Thus a response can be initiated as soon as the target appears. Whilst the appearance of a target in the absence of a cue is sufficient enough to generate a shift of attention, thus explaining why there is only a marginal benefit of the cue in valid compared to uncued trials (Posner, 2013). The cost seen on invalidly cued trials is interpreted as attention must first disengage from the currently attended location, and then re-orientate to the new location, and finally engage the new location. Centrally presented cues, used to guide attention endogenously, generally require ~150 to 300 ms to covertly orientate attention to the cue in simple manual response tasks (where observers are required to maintain fixation; Umiltà, Riggio, Dascola, & Rizzolatti, 1991) and around 150 ms to execute a saccadic response (Rayner, 1998).

Many studies have used the Posner paradigm to selectively bias attention (Jonides, 1983; Lambert & Duddy, 2002; Peterson & Gibson, 2011; Smith, Ball, & Ellison, 2014), although the mechanisms by which centrally presented cues bias attention remain debated. Early claims assumed that these effects would only occur when cues were informative about the target location (Crump, Milliken, & Ansari, 2007; Jonides, 1981). However, several studies have demonstrated cueing effects even when central cues offer no predictive information (Green & Woldorff, 2012; Qian, Shinomori, & Song, 2011) and the likelihood of the target appearing at the cued location is the same as for any other location. Other investigators have suggested that arrow cues tap into a reflexive orienting system (Bayliss, di Pellegrino, & Tipper, 2007; Kuhn & Kingstone, 2009). If the effects of symbolic cueing are largely reflexive, then they should be largely independent of the cue validity, contrary to a number of reports. However, the observation of a validity effect in the face of a non-predictive cue may still reflect an endogenous effect, driven by either an incorrect appraisal of its value, or a sub-optimal utilization strategy.

One strategy which can account for the validity effect produced by uninformative cues is probability matching (Jonides, 1983). Jonides proposed that in a task where the cue correctly indicates the target location less than 100 percent of the time, the cue is only processed on a proportion of trials. Essentially observers behave according to a *two process model* where they are either allocating all available attentional resources to the location indicated by the cue, or they are attending elsewhere. Probability matching assumes that observers will use the cue on a proportion of trials, which match the reliability of the cue (Jonides, 1983). This particular strategy can be a consequence of a simple “win-stay, lose-shift” rule (Gaissmaier & Schooler, 2008), where following a trial in which the cue correctly indicated the location of the target, observers will attend the cued location. Whilst following a trial in which the cue indicates the incorrect target location, the observer will not attend the cued location. In short, participants use the strategy that would have been successful in the previous trial. Jonides (1983) found support for this strategy since it predicted performance better than a single process model, which assumed that a percentage of attentional processes (according to cue validity) were allocated to the cued location on each trial. Though probability matching may seem suboptimal, because it will lead to fewer correct trials than if observers exclusively sampled the highest probability location on each trial, as long as one assumes that the benefits of attending the cued location are larger than the costs of attending the incorrect location. However, it has been suggested that it forms part of a more general strategy when searching for patterns in the face of more complex environments (Gaissmaier & Schooler, 2008).

Subsequently, responses would appear erratic if using a strategy of win-stay, lose-shift when outcomes are random, however such a strategy is more sensitive to finding patterns which humans appear to disposed to identifying (Gaissmaier & Schooler, 2008). Indeed even in studies where stimuli presentation is random, participants will report having identified patterns (Unturbe & Corominas, 2007). An anecdotal and analogous example would be the *gamblers fallacy* applied to a game of roulette, where players try to use previous outcomes to predict future outcomes, despite past events and future events being independent, thus providing no probabilistic information regarding the outcome.

Empirically, a number of studies have observed participants using probability matching during choice tasks. For example, Jonides (1983) tested the idea that observers only attended the cued location on a number of trials proportional to the validity of the cued, against a model predicting participants would distribute attentional resources amongst all possible locations, but with the proportion of attentional allocation matching the cues validity. Thus in this second model, it was proposed that attentional resources would be disproportionally allocated to the cued location according to the cues validity. Jonides predicted that if the two process model was correct, differences in reaction times for reliability would occur because of there would be differences on the proportion of trials where participants were attending to the cued location. Inspection of the data demonstrated that differences in reaction-times were the result changes in the proportion of attended and unattended trials, supporting the idea that attention was fully committed to cued locations, rather than weighted at different locations according to cue reliability. Furthermore, a number of other studies have found that observers use a probability matching strategy (Gaissmaier & Schooler, 2008; Johnson & Yantis, 1995; Unturbe & Corominas, 2007; West & Stanovich, 2003). Nonetheless, despite the empirical support for probability matching as a decision strategy when choosing to use a cue, there is evidence for an alternative explanation of the effects of cue validity on endogenous orienting.

Information theoretical accounts

An alternative, and prominent idea of how observers may internalize estimates of an event probability to optimize response times and accuracy is based on information theoretical accounts (Carpenter & Williams, 1995; Hick, 1952; Hyman, 1953). A crucial aspect of these models is that they consider responses to be the product of a decision making process, based on the accumulation of information transmitted through a limited capacity channel. These models can be considered as the extension to theories providing basic insights into the transmission of information along noisy channels (Shannon, 1948). One of the earliest papers demonstrating a relationship between choice probability and reaction times consistent with information theoretical accounts, was provided by the finding that as the number of decision choices increases, reaction-times also increase, but in a logarithmic manner (Hick, 1952). This logarithmic relationship between uncertainty and reaction times has been replicated by a number of decision-making models (Carpenter & Williams, 1995; McSorley & McCloy, 2009; Ratcliff, 2001; Schall, 2000)**.** One common feature of these models is that all possible decisions, representing the possible target location that an impending eye movement can be directed to, are represented by distinct decision units. For a decision unit to be declared the winner, its level of activation has to reach a certain threshold. This threshold may either be reached by the accumulation of a noisy sensory signal or of a decision signal transmitted along a noisy channel. Once activity of a specific decision unit has reached its threshold, the associated response is then executed (Carpenter & Williams, 1995; Schall, 2000).

Some of the most compelling support for decision-making accounts is provided by neurophysiological studies. In particular, studies demonstrating neuronal activity, which is sensitive to probabilistic information in structures crucial to simple motor responses. Basso and Wurtz (1998) compared activity of buildup neurons, fixation neurons, and burst neurons within the superior colliculus (SC) of non-human primates, whilst systematically varying the target's spatial uncertainty by changing the number of possible target locations. Changes in target probability modulated the baseline activity of SC neurons prior to the stimulus appearance. More specifically baseline activity specific to buildup neurons decreased as the number of possible target locations increased, implying that this indexed the probability that the target would appear at a certain location. Similar findings have been reported in a number of other brain areas considered crucial for covert and overt orienting such as the FEF (Schall, Stuphorn, & Brown, 2002) and the IPS (Heekeren & Marrett, 2008), which suggests that probabilistic information may have widespread effects on neural activity.

LATER Model

Whilst many models attempt to explain the decision processes (McSorley & McCloy, 2009; Ratcliff, 2001; Schall, 2000), one particularly popular information theoretic model is the Linear Approach to Threshold with Erdogic Rate model, known as the LATER model (Carpenter, 2014; Carpenter & McDonald, 2007; Carpenter & Williams, 1995). According to the LATER model, some of the time between the appearance of a salient target and the execution of a saccade towards the target represents decision-making time. The core assumption is that following the appearance of a target, a signal representing the level of activation in the decision unit coding for a saccade toward the target, rises from its baseline level, at a constant linear rate, until it reaches a threshold. Once the rising activity level has reached a predetermined threshold, a decision is executed – in this case, a saccade towards the winning target. Conceptually, the decision signal represents the log-likelihood of the target probability location and the sensory evidence causes the log probability to increase, until a criterion level which is analogous to a significance level, or *p* value, is reached which can only be updated at a finite rate because of the noisiness in the relevant information channel.

Mathematically, the LATER model can be expressed as:

$$\log(\mathbf{L}') = \log(\mathbf{L}) + \mathbf{S}, \qquad \textbf{where} \ \ \mathbf{S} = \log\frac{\mathbf{prob(E|H_1)}}{\mathbf{prob(E|H_2)}}$$

Where **L** represents the Likelihood of some hypothesis **H**, and **E** represents observed evidence. The collection of evidence **E** increases the log likelihood by a constant amount of **S**, which refers to the decision signal representing $\mathbf{H_1}$ against $\mathbf{H_2}$, given **E**.

Empirical support for the LATER model was provided in the seminal paper, the neural computation of log-likelihood theory (Carpenter & Williams, 1995). In a simple experiment, the spatial distribution of the target, the *target probability*, was manipulated over several levels ranging from 5 to 95 percent by changing the odds that the target stimulus would appear either left or right of fixation. The authors reported that after many trials with each probability level, median saccadic latencies for the two observers gradually shifted to reflect the level of target probability (see figure 2). Crucially, the distribution of reciprocal latencies were well described by a normal distribution, a finding that could be accounted for if one assumes that latency variability reflects trial to trial normally distributed variation in the rate of activity accrual. In addition to the main latency distribution of each level of target probability, there was another, earlier distribution comprised of shorter latency saccades called *express saccades*, which are described in greater depth in the chapter on eye movements. The proportion of express saccades also positively increased with higher levels of target probability. According to Carpenter, a second decision unit with a lower decision threshold can account for express saccades. It should be noted that this explanation of express saccades is significantly different compared to the attention-disengagement accounts of express saccades described later in this review. One unique aspect of the LATER model that makes it particularly useful over other models is that reciprocal transformation of the latencies is a feature of this model. These transformed latencies when visualized in reciprobit plots (see figure 2) are more intuitive for visualizing the faster population of saccades, than the more common bell curve method of visualizing data.

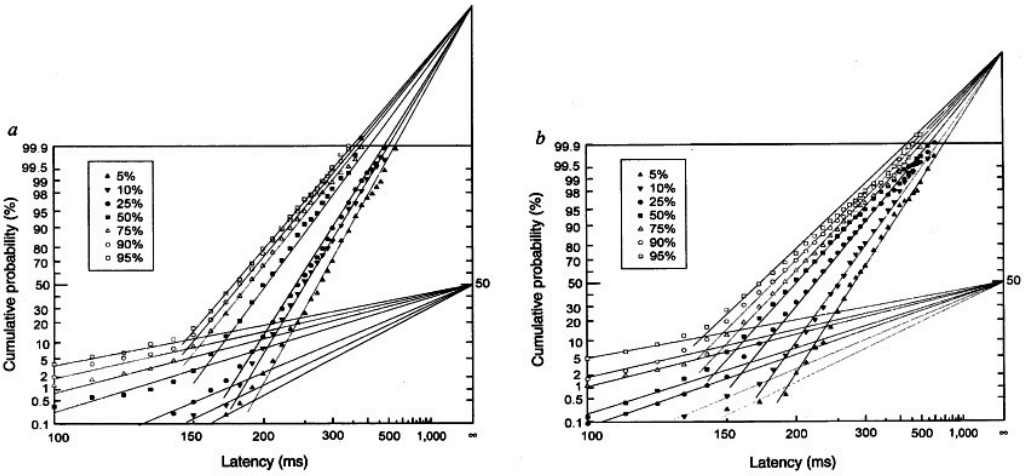

Figure 2 Reciprobit plot of participants' response latencies (ms) scale linearly with target log-likelihood. The first, shorter line reflects a faster population of latencies known as express saccades, whilst the second line represents regular saccades. Figure taken from Carpenter & Williams, 1995.

Summary: response strategies

One issue within the orienting and attention literature is how prior information biases observer responses. Formal models of attention (Petersen & Posner, 2012; Posner & Petersen, 1990) describe expectations as influencing sequential, ballistic processes which control the focus of attention, which include disengaging from the currently attended location, before orientating towards a new spatial location and finally re-engaging attention. These models theorize that expectations influence the orienting process by pre-emptively orienting attention to the cued location. Support for such accounts come from a variety of experiments, where expectations of where a target is likely to appear are provided using a centrally located cue. Typically, reaction times are faster on trials where the target appears in the cued location (valid trials) than trials where the target appears at a location other than where the cue appears (invalid trials). In terms of the pattern of behavioural data, these findings could be accounted for in terms of a probability matching strategy where attention will attend process the cue over a percentage of trials which matches the level of cue reliability (Johnson & Yantis, 1995; Laberge, 1973) thus leading to reaction times scaling linearly with changes in cue reliability.

These explanations are distinct from information theoretical accounts, which take the view that responding is mostly the result of a decision making process. These offer a markedly different account of the effect of expectations on reaction-times, in that responses to the presence of a stimulus are the result of a decision-unit collecting a required amount of sensory evidence which gradually increases the logarithm of a decision signal until a criterion is reached, and subsequently an outcome associated with the winning decision unit (such as a saccade) is executed.

Whilst both models have been overwhelmingly useful and can account for a wide variety of empirical findings, they are in clear disagreement. On one hand, attention models predict that one aspect of the sensory environment is considered during a response and this supports the notion that attention is a process-limited resource. Whilst the other predicts that a competing decision unit represents each probable outcome. Therefore an important question for our understanding of visual attention, is the nature of the effects of target probability on attentional mechanisms - do they influence a decision making process; or alternatively, do they influence a probability matching strategy where attention is deployed only to any one location at a specific moment in time.

Visual search: selecting target from distractor stimuli

Rarely will stimuli important to current task demands be found in isolation. In fact, we spend a large portion of our time awake carrying out visual search tasks. For example, we search for the correct coins amongst a handful of change to pay for a cup of coffee, we may search for a PDF of an interesting journal article amongst a cluttered desktop, or we may scan through the results presented from a Google search to find the one most relevant to our current task demands. In primitive society too, efficient visual search would have been important when scavenging for food, or looking for predators to avoid. The manner in which we achieve this is still under much debate.

Visual search generally involves covert and overt orienting in order to bring attended stimuli into the high-resolution, foveal part of the retina. Search is guided by top down processes, which specify the task relevant aspects of the target and expectations regarding its likely location (Miller, 1988), defining features of colour and shape (Laarni, 2001). Also there may be processes which keep track of previously searched locations and stimuli (Abrams & Dobkin, 1994) to improve search efficiency.

Feature Integration Theory

There are several accounts of visual search (Eckstein, 2011; Wolfe, Cave, & Franzel, 1989). One of the most influential is feature integration theory (Treisman & Gelade, 1980). The core aspect of feature integration is the pre-attentive stage, which occurs early in perceptual processing before visual information enters conscious awareness. During this stage, retinal signals about objects are broken down into different categories of features, such as colour, orientation and motion. The spatial coordinates of each of these features are contained within a separate map, one map for each feature. The second stage is the focused attention stage, where features are combined to create an overall master map, which contains the retinal coordinates of complete objects. Also during the attention stage is when the spotlight is required, and features within its loci are considered to be integrated, or glued together in order to form whole objects (Quinlan, 2003). One beneficial characteristic of this model is that it accounts for visual search. Search can proceed in one of two-ways, either sequential or parallel. The search strategy used depends if search is for an individual feature – such as a red object – versus a collection of objects, such as a red L amongst a sea or red and green T's. Searches for individual features are considered to happen in parallel, whereas object searches happen in serial; naturally, parallel search is faster than serial search.

Distractor suppression in visual search

Top-down signals are used to guide attention when searching for a target amongst task irrelevant stimuli. For example, when searching for a coffee cup, one will usually start from the last location the cup was recalled to be in. Many studies have demonstrated that spatial and feature information regarding the target can improve search performance, including probabilistic information about target location (Geng & Behrmann, 2005), colour (Dunai, Castiello & Rossetti, 2001), information on the spatial location of the target (Geng & Behrmann, 2002). There is some recent evidence that observers can actively suppress the processing of task irrelevant information. For example, it is well documented that previously searched locations are inhibited from being attended again (Klein, 2000; Lupianez, Klein, & Bartolomeo, 2006) since observers are slower to response to targets appearing in previously attended locations.

Other research has shown that responses to a stimulus which share features with a previously identified distractor are delayed (Fox, 1995; Terry & Valdes, 1994; Tipper, Weaver, Cameron, Brehaut, & Bastedo, 1991). Such data suggests that active inhibition of distractors is possible. However whether inhibition can be deployed purely endogenously, or rather requires exposures to distractor stimuli is yet not clear. Several recent studies have suggested that cueing the location or colour of task irrelevant distractors can lead to improved task performance, thought to reflect suppression of the distractor containing location. One of the first studies to argue for endogenous distractor suppression was an fMRI study by Ruff and Driver (2006). In this study, pre-cueing the location of an upcoming task-irrelevant distractor led to a reduced behavioural cost of the distractor. The authors also observed increased preparatory activity in the occipital lobe, in the hemisphere contralateral to where the distractor was expected to appear (as indicated through the cue), as well as increased activation in a parietal and frontal structures. The authors concluded that cueing diminished the distractor related costs, by biasing activity in visual and attentional networks for the purpose of suppressing distractor processing. Additional evidence for active suppression is provided by behavioural studies. Munneke, Van der Stigchel, and Theeuwes (2008) found a reduced flanker effect when subjects were cued about the location of distractor stimuli. Distractor cueing can also modify eye movement trajectories (Van der Stigchel & Theeuwes, 2006) which tend to curve away from the expected location of a distractor, even on trials when no distractor was presented. This suggests that inhibition of the cued distractor location took place during saccadic programming.

Whilst there is evidence to suggest that expectations can enable the system to reduce the impact of a distractor stimulus on attentional orienting, there is another body of research which shows that prior information regarding some element of a distractor can paradoxically result in the observer attending to them instead. For example, observers who have been instructed to actively ignore occasionally appearing distractors perform worse than observers who are not informed about the presence of distractors (Chisholm & Kingstone, 2014). This finding might be accounted for by the so called *white bear effect*, namely that cueing an irrelevant stimulus can lead to increased attention to the distractor (Lahav, Makovski, & Tsal, 2012; Tsal & Makovski, 2006; Wegner & Schneider, 2003) in that trying to actively not think about a stimulus leads to maintenance of the stimulus within memory.

Summary: endogenous spatial inhibition of a distractor containing location.

A large area of the attention research is concerned with the effect of top-down expectations and how they modulate task performance. The idea that information regarding the location of a relevant stimulus improves task performance by modifying top-down expectations is well supported within the literature. Less clear, however, are the effects of programming top-down expectations about the location of task-irrelevant, distractor stimuli. Currently the literature is conflicting, with some studies claiming that cueing the location of a distractor leads to spatial inhibition at the distractor-expected-location, whilst other studies indicate that information regarding the location of distractor stimuli paradoxically impairs performance, by increasing the processing priority of the expected location. Therefore another important question within the literature is to investigate how information regarding the likely location of irrelevant stimuli modulates task performance.

Attention and eye movements

The final section of this review will deal with the relationship between eye movements and attention. First, we will review the anatomy of the eye, then describe different methods of recording eye movements and related research methodology (including the one employed in this body of work), before finally describing the final problem central to this review, the relationship between attention and eye movements.

Anatomy of the eye

The human eye is a wonderfully complex optical system, and its construction and design inspired many of the instruments used in early astronomy research (e.g. Kepler's *camera obscura;* Dupré, 2008). The orientation of the eye in the orbit is controlled by three pairs of antagonist muscles. These extra-ocular muscles are responsible for rotating the eye along three axis – horizontal, vertical, and torsional. Horizontal movements are either adduction (toward the nose) or abduction (away from the eye). Horizontal movements are controlled the medial and lateral rectus muscle. Vertical movements can be either elevation or depression, and are controlled by the superior and inferior rectus muscles, and also the oblique muscles. Torsional movements are either towards the nose (intorsion) or away from the nose (extorsion).

The eye itself is a fluid filled globe comprised of three layers. The outer layer is known as the sclerotic coat, or sclera, and is referred to as the white of the eye. The transparent part of the sclerotic coat is the cornea. The cornea allows light into the anterior of the eye and also bends the light rays so they can be brought into the focus. The middle layer of the eye is known as the choroid coat, and this reduces reflection within the eye as well as forming the iris and also being responsible for eye colour. The final part of the eye is the retina, which is the inner part of the eye and it is here where visual perception begins. Here are contained the rods and cones which are the two types of photoreceptors. The central part of the retina is called the fovea, and is specialized for acuity vision. The first stage of visual perception begins when light enters the retina and falls upon the photoreceptors. This information is then transmitted through the optic nerve at speeds of around 875,000 bits per second (~ 12 megabytes), per eye (Koch et al., 2006) to regions within the brain for further processing.

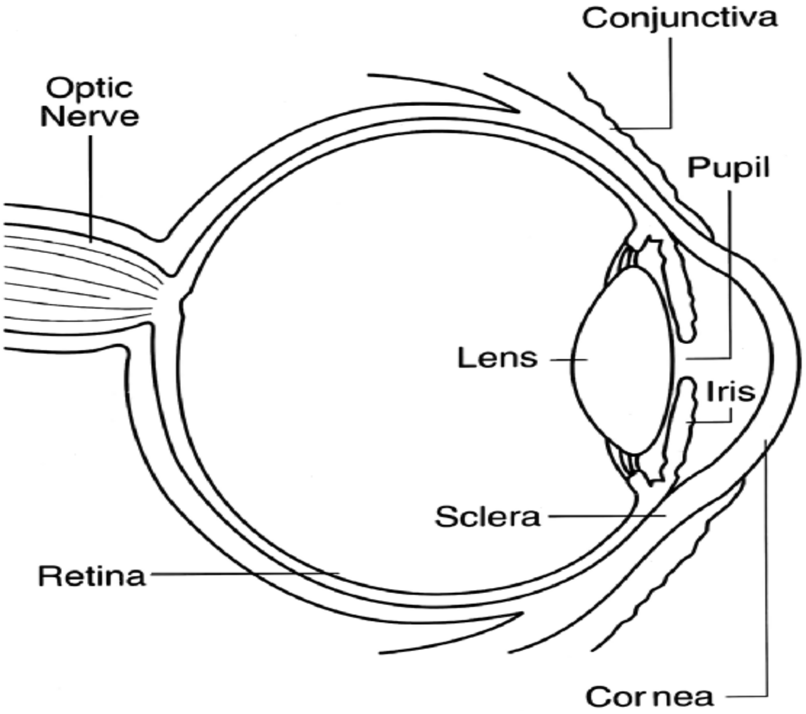

Figure 3: Gross anatomy of the human eye, showing the three layers and the retina. Credit to National Eye Institute, National Institutes of Health.

Eye movement research

Modern eye movement research has a relatively recent history. The term *saccade*, one of the most common movements we make, was originally coined by Javal (Javal, 1878) to describe the jerky ballistic eye movements made whilst reading. One of the early methodologies for measuring eye movements was devised by Delabarre (Delabarre, 1898), who attached a leaver to a plaster of Paris cup, which was placed on the cornea. Raymond Dodge (Dodge, 1903) designed one of the first non-invasive eye trackers. He created a photochronograph, which measured corneal reflections. The equipment was driven by a piano tuning fork and was able to record the eye position at around 100 Hz. Dodge also used such an arrangement to investigate oculomotor control in schizophrenia. Today, contemporary eye tracking methodology is currently used in a broad array of applied basic and translational research (Fairhall, Indovina, Driver, & Macaluso, 2009; Klein, 2008; Smyrnis, 2008).

Recording oculographic data

The equipment employed throughout this body of research is the camera based Eyelink 1000 system (SR Research, Canada). The Eyelink measures an observer's gaze by illuminating the eye with an infrared light, and tracking the position of the pupil and the corneal reflection using a camera. The data are used to estimate the observer's gaze direction. Data are collected through discrete sampling; each sample refers to the image acquired and subsequently processed using a gaze algorithm. The Eyelink 1000 system is able to sample at maximum rate of 1000 Hz, one sample each millisecond. Each sample the system provides gives information about a number of oculomotor events including pupil size and fixation time. The system also calculates a number of other parameters, such as eye velocity, amplitude, and saccadic latency. We were specifically interested in measuring saccadic latencies, which provide a measure of how long it took to initiate a saccade from the onset of an imperative stimulus. Additionally, saccadic amplitude, velocity and duration can be used to define the characteristics of the main sequence, namely the power law which describes the relationship between saccadic amplitude and peak velocity (Bahill, Clark, & Stark, 1975). fFor saccades with an amplitude of < 10 °, the relationship is almost linear when plotted in log – log coordinates. The main sequence data can provide a sensitive index of malfunction within the saccadic system (Garbutt, Harwood, & Harris, 2001; Smeets & Hooge, 2003).

Relationship between attention and eye movements

Another long running theme within the research literature is the relationship between attention and action, or more specifically eye movements and attention. Generally it is known that eye movements and shifts of attention are tightly coupled in primates, providing the basic mechanisms of a saccade-and-sample strategy: where when the eyes saccade to a specific regions of interest within a scene, allowing stimuli to be sampled using the higher sampling resolution provided by the fovea. A useful model of how attention and eye movements are coupled during saccade generation can be explained using express saccades.

Express saccades

One illustrative example of the relationship interaction between shifts of attention and saccades come from the explanation for express saccades (Saslow, 1967), namely a type of extremely fast saccadic eye movement with a latency of ~100 ms (Fischer & Weber, 1993), compared to regular saccades with a latency of around 150 – 180 ms. Whilst the existence of express saccades is contentious, a number of studies have demonstrated a bimodal distribution of saccadic latencies under certain experimental conditions (Carpenter & Williams, 1995). Thus supporting the argument that express saccades represent a special population of response. One explanation is that express saccades are the result of a direct pathway from the retina to the SC, known as the retinotectal pathway (Kato, Takaura, Ikeda, Yoshida, & Isa, 2011). Whilst express saccades can result from manipulations of inter-trial history where variables such as spatial location are kept constant (Carpenter & Williams, 1995), the most common paradigm for eliciting express saccades is the so called *gap paradigm* where the fixation point is removed ~200 ms prior to the onset of the target (Fischer & Ramsperger, 1984). The typical finding is that latencies are shorter in trials when the fixation point is removed prior to appearance of the target, than on trials where the fixation point is visible up to the target onset or beyond (Weber, Dürr, & Fischer, 1998).

The effect of fixation offset cannot be simply accounted by temporal cueing, since they are found even when the temporal uncertainty of the observer is equated by using auditory alerting signals. One account for the gap effect is that removal of the fixation points removes the need for attention to disengage from fixation, before a saccade can be executed towards the target (e.g. Kristjánsson, 2011). Additionally, there is evidence that presenting distractors at the point of fixation leads to greater delays in target evoked saccades than presenting the same distractors at eccentric locations, suggesting that foveal representation may play a prominent role in ensuring stable fixation (Beck & Lavie, 2005). Interestingly, the costs of disengaging from the currently foveated locations on saccadic latencies echoes a similar aspect of attentional orienting (Posner, 1980), namely the proposal that attention must first be disengaged from the currently attended location, before it can be reoriented to the new location. An operation that is thought to underlay the large behavioural costs associated with invalidly cued trials. Although there is currently little evidence to suggest that disengaging attention from an attended location and disengaging fixation both rely on the same neural mechanism, the former operation having been attributed to the parietal lobe (Posner, Walker, Friedrich, & Rafal, 1984) and the maintenance of fixation to the foveal representation of middle and deep layers of the colliculus (Munoz & Wurtz, 1993).

Relationship between attention and eye movements

The relationship between eye movements and attention has attracted much scholarly interest. One popular model is the VAM: the Visual Attention Model (Schneider, 1995). According to this account, limited attentional resources need a selection-for-perception process, which biases which parts of a visual scene are prioritized for processing after a saccade. The second system – selection-for-action – refers to motor systems. Visual environments also contain many stimuli which could be the target of motor actions. However, motor actions are also of limited capacity as generally they are directed to only one target at any one moment in time. According to Schneider, these two, closely related selection systems are coupled by a joint, single process, which selects a single object at any one moment for enhanced processing priority. Schneider's (1995) model is based on several assumptions. Selection-for-visual-perception is the task of the visual ventral pathway, which runs from the primary visual cortex to the inferior visual cortex. This pathway is posited to be the system that processes visual information such as shape. Whereas selection-for-action is considered to be the product of the visual dorsal pathway. This system also begins in the primary visual cortex and ends in the posterior parietal cortex. This system computes spatial information for aiding motor actions, such as the spatial coordinates of the target to be grasped. In this system, the programing of an action will activate the circuit, but the action required a separate release signal to be executed. According to the visual attention model, there is a single, supramodal visual attention mechanism which is communal to the selection-for processes, which controls the processing priority of stimuli represented in the primary visual cortex. Whilst the original model proposed that selection was directed in the primary visual cortex, it has recently been updated with the claim that the selection aspect of the model tasks place in attentional priority maps that are found in lateral intra-parietal region (Bishley & Goldberg, 2010). As a result of this, when a stimuli represented in the primary visual cortex is selected for increased processing priority, which subsequently leads to parallel, increased priority of the selected stimulus in both the ventral and dorsal systems. Thus in the ventral system the prioritized stimuli is recognized faster and enters conscious visual perception faster; whereas within the dorsal pathway, motor programs for foveating, or grasping, or stepping on the high priority object, are programed with the highest level of processing priority. Whilst VAM proposes that attention is therefore a supramodal process, which is common to perception and action systems, there is a competing and highly influential model discussed below.

One of the most influential studies within the literature on attention and eye movements was conducted by (Rizzolatti et al., 1987; see figure 3) which demonstrated the so called *meridian effect*. That is, in a covert orienting task when attention is invalidly cued to the hemifield opposite the one where the target stimuli appears, there is a larger cost (in terms of increased manual reaction times) than when responding to invalidly cued targets within the same hemifield. The authors reasoned that no attentional account can explain why a purely cognitive, supramodal process should bear an extra cost for crossing the main visual meridians. Instead the authors suggested one plausible explanation that could account for the meridian effect would be if covert shifts of attention arose because of an ocular motor plan, which was not executed. Subsequently the increased cost of changing meridians is reflective of erasing a previously prepared oculomotor movement and preparing a new one; whereas reorienting to invalidly cued targets within the same hemifield simply requires an adjustment of saccadic amplitude.

In addition to the so-called meridian effect, the authors drew on several other studies to argue that attention and eye movements arise from the same cortical circuits. Proponents of premotor theory suggest that cortical pragmatic maps are used to code the metric of covert and overt orienting. Moreover, signals generated within these maps are used to enhance processing at corresponding locations in sensory representations, whilst increasing motor readiness for the activated vectors.

The core essence of premotor theory can be captured as thus:

"Attention does not result from, nor require a control system separated from sensorimotor circuits. Attention derives activation of the same circuits that under other conditions, determine perceptual and motor activity." (Craighero & Rizzolatti, 2005, p. 181).

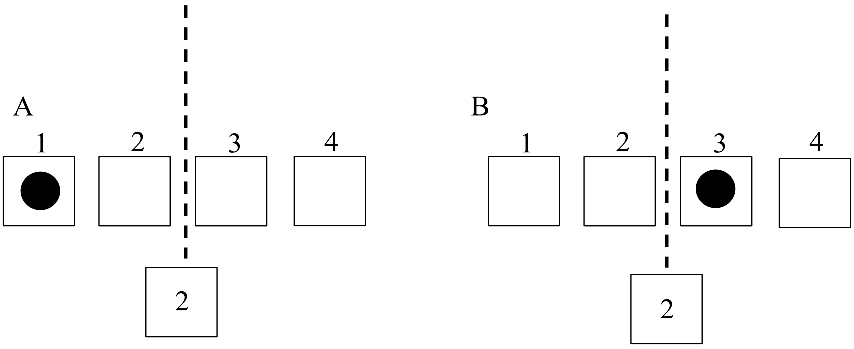

Figure 4 Schematic illustration of the paradigm used to demonstrate the meridian effect by Rizzolatti, Riggio, and Dascola, 1987. A number would appear in the central fixation box, acting as cue to indicate the likely location of the target (with a reliability of 80%). Participants were required to maintain central fixation and respond to the appearance of the target using a manual button press. Dashed line represents the vertical meridian. The meridian effect was not present for invalidly cued targets in the same hemifield **(A),** only when the target was invalidly cued across vertical or horizontal meridians **(B),** despite that in both types of trials, the distance of the target from the cued location is the same.

Neurophysiological investigations

A number of fMRI studies provide support for shared neural mechanisms between attention and eye movements. Corbetta and collegues (Corbetta et al., 1998) measured BOLD responses whilst observers responded to stimuli either covertly or overtly. Covert and overt orienting evoked BOLD signals in the same overlapping regions of parietal, frontal and temporal cortex, suggesting that cortical networks engaged by shifts of attention and eye movements are largely similar. These findings have been replicated in a number of neuroimaging studies. For example; Nobre, 2000; Beauchamp, Petit, Ellmore, Ingeholm, and Haxby (2001) also found overlapping signals following covert and overt shifts of attention, however the amplitude of the evoked BOLD response was higher for overt than covert shifts. The authors claim that the increased activity represents the increased level of effort required to program an eye movement. More recently, overlapping ocular and attention pathways have been observed in the cerebellum (Striemer, Chouinard, Goodale, & de Ribaupierre, 2015), suggesting that subcortical structures also contribute to both covert and overt orienting.

Patient studies

Patient studies also provide compelling evidence for a shared neural mechanism. Several studies have demonstrated impaired attentional orienting in the presence of oculomotor disorders (Craighero, Nascimben, & Fadiga, 2004; Craighero, Carta, & Fadiga, 2001; Gaby, Henik, & Gradstein, 2010; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988**.** For example it has been shown that patients with ophthalmoplegia show a reduced validity effect when attention is directed to locations where such individuals have difficulty executing a saccade. Remarkably, deficits due to peripheral issues such as muscle weakness can also be associated with impairments in covert orienting (Smith, Rorden, & Jackson, 2004), suggesting that disruption of overt orienting will eventually result in disruption of covert orienting as well. Even in healthy observers, attending to cued targets placed beyond the oculomotor range, thus cannot be directly foveated, but still within peripheral vision, is greatly diminished compared to attending to cued targets placed with the oculomotor range (Smith et al., 2014).

Behavioural evidence

There appears to be a tight coupling between eye movements and attention. Katnani and Gandhi (2013) studied the relationship between attentional shifts and saccades using a blink perturbation method. During blinks, activity in a set of neurons known as omnipause neurons decreases. Omnipause neurons are believed to gate the saccadic system, since activity in these neurons is associated with preventing a programed saccade from being performed. Therefore by invoking a blink at various epochs of a task, which leads to prematurely releasing the saccade, it is possible to delineate the temporal properties of saccadic programming. In an antisaccade task, Katnani and Ghandi (2013) found that a blink delivered during early epochs of the task (around 60-200 ms after the presentation of the singleton) elicited a saccade towards the singleton, irrespective of the trial being pro or anti-saccade. At later epochs however, the end point of elicited saccades were closer to the correct endpoint for pro (towards the singleton) and anti saccade trials (away from the singleton). The main interpretation of these observations is that as attention is captured by a new onset singleton, an eye movement is concurrently programmed, which is executed when gaze holding mechanisms are turned off.

Further evidence for a relationship between saccades and attention comes from the observation that perception is facilitated at the location of an impending saccade, before the saccade is executed. For example, Smith and colleagues (Smith et al., 2014) asked observers to identify letters presented, prior to the execution of a saccade, at various locations. Letter discrimination was at chance, except for letters that were presented at the saccadic goal. This coupling between the location of the saccadic target and the locus of increased perceptual acuity suggested that attention is automatically, if transiently, deployed to the upcoming saccadic goal (Smith et al., 2014).

Whilst there is strong evidence for a tight coupling between attention and eye movements, recent research has started to question the assumption that they are structurally the same. The functional data suggests a shared circuitry for covert and overt responses, thus providing a compelling case that eye movements and attention are linked. However independence has been demonstrated within these structures using single cell recordings, which provide a higher spatial resolution than is available with fMRI. Schall (2004) showed with single cell recordings in the frontal eye fields of primates that different populations of neurons are recruited when programming an eye movement than are recruited when covertly orienting to a stimuli; demonstrating that dissociation of covert and overt attention appears within the structure at the neuronal level. Additionally, whilst the behavioural data from Katnani and Ghandi (2013) using the blink perturbation method demonstrates a tight temporal and spatial coupling between saccadic programming and attention, it is unable to establish if this activity is the product of a single system. Therefore the claim from premotor theory that preparation of an eye movement is sufficient to generate a covert shift of attention is not fully supported at the neuronal level.

Counter evidence

Recent behavioural evidence has also been used to question the link between covert and overt orienting. Juan and Shorter-Jacobi (2004) used microstimulation of the frontal eye fields in an anti-saccade paradigm in order to elicit premature saccades. Participants were instructed to perform either an antisaccade if the singleton was vertically orientated, or a prosaccade if the singleton was horizontally orientated. They reasoned that if an eye movement were programed when attention is captured by a new onset singleton, then one would expect to see saccades first directed towards the singleton as observers would first have to orientate towards the singleton in order to ascertain the appropriate response. Juan and Shorter-Jacobi found that all eye movements evoked by microstimulation during antisaccade trials were executed away from the singleton, whilst on prosaccade tasks were executed towards the singleton. The author's main interpretation of these results is that attention could be orientated towards the singleton without having to program a concurrent eye movement. However it is possible that microstimulation of the FEF somehow interfered with saccade programming thus explaining why these results contradict the data obtained using the blink perturbation method.

A number of behavioural studies have also demonstrated differences in how behavioural effects may differently affect different response modalities. For example, Hick's Law is the finding that manual reaction times increase in accordance with the number of response alternatives, until a point is reached when reaction time remains constant (Hick, 1952). However, Kveraga, Boucher, and Hughes (2002) investigated if Hick's Law is multimodal across different response types. That is, they manipulated the number of response alternatives and participants were required to either perform a manual key press in response to the target, look at the target (prosaccade), or look at the target outline opposite the target (anti-saccade). The authors found that response times only increased as a function of the number of potential target locations for manual button presses, and antisaccades, indicating that different response systems are recruited for prosaccades, than are employed for manual responses and antisaccades. Another instance of a well-documented behavioural effect not extending across response modalities is the gap paradigm, discussed in the section on express saccades. Whilst studies have found the gap paradigm results in faster reaction-times in simple manual response tasks and choice manual response tasks, they do not result in the same bimodal distribution of regular-express responses observed in saccadic versions of the task (e.g. Machado-Pinheiro, Gawryszewski, Riberio-do-Valle, 1998).

Compelling evidence for the dissociation between saccades and shifts of attention was found in a patient with unilateral optic ataxia (Khan et al., 2009). Whilst this patient's saccadic latencies were slower than controls, he showed no differences in in latencies between his affected and unaffected visual field. However, in a secondary discrimination task where the target appeared at the saccadic endpoint, his performance in the unaffected field was comparable to controls, whilst performance in the affected field was at chance. These findings were taken as evidence that oculomotor planning and presaccadic facilitation can be dissociated (Khan et al., 2009).

Summary: attention and eye movements

The end of this section brings us onto third second problem. Despite claims from the influential premotor theory that the oculomotor system and the attention system are functionally similar, this position has been undermined by a number of recent studies, which have shown that instances where the two processes can be behaviourally and functionally dissociated. Therefore an important question to enhance our understanding of covert and overt orienting is under what conditions can the two processes be dissociated. One limitation of the present literature is that studies often attempt to delineate the two processes by showing they are dissociable. However this overlooks that one of the arguments of premotor theory is that attention arises from oculomotor planning, and is independent of motor execution (e.g. Smith & Shenk, 2012). Therefore an alternative proposal to investigate the relationship between eye movements and attention would be to simply compare saccadic latencies with simple manual reaction times across the same tasks. Particularly suited to this would be tasks manipulating expectations, such as discussed so far. This would allow an adequate comparison of behavioural responses which were collected within the same paradigm, and if a single system is responsible for the orienting stage for both covert and overt responses, then one could expect similar patterns of behavioural results for both covert and overt responses. Furthermore, any differences between patterns would be indicative of different computational processes having processed expectations.

A further problem within the premotor literature comes in the way that whilst patient studies are useful, often grouped patient data can be problematic in that lesions are rarely isolated to the exact same location, therefore a single patient's impaired performance arising from subtleties can be lost within a broad group analysis due lack of homogeneity across patient lesions. Whilst group methods are useful for broad structural investigations, such an approach may not be adequate within the framework of premotor research when considering that eye movements and attention can be dissociated at the neuronal level but not at the structural level. Therefore single patient case studies may provide a more powerful approach to investigate premotor theory neuropsychologically.

Final statement

The purpose of this literature review was to show that the topic of attention is an exciting, challenging, and important one. It was also the aim to show that despite the huge amount of effort that has gone into understanding the topic, there are still a number of unresolved problems. The aim of this thesis is to make a contribution to each of the three main areas reviewed; therefore the rest of the thesis will flow as follows. The problem regarding how expectations influence attentional orienting will be examined in chapter two. The second problem, can inhibition of irrelevant information be initiated endogenously will be explored in chapter three. The final question, which is central to this thesis, will be an investigation of the relationship between attention and eye movements. This will be investigated behaviourally in chapters two and three. Furthermore, chapter four will describe a neuropsychological case study of a single patient, who presented with ocular impairment. The fifth and final chapter will then conclude with a discussion regarding the broader implications and contributions of the findings to the current state of the literature.

Chapter II

Comparing Target Probability and Cueing Effects on Covert and Overt Orienting

Abstract

Shifts of attention are spatially and temporally yoked to saccades, suggesting that covert and overt orienting are controlled by the same premotor circuitry.

However, manipulations of target spatial probability have suggested different computational constraints on covert attentional shifts and overt oculomotor responses (e.g. Posner, 1980; Carpenter & Williams, 1995). While latencies of covert orienting are thought to depend on the number of sequential operations needed to be performed to align attention with the target, overt orienting latencies are thought to be contingent on the time taken to transmit a decision signal along a limited capacity channel. The two models predict that response latencies will either vary linearly (attention model) or logarithmically (information theoretic model) with target probability. To examine this apparent inconsistency, we measured how prior knowledge of a target location affects simple detections and visually evoked saccades, under conditions that equate all remaining experimental factors. Naïve observers were informed about the location of an upcoming target either by blocking its spatial probability distribution, or by a central cue. When the target spatial distribution was blocked, the effects of target probability on covert and overt orienting were of similar magnitude, with changes in detection and saccadic latencies, relative to a condition where target locations were equiprobable, greater for low than high probability targets. This finding is inconsistent with both the attentional account and the information theoretic account. When the target location was cued, latencies were shorter for high rather than low probability targets, and for validly rather than invalidly cued targets. The effects of target probability and validity being greater for overt than covert orienting responses. Saccadic, but not detection, responses varied logarithmically with target probability following central cues, while validity effects were found even when the cue was uninformative. We conclude that similar computational constraints affect covert and overt orienting. Although, central cues also engage mechanisms specific to overt orienting. Finally, neither the attentional nor information theoretic models fully account for response latencies in covert and overt orienting paradigms.

Initial and more recent reports examining the effects of an observer's uncertainty about the position of a upcoming target on manual and oculomotor responses found that latencies varied logarithmically with the target probability or the spatial precision of the required response (Hick, 1952; Hyman, 1953; Carpenter & Williams, 1995). Responses being faster for targets appearing at probable locations, than targets appearing at improbable locations. These findings support the notion that response latencies reflect the combined effects of the observer's initial spatial uncertainty and, once the target becomes visible, the finite rate at which a decision signal, which determines the metric of the motor response, is transmitted along a limited capacity channel (Hick, 1952; Hyman, 1953).

An alternative model of how spatial expectations influence response latencies comes from the attention literature. The prototypical paradigm is based on the use of central cues, which indicate the likely location of an upcoming target (Posner, 1980). Results from studies of brain injured patients and functional imaging have provided evidence that separate brain networks are recruited when preparing and responding to visual targets (Posner et al., 1982; Rafal & Posner, 1987; Posner & Petersen, 1990; Corbetta & Shulman, 2002; Petersen & Posner, 2012) supporting the proposal that various operations are carried out when the observer orients to a novel stimulus. The core assumption is that for the response to be executed, even following the simple detection of a clearly visible target, attention has to be spatially aligned with the target. This alignment is carried out by sequentially ordered operations, either voluntarily or reflexively (Posner & Petersen, 1990), which include shifting the attentional vector across the visual field, engaging and locking attention at a particular location and, finally, disengaging attention from its current location, before orientating to a new location (Laberge, 1973; Posner, 1980; Posner & Cohen, 1984; Rafal & Posner, 1987; Posner & Petersen, 1990; Petersen & Posner, 2012). This scheme accounts for shorter response latencies when the target appears at the expected location, and longer latencies when it appears elsewhere, because in the latter condition, attention has to be disengaged before it is reoriented toward the target (e.g. Posner & Petersen 1990).

While both the information based and attention based viewpoint have been widely influential in the respective field, they are clearly at odds with the implications of several studies indicating that covert and overt orienting rely on shared processes (Rizzolatti et al., 1987; Kowler et al., 1995; Deubel & Schneider, 1996; Godijn & Theeuwes, 2003; Doré-Mazars, Pouget, & Beauvillain, 2004). How can one reconcile these diverging accounts of the computational constraints on covert and overt orienting with the view that the underlying mechanisms are basically identical? Before addressing this issue, we summarize previous evidence regarding the effects of spatial probability on response latencies.

Effects of target probability on response latencies are variable

It seems obvious that an observer's expectation regarding the location of an upcoming target should depend on internal estimates of the target's spatial distribution. Indeed, the importance of learning in shaping spatial expectations was confirmed in highly trained observers, by the finding that visually evoked saccades had briefer latencies when the targets appeared at high than low probability locations, even when the only information about the target' spatial distribution was repeated exposures to the target over thousands of trials (Carpenter & Williams, 1995). Presumably, in this and similar tasks, observers keep a tally of visual events, in order to build an internal representation of a target's spatial distribution (Carpenter & Williams, 1995; Geng & Behrmann, 2005; Bestmann et al., 2008). Moreover, neural correlates of internal estimates of the target spatial probability have been described in both cortical and subcortical structures of highly trained, non-human primates performing visually evoked saccades (Basso & Wurtz, 1998; Churchland et al., 2008) suggesting that representations of the target spatial distribution, shaped by experience, can directly bias processes in the oculomotor centres of the primate brainstem. However, spatial expectations do not only influence preparatory signals, but also which neural circuits may be engaged by a visual target. In fact, participants execute more frequently express saccades, a distinct population of short latency ballistic eye movements generated mostly sub-cortically (Fischer & Ramsperger, 1984), when targets appear at probable than improbable locations (Carpenter & Williams, 1995; Dorris & Munoz, 1998; Haushofer et al., 2002; Schiller et al., 2004). The presence of distinct populations of oculomotor responses, whose frequency is affected by target probability, thus suggests that spatial expectations can determine which neural circuits will be engaged by the target.

Spatial expectations have also been manipulated in simple detection tasks by pre-cueing the target location on every trial (Posner, 1980), or by varying the number of possible target locations (Hick, 1952; Hyman, 1953). These manipulations do not require repeated exposures to the target for the behavioural effects of target probability to be observed. However, cues and the number of possible target locations affect response latencies in ways that are not always consistent with those reported when the target spatial probability is fixed and learned through repeated exposures. For example, as the number of possible target locations is increased, latencies of arm movements show asymptotic rather than linear increments with diminishing target log-likelihood (Corbetta et al., 2000; Pellizzer & Hedges, 2004), or no change at all (Favilla, 1996). Similarly, the latency of visually evoked saccades performed by naïve participants does not change (Kveraga & Hughes, 2002) or, paradoxically, may even decrease (Lawrence et al., 2008) as the number of target location, and hence spatial uncertainty, decreases. Additionally, the effects of target probability on reaching and saccadic latencies can depend on seemingly unrelated factors, such as whether the end-point is instructed exogenously or endogenously (Lawrence, 2010), or whether the fixation point is visible or not at the time of target onset (Carpenter, 1999; Marino & Munoz, 2009). Indeed, a previous study showed that observers, after they had become familiar with the spatial distribution of the target, responded more quickly when the target appeared at a high than a low probability location, indicating that search may be initialized at the expected target location (Geng & Behrmann 2005). When a central cue was introduced, which provided additional information about the target position, additive effects were found possibly suggesting that the effects of cueing were mediated by independent mechanisms.

Comparing the effects of spatial expectations on covert and overt orienting.

The above evidence clearly shows that the effects of target probability on covert and overt orienting can only be adequately compared when testing conditions are closely matched. Therefore to understand the computational constraints on covert and overt orienting, we examined the effects of target probability on saccadic and simple manual detection latencies. The empirical results were compared to predictions of the attentional and information theoretic models. Information theoretic accounts of response selection predict a logarithmic relation between target probability and response latencies (Carpenter & Williams, 1995) while attentional accounts predict that response latencies are either not modulated, or according to the probability matching hypothesis, vary linearly with target probability (Jonides, 1981; Yantis & Johnson, 1990). The latter prediction stems from the conceptualization of attention as a finite state machine, whose basic operations are either performed or not, but cannot otherwise be adjusted. Therefore, the only way target probability can affect the workings of such a mechanism is by changing the probability that a specific operation, such as attending the cued location, will be performed (Jonides, 1981). Specifically, the assumption is that observers will attend the cued location on a proportion of trials, which matches the probability that the target will appear there. Response latencies will therefore depend on the proportion of trials in which the observer attended the high probability location, rather than all locations. In valid trials, for example, response latencies will decrease linearly with increasing cue reliability whereas on invalid trials they will increase linearly with the cue reliability.

The rates of increase and decrease in valid and invalid trials respectively, will be determined by the relative benefits and costs associated with attending the cued location, relative to keeping attention in a diffuse state. Previous studies have suggested that cost and benefits are generally matched, at least following central cues, suggesting that also rates of latency change as a function of cue reliability should be similar for valid and invalid trials (Posner et al., 1980; Theeuwes, 1989). When the target spatial distribution is blocked, a similar prediction follows except that whereas a non informative cue, for example a 50% reliable cue indicating one out of two possible target location, is still predicted to bias attention in 50% of the trials toward the cued side, knowledge that the target appears with equal probability at two possible locations should not bias attention to either side. Despite its simplicity, whether probability matching is able to account for response latencies has not been conclusively established, since previous work used tasks which required fine discriminations in crowded displays (Jonides, 1981; Johnson & Yantis, 1995) and thus confounded effects of spatial expectations on the accumulation of sensory evidence with those on orienting. Both Posner (1980) and Carpenter and Williams (1995) were careful to avoid this confound, by using highly visible targets presented in isolation. Thus diminishing the distinctiveness of the target, either by decreasing its contrast (Carpenter, 2004), adding distractors to the display or changing the task from a simple to a choice detection (Posner et al., 1980), paradoxically decreases the effects of target probability on response latencies.

In the following series of experiments we carried out, highly visible targets were used to minimise the effects of sensory factors on response latencies. Simple detection reaction times and saccadic response latencies were collected, under the same experimental conditions and in separate groups of participants, to allow a direct comparison of the effects of spatial expectancy on covert and overt orienting. Spatial expectations were instructed either by cueing the likely target location, or by blocking the spatial distribution of the target. The target probability was varied over multiple levels to allow us to determine the nature of the relation between the nature of response latencies and target probability. Our results indicate that covert and overt orienting exhibit largely similar effects of spatial expectations whether they were instructed by blocking target probability or by cueing the likely target location, suggesting that in naïve participants the computational constraints on covert and overt orienting are largely shared. Moreover, the effects of target probability on response latencies were not well accounted by simple information theoretic or attentional models of orienting.

Methods

Participants. All participants were right handed naïve observers, with normal or corrected to normal vision, recruited among students at Bangor University School of Psychology. In the first experiment, which investigated the effects of a fixed spatial distribution of the target on simple detection latencies, ten participants (six females) with a mean age of 25 (range: 19-40) were recruited. In the second experiment, which investigated the effects of fixed spatial distribution of the target on saccadic latencies, ten participants (three males) with a mean age of 28 (range: 23-52) took part. Nine participants (four males) with a mean age of 27 (range 22-31) completed the third experiment, which examined the effects of partially valid cues on detection latencies. In the fourth experiment, investigating the effect of partially valid cues on saccadic latencies, nine observers (five males) took part. The mean age was 26 years (range: 19-39). The experimental protocols had been approved by the Ethics Committee at Bangor University, School of Psychology. Participants gave written consent prior to commencing any experimental procedure and received monetary compensation for their time.

Apparatus and procedure. Participants were tested in a dark room. Head position was restrained by a chin and forehead rest. Stimuli were generated and displayed using a custom coded MATLAB™ script and a set of procedures, which allow precise timing of the display and synchronization with the eye-tracker (Brainard, 1997; Cornelissen et al., 2002; Pelli, 1997). Visual stimuli were presented at a distance of 57 cm from the observer, on a 19” Viewsonic G90fB Graphics Series Monitor, set at a 1024 x 768 resolution and a 60 Hz refresh rate. Eye movements were recorded using an infrared camera based Eyelink CL 1000 system (SR Research, Mississauga, Canada), set at a 1000 Hz sampling rate. Calibration took place at the start of each block, using a nine-point calibration and validation procedure. Calibration was considered successful when the error was < 1° of visual angle.

In the first experiment, each trial began when the fixation point turned from black to red for 400ms. The fixation point was visible throughout the trial. This was followed by a non-aging foreperiod, lasting between 600 and 1200 ms. Its duration, namely the stimulus onset asynchrony (SOA), was obtained by sampling the following exponential distribution, with replacement:

$$p(\text{SOA}) = e^{-\frac{\text{SOA}-0.6s}{\tau}} \quad \text{iff } 0.6\text{s}<\text{SOA}<1.2\text{s}$$

else

$$p(\text{SOA}) = 0$$

where $\tau = 0.2$ s.

A bright, highly salient circular target appeared on 95% of trials. The target had a Gaussian luminance profile with a standard deviation of 0.25°, and appeared in one of the four visual quadrants, at an eccentricity of 7° along the main diagonals. The background luminance was 12.75 cd/m^2, and the peak target luminance was 62.4 cd/m^2. Participants were required to press a spacebar whenever the target appeared on the screen, whilst maintaining central fixation. Fixation was monitored using the eye tracker. The target remained visible for 900 ms. An auditory tone indicated the end of the trial and prompted the participant to press the spacebar to initiate a new trial. At this time, a drift correction was performed. In half of the blocks, one of the locations contained the target in 75% of the trials, while each of the other locations contained the target in approximately 8% of the trials. In the other half of the blocks, the four locations were equally likely to contain the target. At the start of each block, participants were informed of the spatial distribution of the target verbally by the experimenter and also by written instruction that appeared prior to the commencement of each block. Each participant took part in three sessions. In the initial training session, participants' performance was monitored, and participants were informed when errors, such as breaks of fixation, occurred. The final two sessions comprised twelve blocks, six for each target probability distribution. Each block consisted of one hundred trials, plus five catch trials.

In experiment 2, the trial structure was identical to experiment 1, except that observers had to fixate the target as quickly as the target appeared or, on catch trials, maintain fixation until the trial was over. In experiment 3 and 4 (see figure 5) the target location was cued by a centrally presented line.

Each trial began when a red diagonal line abutting the fixation point was presented for 400 ms. The trial structure was otherwise identical to the one in blocked probability trials. In half of the blocks, the cue correctly indicated the location of the target in 75% of the trials. In the other half, an uninformative cue correctly indicated the target location on 25% of the trials. Participants were informed of the cue reliability at the start of each block. The order in which blocks containing cues of different reliabilities were presented was alternated and counterbalanced across participants. In all experiments participants were tested on three consecutive days. The first session comprised two training blocks of one hundred trials, one for each level of cue reliability. During the training session, subjects' performance was monitored by the experimenter who emphasized timely and accurate responses, while discouraging anticipatory saccades. The other two experimental sessions comprised a total of twelve blocks of one hundred and five trials each. No feedback was given during these sessions. Experiment 3 required participants to press a key as soon as the target appeared, whereas in experiment 4 participants had to foveate the target as soon as it appeared.

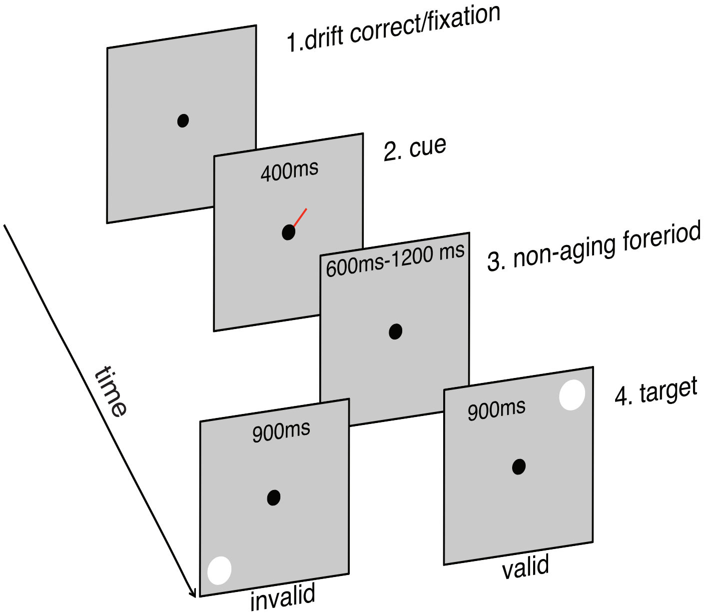

Figure 5. Schematic illustration of the experimental paradigm used in experiments 3 and 4. 1) Subjects maintained fixation on a central fixation point. 2) A red central cue was then displayed for 400ms, which indicated the likely location of the subsequent target. The cue reliability was varied over two levels, 25% and 75% valid. 3) Following a non-aging foreperiod, 4) the target stimuli appeared.

Data analysis. For each experiment, a total of 1200 trials were collected from each participant over the last two testing sessions; except for the cued and blocked probability saccadic experiments, where due to a technical error, 1100 trials were collected from one of the participants in both instances. Saccadic latency was defined as the period between target onset and initiation of the saccade. Correct responses were defined as saccades starting within 2° of the central fixation point and landing within 2° of the target. Only the first saccade made in a trial was analysed. Saccadic latencies briefer than 80 ms and longer than 800 ms were excluded from further analysis. The oculomotor traces for each trial were visually inspected, and trials containing artefacts or blinks were discarded. Overall, in experiment one 90% of trials, and in experiment three 97% of trials were used in the group analysis. When a manual response was required, responses briefer than 150 ms or greater than 800 ms were excluded from further analysis. Oculomotor traces for each individual trial were examined and trials containing artefacts, such as blinks, or saccadic responses to the target were discarded. Overall, 94% and 95% of trials were used for the analysis in the second and fourth experiments respectively. Finally, to remove outlier responses, for each participant and condition latencies were calculated by averaging 10,000 bootstrapped estimates of the median latency.

Separating express from regular saccades. In order to examine the effect of spatial expectations on the distribution of saccadic latencies, we estimated the proportion of express and regular saccades and their mean latencies. A maximum likelihood procedure was used to obtain separate estimates of the mean and spread of the reciprocal values of regular and express saccadic latencies distributions, which was similar to a previously published analytical protocol (Guan et al., 2012). The steps taken to perform the de-convolution of the latencies distribution included computing the reciprocal saccadic latencies lat^{-1} and then fitting a mixture model, which assumed the overall distribution of reciprocal saccadic latencies reflected the mixture of two Gaussian distributions N, which differed in their location and spread:

$$p\left(lat_i^{-1} \middle| m, \overline{lat_{\mathrm{reg}}^{-1}}, \sigma_{\mathrm{reg}}, \overline{lat_{\mathrm{exp}}^{-1}}, \sigma_{\mathrm{exp}}\right) = m \cdot N\left(\overline{lat_{\mathrm{reg}}^{-1}}, \sigma_{\mathrm{reg}}\right) + (1-m) \cdot N\left(\overline{lat_{\mathrm{exp}}^{-1}}, \sigma_{\mathrm{exp}}\right)$$

Thus, we estimated five parameters: the proportion of regular saccades, m, the average reciprocal latencies, $\overline{lat^{-1}}$, and standard deviations, σ, of the distributions of regular, lat_{reg}, and express, lat_{exp}, saccadic latencies, respectively, by maximizing the log-likelihood Λ, of the data.

$$\Lambda\left(lat_{1\ldots n}^{-1} \middle| m, \overline{lat_{\mathrm{reg}}^{-1}}, \sigma_{\mathrm{reg}}, \overline{lat_{\mathrm{exp}}^{-1}}, \sigma_{\mathrm{exp}}\right) = \sum_{i=1}^{n} \log\left[p\left(lat_i^{-1} \middle| m, \overline{lat_{\mathrm{reg}}^{-1}}, \sigma_{\mathrm{reg}}, \overline{lat_{\mathrm{exp}}^{-1}}, \sigma_{\mathrm{exp}}\right)\right]$$

When the average latency of express saccades was estimated to be greater than 140 ms, suggesting that the latencies distribution included no express saccades, the model was simplified and made to include a single distribution of regular saccades, with m=1.0.

Group level statistics were calculated after normalizing the estimated probability of regular saccades, for each participant, using the inverse sine of the square root transformation. Latencies of express saccades were not further analysed at the group level, since no express saccades were effectively found in a number of participants and conditions.

Results

Overview of the analysis and models' predictions

We report the reaction times of covert and latencies of overt orienting responses when spatial expectations were either instructed by i) blocking the target spatial distribution (manipulating the probability of where the target would appear across blocks) or ii) using a central cue to indicate likely location of the target. Our aim is to compare these results to the predictions of information theoretic and attentional, probability matching models of orienting in order to establish which of the two models are able to account for the results. While the information theoretic model's predictions are determined simply by the target spatial probability, the predictions of the probability matching model depend also on how target probability is instructed: the reason is that when all locations are equiprobable, according to the probability matching model, attention will be kept diffuse in every trial when the spatial target probability is blocked. However, following a cue, attention will be focused at the cued location in a proportion of trials matching the target probability, even following uninformative cues. The implication is that when the target spatial distribution is blocked or its likely location cued, the latency difference between responses to high probability and equiprobable targets should be the same as the latency difference between equiprobable and low probability targets, if the costs and benefits of breached and met expectations, respectively are matched. However, following uninformative cues, the probability matching model predicts a validity effect whilst the information theoretic account does not.

Effects of blocked probability on reaction times

In experiment 1, we examined the effects of blocking the spatial probability of the target on simple detection reaction times. Two levels of probability were used. The target was either equally likely to appear at each of four eccentric locations or it had a probability of .75 of appearing at one of the four locations and approximately .08 of appearing at each of the other three locations. Figure 6A shows the overall, group averaged reaction times as a function of target probability. A one-way, repeated measures ANOVA indicated that target probability had a significant effect *F*(2, 18) = 20.86, *p* > .001, *ηp2* = 0.70, reaction times being faster to targets appearing at probable (probability = .75) than equiprobable (probability = .25) or improbable (probability ≈ .08) locations, Moreover, figure 6B shows that the reaction time difference between low probability and equiprobable targets was greater in size than the difference between equiprobable and high probability targets *t*(9)= -2.769, *p* = .02, *d' = -0.88*. The finding is inconsistent with both the information theoretic account, which predicts that the latency differences should be identical, and the attentional accounts, which predicts that the latency difference should be equal if the cost and benefits are matched.

Effects of blocked target spatial probability on saccadic latencies

In experiment 2 we examined the effects of blocking the spatial probability of the target on saccadic latencies. The experimental conditions were exactly matched to those used in experiment 1, except that participants were instructed to foveate the target as soon as the target appeared. Group averaged saccadic latencies are shown in figure 6C. Moreover, to discount the effects of target location on saccadic latencies (see below), latencies to high and low probability targets were rebased using the latency values obtained in trials in which targets appeared at the same locations during the equiprobable blocks. Figure 6D shows that target probability had a significantly greater effect on saccadic latencies to low probability than high probability targets, since the latency difference between responses to high probability and equiprobable targets was smaller than the difference between equiprobable and low probability targets *t*(9) = 4.89, *p* < .001, *d'* = 1.54. This finding is again inconsistent with the predictions of the attentional model and information theoretic models, which predict an equally sized difference.

Finally, a mixed factor was used to examine whether covert and overt orienting showed differences in the effects of target probability. As expected there was an overall effect of probability *F*(1, 18) 34.085, p < .001, *ηp2* = 0.65, although the interaction between probability and response type *F*(1, 18) = 0.004, *p* = .950, was not significant, consistent with the impression that differences between tasks were, if present, minimal.

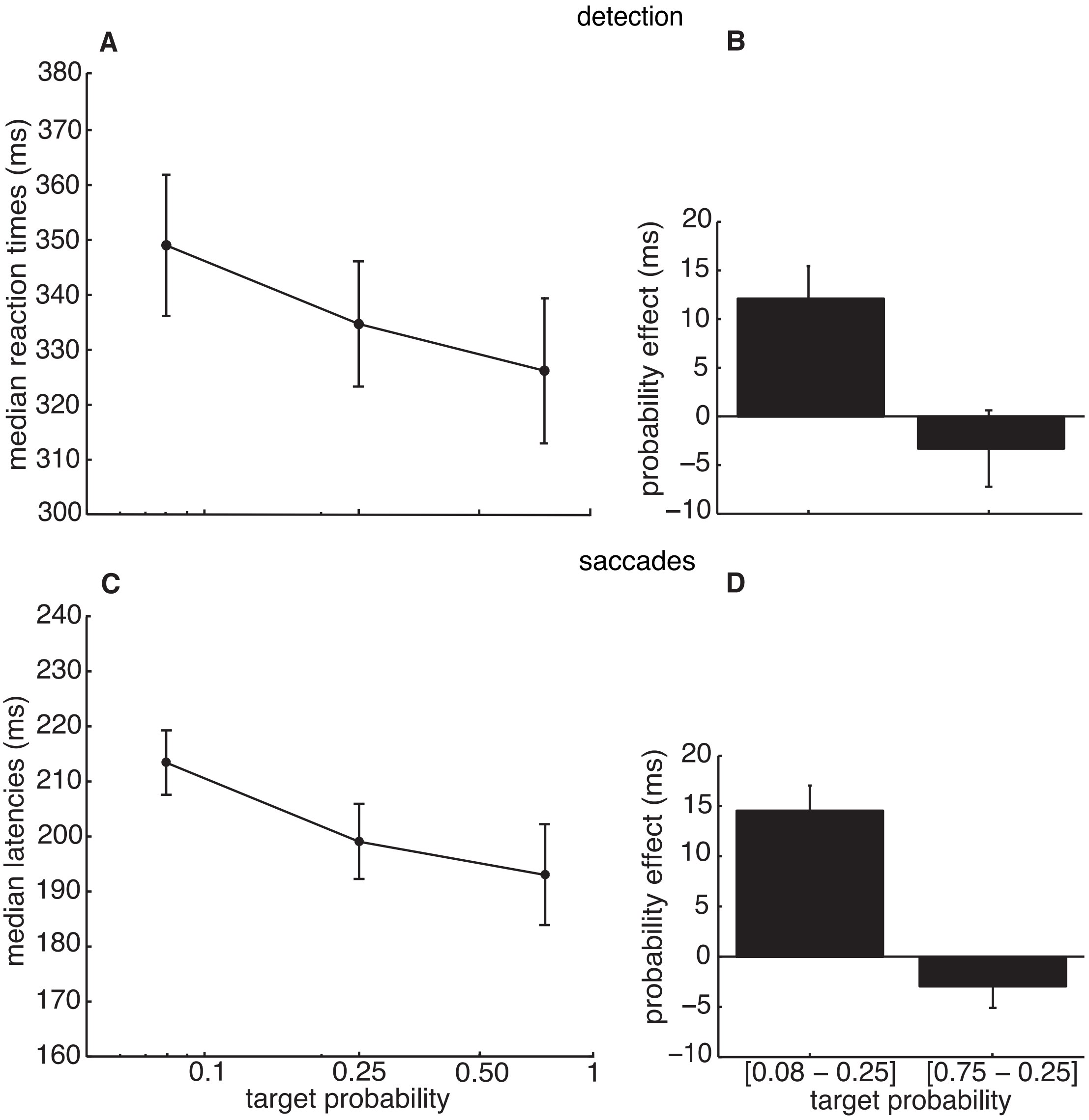

Figure 6. Blocked target probability effects on manual and saccadic latencies. **A**. Group averaged saccadic latencies are plotted as a function of the target log-likelihood. **B.** Group averaged differences between saccadic latencies to high probability and equiprobable targets, and between low probability and equiprobable targets. **C.** Group averaged manual responses latencies are shown as a function of target probability. **D.** Group averaged differences between latencies to high probability and equiprobable targets, and low probability and equiprobable targets. Error bars represent standard error of the mean.

Target probability mainly affects regular saccades latencies

Humans can generate saccades with very brief latencies, so called express saccades (Fisher & Weber, 1993). In order to understand the contribution of express saccades to the effects of target probability, we estimated the proportion of express saccades and the median latency of express and regular saccades for each target probability level. A repeated measures ANOVA was used to assess the effects of spatial probability on the proportion of express saccades and regular saccades latencies. The group Averaged proportion of express saccades when targets appeared at the high probability location was 0.07, at equiprobable locations 0.04, and the low probability location 0.01. While this data suggest that express saccades were more likely to high than low probability targets, this effect was not significant *F*(2, 18) = 1.75, *p* = .202. On the other hand, the group averaged latency of regular saccades to high probability targets was 190 ms (SD = 22.5 ms), to equiprobable targets 196 ms (SD = 14.4ms), and to low probability targets 209 ms (SD = 13.5 ms). The effect of target probability on the latency of regular saccades was significant *F(2, 18)* = 7.914, *p* = .003, *ηp2* = 0.47. These data suggest that most of the effects of blocked target probability on saccadic latencies were attributable to modulations of the latency of regular saccades rather than changes in the proportion of express saccades.

Effects of target probability and validity on manual reaction times

In experiment 3, we examined the effects of cueing the likely target location on simple manual reaction times. The cue was a central line pointing to one of four eccentric locations. Two levels of cue reliability were used. The cue reliability was either 25%, and the cue did not provide any information about the upcoming target location, or 75%, and the informative cue indicated the location containing the target on 75% of the trials. Both cue types resulted in trials in which the target appeared at the cued location (valid trials) and at an uncued locations (invalid trials).

Figure 7A shows the group averaged median latencies on valid and invalid trials for the two levels of cue reliability. The effect of cue validity on reaction times was highly significant *F*(1, 8) = 21.53, *p* < .002, *ηp2* = 0.73, being longer to invalidly than validly cued targets. The effect of cue reliability was not significant *F*(1, 8) = 2.91, *p* < .127. The interaction between cue validity and cue reliability was also significant *F*(1, 8) = 8.45, *p* < .02, *ηp2* = 0.51, indicating that the size of the validity effect was affected by the reliability of the cue. Lastly, figure 7B shows that a significant validity effect was found even when the cue reliability was 25% and the cue was uninformative *t*(8) = -3.181, *p* < .013, d’ = -1.06, suggesting that cue validity and target probability may exert partly independent effects. Moreover, the validity effects were about three times larger following high reliability than low reliability cues, consistent with the probability matching, attentional model, which predicts a threefold change in the size of the validity effect for a threefold change in cue reliability. The probability matching model could account for the validity effects following uninformative, 25% reliable cues, as it assumes that on these trials the participant will attend the cued location on 25% of the trials and attend all locations on the remaining 75% of the trials. On the other hand, the latency differences between valid trials following 25% and 75% reliable cues were larger than the latency difference between invalid trials following 25% and 75% reliable cues *t*(8) = -2.825, *p* = .022, *d'* = -.094, contrary to both the information theoretic and probability matching models' prediction that these differences should be identical.

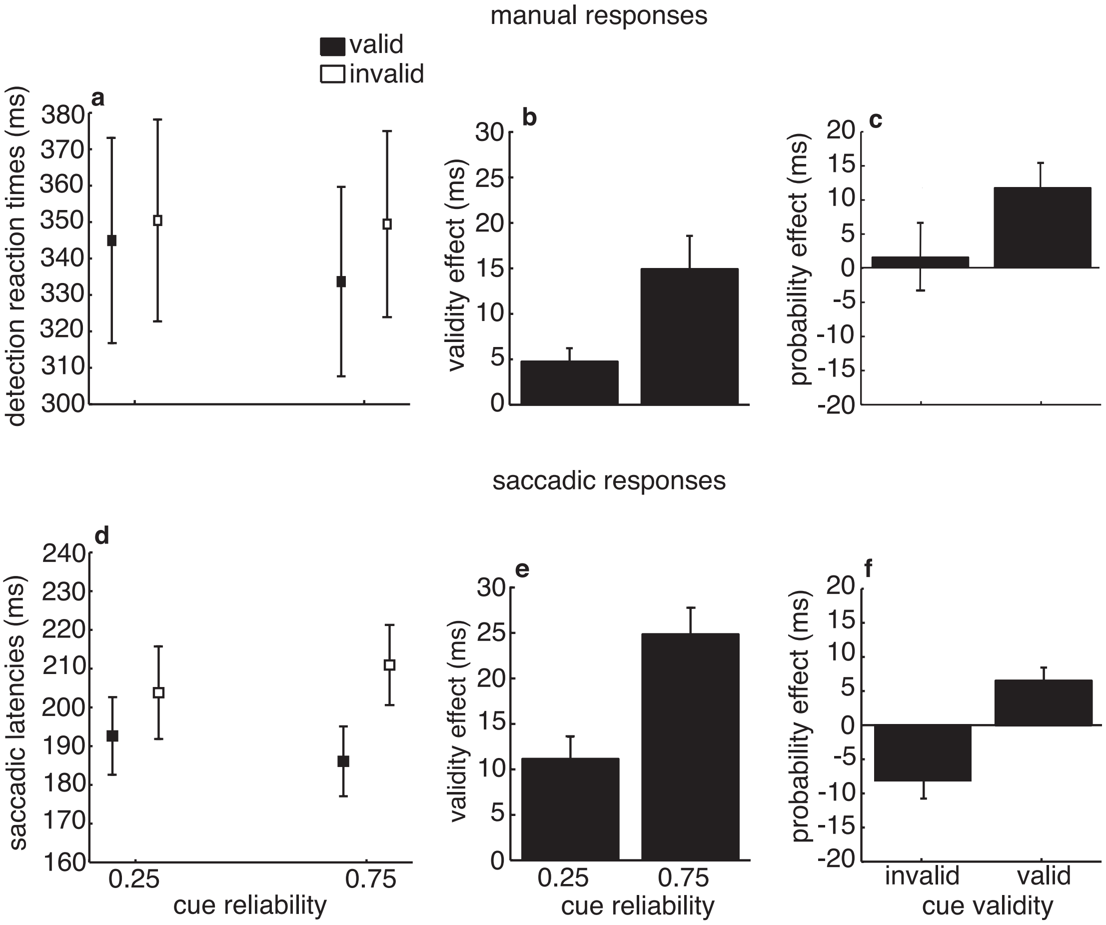

Figure 7. Manual and saccadic latencies following probabilistic, central cues. **A.** Group averaged manual latencies are shown by cue reliability and validity. **B.** The size of the validity effect was calculated separately for valid and invalid trials by subtracting response latencies following 75% and 25% reliable cues. **C.** The size of the probability effect was calculated by subtracting manual latencies following 25% reliable cues from latencies following 75% reliable cues, separately on valid and invalid trials. **D.** Group averaged saccadic response latencies are shown by cue reliability and validity. E. The validity effect was calculated separately for the two levels of cue reliability by subtracting response latencies on invalid from valid trials. **F.** The size of the probability effect was calculated separately for valid and invalid trials by subtracting saccadic response latencies following 25% reliable cues and 75% reliable cues.

Effects of cue validity and target probability on saccadic latencies

In experiment 4, we examined the effects of cueing the target location on saccadic latencies. The same testing procedure used in experiment 3 was utilized here, except that participants were instructed to foveate the target as soon as it appeared. Figure 7D shows the group averaged median latencies on valid and invalid trials for the two levels of cue reliability. The effect of cue validity was highly significant $F(1,8) = 47.39$, $p < .001$, $\eta p2 = 0.86$, longer latencies being observed on invalid than valid targets. The main effect of cue reliability was not significant $F(1, 8) = 0.03$, $p = .874$, but the interaction of validity by cue reliability was $F(1, 8) = 97.89$, $p < .001$, $\eta p2 = 0.92$. A paired samples t-test confirmed that the magnitude of the validity effect was modulated by the reliability of the cue, $t(8) = 9.89$, $p < .001$, $d' = 3.30$, and, by extension, target probability. Additionally, a significant validity effect was found following uninformative, 25% reliable cues $t(8) = -4.50$, $p < .002$, $d' = -1.47$, with shorter latencies on valid than invalid trials. Saccadic latencies, following central cues, were affected by the target probability in a manner consistent with the predictions of both models. They also demonstrated an effect of validity following uninformative cues, which is inconsistent with information theoretic accounts. A three-way, repeated measures mixed ANOVA was used to compare the effects of cueing on covert and overt orienting. The repeated factors were cue reliability (75% vs. 25%) and validity (valid vs. invalid), the between subject factor was task (covert vs. overt). There was a significant effect of validity $F(1, 16) = 67.809$, $p = < .001$, $\eta p2 = 0.81$, but no overall effect of cue reliability $F(1, 16) = 1.714$, $p = .209$. The interactions between validity and cue reliability $F(1,16) = 38.628$, $p < .001$, $\eta p2 = 0.71$, and validity and task $F(1, 16) = 5.011$, $p = .04$, $\eta p2 = 0.24$, were significant, the magnitude of the validity effect, as shown in figure 7B and figure 7E being larger on overt than the covert orienting. The three-way interaction was not significant $F(1,16) = 0.731$, $p = .405$.

Cueing effects on express saccades

We examined the effects of target validity and target probability on the proportion of express and regular saccades as well as the latency of regular saccades. Two-way, repeated measures ANOVAs were used to assess the effect of cue reliability and validity on the proportion and mean latency of regular saccades. Figure 8 shows the group averaged proportion of regular saccades for valid and invalid targets following 25% and 75% reliable cues. Validity had a significant effect on the proportion of express and regular saccades $F(1, 8) = 20.97$, $p = .002$, $\eta p2 = 0.72$, express saccades being more frequent in valid than invalid trials. Neither cue reliability, $F(1,8) = 2.30$, $p = .168$, while the interaction of reliability by validity affected the proportion of express saccades only marginally $F(1,8) = 3.76$, $p = .089$, $\eta p2 = 0.32$.

The group averaged mean latencies of regular saccades are shown in figure 8B. There was a significant effect of cue validity $F(1, 8) = 24.32$, $p = .001$, $\eta p2 = 0.75$, the latencies of regular saccades being shorter to valid than invalid targets. There was no significant effect of cue reliability *F*(1, 8) = 0.51, *p* = .494, but there was a significant interaction between cue validity and reliability *F*(1, 8) = 5.65, *p* = .045, *ηp2* = 0.41. We conclude that target validity affected both the proportion and the latency of regular saccades, while target probability affected the latency of regular saccades, but had negligible effects on the proportion of express saccades. We conclude that cueing causes larger validity effects on overt than covert orienting, partly because validity affects the proportion of express saccades.

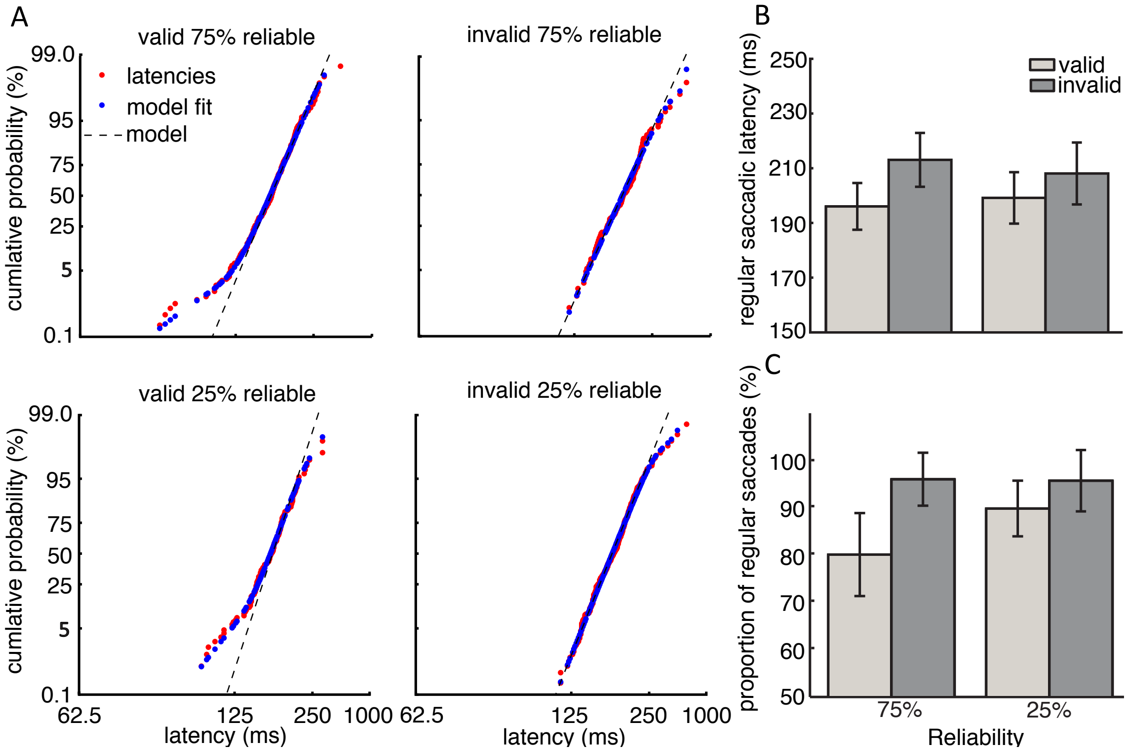

Figure 8. Effect of cue reliability and validity on the proportion and latency of regular saccades. **A.** Reciprobit plots illustrate the cumulative distribution of saccadic latencies following both informative (75% reliable) and non-informative cues (25% reliable), on valid and invalid trials for one representative subject. Red and blue circles represent, respectively, latencies on a single trial and the model fits. The dash line represents the estimated distribution of regular saccades latencies**. B.** Group averaged estimates of regular saccadic latencies as a function of cue reliability and validity. **C.** Group averaged estimates of the proportion of regular saccades as a function of cue reliability and validity. Error bars show the standard error of the mean.

Saccadic latencies, but not detection reaction times, show spatial anisotropies

We found that target location affected the latency of saccadic, but not detection responses both when the target spatial distribution was blocked and cued. These results are reported next. A two-way ANOVA was used to examine the effect of target location in the blocked conditions. The first factor was the vertical location of the target, i.e. lower vs. upper visual field; the second was its horizontal location, i.e. left vs. right visual field. In the detection task, reaction times were not significantly modulated either by the vertical $F(1, 9) = 1.09$, $p = .32$ or horizontal $F(1, 9) = 0.53$, $p = .49$, position of the target nor by the interaction $F(1, 9) = 0.001$, $p = .91$. However, saccadic latencies showed a significant effect of the target vertical position $F(1, 9) = 70.41$, $p < .001$, $\eta p2 = 0.89$, saccadic latencies being longer for targets in the lower (m = 214 ms, SD = 18.78 ms) than upper visual field (m = 184 ms, SD = 21.39 ms). The horizontal position did not have a significant effect $F(1, 9) = 0.94$, $p = .357$, nor the interaction of vertical and horizontal target position $F(1, 9) = 0.042$, $p = .843$.

A three-way, repeated measures ANOVA was used to examine the effect of target location and validity on responses following central cues. The first factor was the vertical location of the target, the second factor was its horizontal location, the third factor was cue validity. In the detection task, there were no significant reaction time differences $F(1, 8) = 2.37$, $p = .162$, for targets appearing in the upper versus lower visual field. Additionally, there was no significant effect of the horizontal target location, $F(1, 8) = 1.288$, $p = .289$. As expected, there was a significant effect of cue validity $F(1, 8) = 35.121$, $p < .001$, $\eta p2 = 0.81$. The interaction between the horizontal and vertical position, $F(1, 8) = 0.041$, $p = .845$, the horizontal position and validity $F(1, 8) = 1.273$, $p = .292$, vertical position and validity $F(1, 8) =1.627$, $p = .238$, and the three-way interaction $F(1, 8) = 1.06$, $p = .333$, were all not significant. In the saccadic task, there was a highly significant effect of the vertical position of the target $F(1, 8) = 33.153$, $p < .001$, $\eta p2 = 0.81$, with shorter latencies when the target appeared in the upper (m = 185 ms, SD = 31 ms) than the lower visual field (m = 208 ms, SD = 30 ms). The effect of the target horizontal position was nearly significant, $F(1, 8) = 5.09$, $p = .054$, $\eta p2 = 0.39$, with shorter latencies for targets in the left (m = 193 ms, SD = 31 ms) than right visual field (m = 199 ms; SD = 33 ms). The interaction between the horizontal and vertical position, $F(1, 8) = 1.974$, $p = .198$, the interaction of the horizontal position and validity $F(1,8) = 2.03$, $p = .192$, vertical position and validity, $F(1, 8) = 0.552$, $p = .479$, and the three-way interaction $F(1, 8) = 0.430$, $p = .530$, were all not significant. We conclude that saccadic latencies, but not detection reaction times, show effects of target location. These effects do not interact with those of target probability and validity.

Discussion

Spatial expectations affect orienting when observers respond to the onset of visual stimuli. The finding that animals faced with unexpected sensory stimuli exhibit a complex, but stereotypical set of responses (Pavlov, 1927), liable to the effects of repeated exposures (Sokolov, 1963) and that the spatial probability of a target affects detection reaction times, lead to the proposal that spatial expectancies engage specific preparatory processes (Posner, 1980; Posner et al., 1982). These were envisioned as sequentially organized operations aligning an attentional vector with the expected target location (Posner & Petersen, 1990). This view has been highly influential in the field of visual attention and has lead, for example, to a number of specific neuroanatomical models of visual attention (Posner & Petersen, 1990; Corbetta & Shulman, 2002).

A separate conceptualization of response selection and overt orienting draws from basic insights into the nature of information and its transmission (Shannon, 1948). These ideas lead to the finding that the time taken to make the instructed response, following an imperative stimulus, varies with either the initial number of response alternatives or the precision of the response required (Hick, 1952; Hyman, 1953). This suggests that response latencies reflect central procedures that incrementally select the response to be made from a pre-specified script of response alternatives, the greater the initial uncertainty and therefore the amount of information required to uniquely specify the response, the longer the reaction time. The finding that latencies increase logarithmically with the number of alternatives was taken as evidence that information may be coded similarly in the brain and digital circuits. While the generality of this phenomenon has been challenged and response distributions more consistent with analogical processes have been reported (e.g. Pellizzer & Hedges, 2004; Kleiner et al., 2007), others have endorsed this computational view of response selection. In a seminal study, Carpenter and Williams (1995) examined the latency distribution of visually evoked saccades under conditions in which the spatial probability of a target was manipulated directly, rather than by changing the number of possible target locations. A simple race to threshold model of the neural activity was proposed, which could replicate the distribution of saccadic latencies as a function of target probability. One crucial feature of the model was that preparatory, baseline activity varies with the logarithm of the target probability, in accordance with neurophysiological evidence regarding the coding of spatial expectancies in subcortical and cortical structures (Basso & Wurtz, 1994; Churchland et al., 2008). These information theoretic models, which regarded decision making in the brain as a two stage computation, first the uncertainties of the response set are computed and, once the target appears, the response is specified by transmitting information along a limited capacity channel, also maps quite naturally into the idea, popularized more recently, that the brain computes perceptual and motor decision by combining expectancies with sensory data to maximize the likelihood of a correct response (e.g. Gold & Shadlen, 2007).

One crucial difference between attentional and information theoretic conceptualizations is that the former has a limited ability to track changes in target probability, except if one assumes that observers engage in probability matching (Jonides, 1981), attending the likely target location in some and maintaining attention in a diffuse state, in the remainder of the trials. Thus an obvious way to distinguish between the two models is to examine the effects of target probabilities on orienting responses. Accordingly, the former model would predict response latencies that are either independent of target probabilities or, if the observer matches the target probability, vary linearly with target probabilities. Whereas the information theoretic account would predict that response latencies vary logarithmically with target probabilities.

Target spatial probability affects covert and overt orienting

When participants oriented covertly and overtly to targets appearing at locations of varying probabilities, responses were briefer for targets at likely than unlikely locations, suggesting that target probabilities shaped spatial expectations. Although detection reaction times were consistently slower than saccadic latencies, the effects of target probability on covert and overt orienting were similar in magnitude, suggesting that target probability effects arose independently of central and biomechanical constraints specific to covert and overt orienting responses. Interestingly, the effects of target probability on overt responses were larger for low probability than high probability targets, relative to equiprobable targets. This finding is inconsistent with both the attentional, probability matching model, if one assumes that the benefits of attending the cued location on valid trials match the costs of attending the cued location on invalid trials, as well as the information theoretic model, since the both predict equally sized effects. Nevertheless this finding is not novel. Already (Posner et al. 1980) reported greater spatial expectancy effects on low than high probability targets, relative to equiprobable targets, when the target spatial probability was blocked. Similarly, when the reliability of central cues is learnt implicitly from sequential exposures to several cue-target pairings (Daunizeau, Bauer, Driver & Friston, 2014), or the reliability of the cued is explicitly communicated to the participant and the time taken to identify a poorly visible target is measured (Giordano et al., 2009), target probability effects are found to be greater on low, invalid than high probability, valid trials. These data suggest that target probability may affects processes specifically engaged when spatial expectations are violated by invalid or low probability targets. A number of explanations have been put forward to account for the greater cost of breached expectations. These have included habituation to repeated stimuli (Sokolov, 1963), or the need to interrupt on-going neural processes in order to examine a novel, unexpected target, (Corbetta & Shulman, 2002; Pavlov, 1927) or the disengagement of visual attention from the currently attended location to examine the location containing the target (Laberge, 1973). Regardless of the exact reason for the disproportionally large cost found when orienting to low probability targets, an imaging study recently examined the consequences on preparatory neural activity of the probability that an endogenous signal will instruct either to maintain attention at the current location or shifting attention to the contralateral side (Shulman et al., 2010). It was found that when the instruction is to shift attention the effects of the instruction probability on BOLD signals evoked in frontal and basal ganglia regions is much greater than when the instruction is to maintain attention. This suggests that disengagement of attention and shifting attention may be specifically modulated by probability, in agreement with the results from the blocked probability experiments.

Cueing affects differentially saccadic and detection latencies

Participants were faster to orient to and detect supra-threshold visual targets, when they appeared at cued than uncued locations, suggesting that observers used the cue when preparing to respond to an upcoming target (Posner, 1980; Jonides, 1981**).** Furthermore, cueing effects on detection and saccadic latencies were modulated by the cue reliability, suggesting that target probability affected preparatory processes engaged by the cue. Saccades showed a 8ms latency difference between valid targets that followed a 75% reliable cue and a 25% reliable cue. A similar difference was found for invalid targets. Since the difference in target log-likelihood following high and low reliability cues was equated for valid and invalid targets, this result is consistent with the predictions of the information theoretic model, and the probability matching model. This latency difference is smaller than previously reported in a study using highly practiced participants, a three fold change in target probability resulting instead in a 30 to 50ms change in response latency (see Table 1 in Carpenter & Williams, 1995), but closer to values reported in later studies (Carpenter, 2004). Moreover, we found a validity effect in both the covert and overt orienting task following low reliability cues, when the target was equally likely to appear at any of the four locations. This latter finding is inconsistent with the predictions of the information theoretic account and with the long held view that central cues engage attention only when they provide task relevant information (Jonides, 1980). However, a number of authors have found that symbolic cues can engage attention even if uninformative (Eimer, 1997; Tipples, 2002). Various reasons have been invoked to account for this effect, including that central cues engage top-down processes, which then lead to both voluntary and automatic orienting (Kuhn & Kingstone, 2009). Alternatively, the validity effect following uninformative cues could simply reflect a probability matching strategy.

Covert orienting response latencies were affected by target probability more so in valid than invalid trials, the latter showing little if any effect of target probability. This finding is neither consistent with the attentional, probability matching model, nor the information theoretic model, since both predict equally sized probability effects on valid and invalid trials. Additionally, the size of the validity effect on covert orienting response latencies approximately tripled following highly reliable cues compared to low reliability cues, which is consistent with the attentional, probability matching model. Saccadic latencies showed similar validity effects. However, the size of the validity effect was larger in the overt than covert orienting task, following both low and high reliability cues (see figure 7). This difference is likely accounted by fact that in the overt orienting task express saccades are made more frequently to valid than invalid targets, while in the covert orienting tasks there is no separate population of express, short latency responses (data not shown, but see Bekkering & Abrams, 1996; Pratt & Nghiem 2010 for extensive analysis of response distribution in manual and saccadic tasks).

Overall, our data can be taken to imply that the central constraints on covert and overt orienting are largely shared, albeit their computational nature is incompletely captured by both information theoretic and probability matching models. Differences between the effects of target probability and validity on covert and overt orienting latencies could then be interpreted conservatively, by assuming that processes specific to overt, but not covert orienting, exists which are also amenable to cueing effects. This proposal is consistent with independent observations indicating dissociable effects on response latencies in covert and overt orienting tasks when experimental manipulations which specifically affect the proportion of express saccades are introduced (Bekkering & Abrams, 1996; Pratt & Nghiem, 2010). A straightforward account for the limited differences we found between covert and overt orienting in experiments, where the target spatial distribution was instructed by a cue, would then be that overt orienting can recruit neural short-cuts leading to express saccades, when responses to highly expected targets are elicited, however, we cannot exclude that other differences may be present as well: we found faster saccadic latencies to targets presented in the upper than lower visual field, confirming previous observations in both human participants (Heywood & Churcher, 1980) and non-human primates (Schlykowa et al., 1996). We did not find a difference in detection reaction times when targets appeared in the upper versus lower visual field, nor was the effect of target location on saccadic latencies modulated by cue validity, leading us to conclude that the effects of target location on saccadic latencies are purely oculomotor. However, our conclusion differs from that drawn on the basis of data obtained in non-human primates by Zhou and King, 2002*,* who suggested that this spatial anisotropy may reflect a orienting effect, having found smaller validity effect for vertical than horizontal saccades made to exogenously cued targets.

Target probability effects depend on behavioural context

A potential account of the differential effect on response latencies, of blocking the target spatial distribution and manipulating the reliability of a central cue can be drawn from the body of work concerning choice behaviour under risk. These studies have shown that the internal representation of probability and utility is frequently biased in human participants, and shaped by the manner in which expectations and financial prospects are instructed (e.g. Allais, 1953; Kahneman & Tversky 1979). Indeed, comparison of our data to data obtained under conditions in which the target probability was manipulated by changing the number of possible target locations is supportive of this suggestion. Both arm (Favilla, 1996; Dassonville et al., 1999; Pellizzer & Hedges 2003; Pellizzer and Hedges 2004) and saccadic eye movements (Heywood & Churcher 1980; Kveraga & Hughes, 2002) display latencies, which plateau as the stimulus probability decrease. Paradoxically, saccadic latencies can even decrease as target probability decreases (Lawrence et al., 2008; Lawrence & Gardella, 2009). These effects depart considerably from those demonstrated here, especially when blocking the target spatial distribution. This discrepancy has no plausible explanation other than to conclude that spatial expectations and the preparatory processes which depend on them are shaped by the way possible outcomes are presented.

Chapter three

Distractors are suppressed during reorienting to invalidly cued targets: support for the filtering hypothesis

Abstract

The finding that the same brain regions deactivated by distractors, respond prominently to invalid targets, lead to the hypothesis that distractors are prevented from capturing attention by increasing the selectivity for the target defining feature of reorienting mechanisms (Shulman et al., 2004). On the other hand, whether endogenous spatial attention can prevent distractors capturing attention remains contentious. We examined detection reaction times and saccadic latencies following central cues. Cues indicated either the target or a distractor's likely location. Distractors slowed orienting, except when the target was invalidly cued. Cueing the distractor lead to faster responses, when a distractor or the target appeared at the cued location. Finally, orienting was faster when the previous several trials contained a target than when they did not. Smaller, but spatially specific effects were also found for the distractor. We conclude that, 1) when reorienting to invalidly cued target, distractors do not capture attention, in keeping with the filtering hypothesis; 2) cueing the distractor does not lead to inhibition of the cued location; 3) orienting is facilitated by a slowly decaying tonic signal, associated with previously observed stimuli.

Introduction

Processing of sensory data is constrained by slow neural processes of limited capacity. To accommodate these limitations, human observers are thought to prioritize those elements of the sensory array relevant to their current behavioural goals, leading, for instance, to faster responses to attended than unattended stimuli (Bundesen, 1990). These prioritizing processes have been commonly identified with attention (Carrasco, 2011).

Mechanisms of attention

The facilitatory effects of attention on sensory and motor processes are well documented. For example, faster and more accurate responses are found for visual targets appearing at expected than unexpected locations (e.g. Posner, 1980; Jonides, 1981; Posner, Snyder & Davidson, 1980; Carpenter & Williams, 1995; Geng and Behrmann, 2005). When the target is highly visible and appears without competing distractors, valid cues are thought to affect behavioural performance by facilitating the motor response, which requires attention to be deployed at the location of the imperative stimulus (Posner, 1980). Others have suggested instead that spatial expectations shorten response time by lowering the decision threshold, required to generate a directional response to a highly visible target (Carpenter & Williams, 1995). Under conditions of low target visibility, attention may increase the apparent contrast of a target (Carrasco, Penpeci-Talgar & Eckstein, 2000) and its resolution (Carrasco, Williams, & Yeshurun, 2002), implying that attention can change the grain of sensory sampling. In the presence of distractors attention may diminish their interference on sensory and decision processes (e.g. Desimone & Duncan, 1995; Dosher & Lu, 2000). A number of these proposals can be captured using well-established analogies. For example, attention may act as an internal s*potlight* or a *zoom lens*, which highlights internal representations of selected parts of the visual scene to the exclusion of the remainder (Eriksen & St James, 1986; Eriksen & Hoffman, 1972).

Distractor suppression: automatic vs. voluntary effects

The proposals listed above insinuate that ignoring particular locations, objects, or features, is simply a consequence of not being selected. Nevertheless, inhibitory mechanisms are known to be important in the deployment of attention. For example, inhibitory interactions among homogenous distractors diminish their saliency, while increasing the saliency of odd elements, in a purely bottom-up fashion (Koch & Ullman, 1987). There is also recent evidence for top-down control of inhibitory processes. For example, distractor interference is diminished when the display is expected to contain distractors, compared to when it is not (Awh, Matsukura & Serences, 2003).

Posner and Klein (1984) were the first to report spatial inhibition of orienting, having found that detection reaction times were delayed when the target appeared at a location where an exogenous cue had previously been shown. They suggested that previously attended locations are inhibited (Klein, 2000). Others have shown that the processing of target stimuli is slowed when they share visual features with distractors shown in preceding trials (Tipper, 1985; Tipper & Cranston, 1985). This phenomenon may indicate that distractors and their features are actively inhibited and that this inhibition lingers into the next trial.

Like facilitatory mechanisms, some studies have suggested that inhibitory mechanisms can be engaged voluntarily ahead of the main stimulus (e.g. Munneke, Van der Stigchel, & Theeuwes, 2008; Van der Sitgchel & Theeuwes, 2005; Ruff & Driver, 2006). For example, a *preview benefit* is observed in conjunction search tasks. When observers are shown distractors prior to the display containing the target, the previewed distractors have minimal effects on search times (Watson & Humphreys, 1997), suggesting that previewed distractor locations are inhibited. However, other accounts of this phenomenon have been offered that do not invoke spatial inhibition (Donk & Theeuwes, 2003; Pratt, Theeuwes, & Donk, 2007). Munneke, Van der Stigchel, and Theeuwes (2008) found a reduced flanker compatibility effect, when flankers appeared at the location cued by a central arrow, suggesting that observers voluntary inhibited cued locations and therefore experienced diminished interference when distractors appeared there**.** However, cues sped up responses to both congruent and incongruent trials, suggesting that cues had additional effects beyond inhibiting the locations cued. Van der Stigchel and Theeuwes (2006) found that saccadic trajectories deviated away from the expected distractor location, even if no distractor appeared, under conditions in which the relative position of the target and distractor was fixed. This suggested that purely endogenous, preparatory signals can affect oculomotor programming either through spatial inhibition or other mechanisms.

Neuroimaging and electrophysiological data have provided some support for the idea that distractor suppression can be initiated endogenously. Ruff and Driver (2006) examined the consequences of informing the observer whether a distractor would appear in the hemifield opposite the target. In the presence of a distractor, faster discrimination responses were found in cued than uncued trials. Moreover, increased preparatory BOLD signals were observed, following the cue, in retinotopic regions of the hemisphere contralateral to the expected distractor location, as well as higher order regions. The authors suggested that this preparatory activity indexed suppression of sensory processes at the expected distractor location. Other studies confirmed that prior information regarding the location and timing of distractors results in both diminished distractor interferences and increased preparatory BOLD signals at corresponding locations in retinotopic cortex (Serences, Yantis, Culberson & Awh, 2004). However, these studies also allow a different interpretation, namely that the same preparatory signals used to improve target related responses can also minimize distractor interference (Lahav & Tsal, 2013). Overall, neuroimaging data are more consistent with the latter interpretation. Decrements in preparatory BOLD signals, following a cue indicating the likely target location, are found in retinotopic cortex at locations corresponding to the expected position of task irrelevant stimuli (Sylvester et al., 2008). Preparatory BOLD signal decrements in non-target regions are found in somato-sensory cortical areas as well (Drevets, Burton, Videen, Snyder, Simpson & Raichle, 1995), suggesting that suppression of task irrelevant sensory inputs is not specific to visual processes. Negative BOLD responses to task irrelevant visual stimuli are found in both thalamic and cortical areas (Gouws, Alvarez, Watson, Uesaki, Rogers, & Morland, 2014), suggesting that negative BOLD responses, whether endogenously or exogenously generated, may index diminished sensory processing of suppressed distractors. In summary, the finding that expectation of a distractor can result in both increases and decreases of BOLD signals, suggests that preparatory processes for distractors may reflect a variety of strategies. While all can result in diminished distractor interference, only some are inhibitory in nature.

In contrast to the above accounts, several researchers have found that cueing the location of distractors is not effective. Chisholm and Kingstone (2014) examined how expectations affected distractor interference in a speeded choice task. Performance was worse when participants were instructed to actively avoid the distractor, compared to when participants were not informed that a distractor could appear on some trials. Thus when participant are actively encouraged to ignore distractors, they fail singularly to do so. Instead, they attend them more than they would otherwise (e.g. Stale & Makovski, 2006; Moher & Egeth, 2012). One interpretation is that cueing the distractor results in an *attentional white bear* effect. That is, when prompted to ignore a location or a feature, observers activate the corresponding representation in working memory (Kahnemen & Treisman, 1984; Tsal & Makovski, 2006; Wegner, Schneider, Carter, & White, 1987), which biases attention toward the location and feature, regardless of task relevance (Lahav, Makovki & Tsal, 2012; Lahav, Makovski, & Tsal, 2012; Tsal & Makovski, 2006). However, the idea that the contents of working memory draw attention automatically (e.g. Woodman, Carlisle, and Reinhart, 2013; Downing 2000; Awh, Jonides, and Rueter-Lorenz,1998) has not gone unchallenged. Several studies have suggested that working memory can guide attention in a flexible manner (Close, Sapir, Burnett, & d'Avossa, 2014; Downing, 2000; Downing & Dodds, 2004; Woodman and Luck, 2004; Olivers, 2009). Others have suggested that inhibition is commonly recruited to diminish distractor interference with target processing, but that inhibitory mechanisms are inherently slower than processes associated with target selection (Moher & Egeth, 2012; Moher, Lakshmanan, Egeth, & Ewen, 2014).

In conclusion, whether spatially selective inhibitory processes can be initiated purely voluntarily and independently of processes associated with target selection has not been conclusively demonstrated. In the present work, we aimed to probe whether endogenous inhibition of locations where distractors are expected to appear, can be demonstrated in tasks requiring a simple orienting response, either covert or overt. If cueing the distractor location leads to suppression of processes evoked by stimuli appearing at the cued location, then orienting latencies should be faster when the distractor appears there, but slower when the target does. Instead, if cueing leads to enhanced processing of any stimulus presented at the cued location, then similar cueing effects should be found whether the target or a distractor appear at the cued location; regardless of whether the target or a distractor location has been cued.

Effects of partially valid cues on distractor suppression

In this study, we also examined the interaction between target validity and distractor presence. Previous imaging data have shown that during visual search through sequentially presented distractors, regions related to reorienting to invalidly cued targets are deactivated (Shulman, McAvoy, Cowan, Astafiev, Tansy, d'Avossa, & Corbetta, 2003; Shulman, Astafiev, McAvoy, d'Avossa & Corbetta, 2007). This finding lead to the suggestion that deactivations in these regions reflect distractor suppression to prevent attentional capture by task irrelevant stimuli. If this interpretation is correct then one would predict that reorienting to invalidly cued targets will be particularly robust to distractor interference and the interaction between distractor capture and reorienting.

Detection reaction times and overt orienting latencies were compared since it is still debated whether a simple detection requires a covert shift of attention. It has been suggested that while detection of a pop-out target does not (Bravo & Nakayama, 1992), visually guided saccades are obligatorily preceded by a shift of attention to the target location (McPeek, Maljkovic, & Nakayama, 1999). However, others have suggested that simple detection latencies reflect the time taken to covertly orient to the target location (Posner, 1980). If the latter view is correct, then both simple detection and saccadic latencies can be used to examine orienting independently from the effects of attention on visual sensitivity. Thus, highly visible targets and distractors, preceded by partially valid cues are particularly well suited to understand whether basic mechanisms of spatial attention are deployed similarly during covert shifts of attention and overt eye movements (e.g. Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Sheliga, Riggio, & Rizzolatti, 1995).

Method

Participants. Twelve right-handed observers (five males) with a mean age of 26 years (range 19-40) and normal or corrected to normal vision were recruited among students at Bangor University School of Psychology. All experimental protocols were approved by the local Ethics Committee. Participants gave written consent prior to commencing any experimental procedure and received monetary compensation for their time.

Materials. All aspects of stimuli presentation and data collection were carried out via a custom coded MATLAB™ program, using psychtoolbox for the accurate display and timing of visual stimuli and the recording of behavioural responses (Brainard, 1997; Cornelissen, Peters and Palmer, 2002; Pelli, 1997). Visual stimuli were presented on a 19” Viewsonic G90fB Graphics Series Monitor, set at a 1024x768 resolution and a 60 Hz refresh rate. Participants were tested in a darkened room. Head position was restrained by a chin and forehead rest.

Eye movements were recorded from the left eye using an infrared camera based Eyelink CL 1000 system (SR Research, Mississauga, Canada), set at a 1000 Hz sampling rate. The eye tracker was calibrated at the start of each block, using a nine-point calibration and validation procedure. This was considered successful when the difference between estimates and actual gaze position was < 1° of visual angle. Manual responses were collected via button press using the Cedrus RB-540 Response Pad (Cambridge Research Systems, Rochester UK).

Stimuli and Procedure. We compared the effects on response latencies of cueing the location of the target or a task-irrelevant distractor. In half of the blocks, participants performed a simple reaction time task. In the other half, participants performed a choice reaction time task instead: the appearance of the target required an overt saccade directed at the target. The target display was preceded by a central cue, which, in separate blocks, indicated the likely location of either the target or the distractor. Thus, participants engaged in four different block types.

The basic trial structure is illustrated in figure 9. A 0.8°, black fixation square was visible at the centre of the screen throughout each block. After performing a drift correct, the trial began when the participant pressed the response key. A 0.8° long white line, abutting the fixation point, was then shown for 400ms. The line was the cue, which indicated, either the likely location of the target, or the likely location of a distractor. Depending on the block, the cue was either 75% valid for the target and 25% valid for the distractor, or the other way around. On 7% of trials a non informative cue was used instead. This was a white circle with a 0.8° diameter. A non-aging foreperiod, lasting between 600 and 1200ms followed the cue offset. The trial-wise distribution of foreperiods was obtained by sampling an exponential distribution with a time constant of 0.2s. The sample values were truncated to a 0.6s and 1.2s.

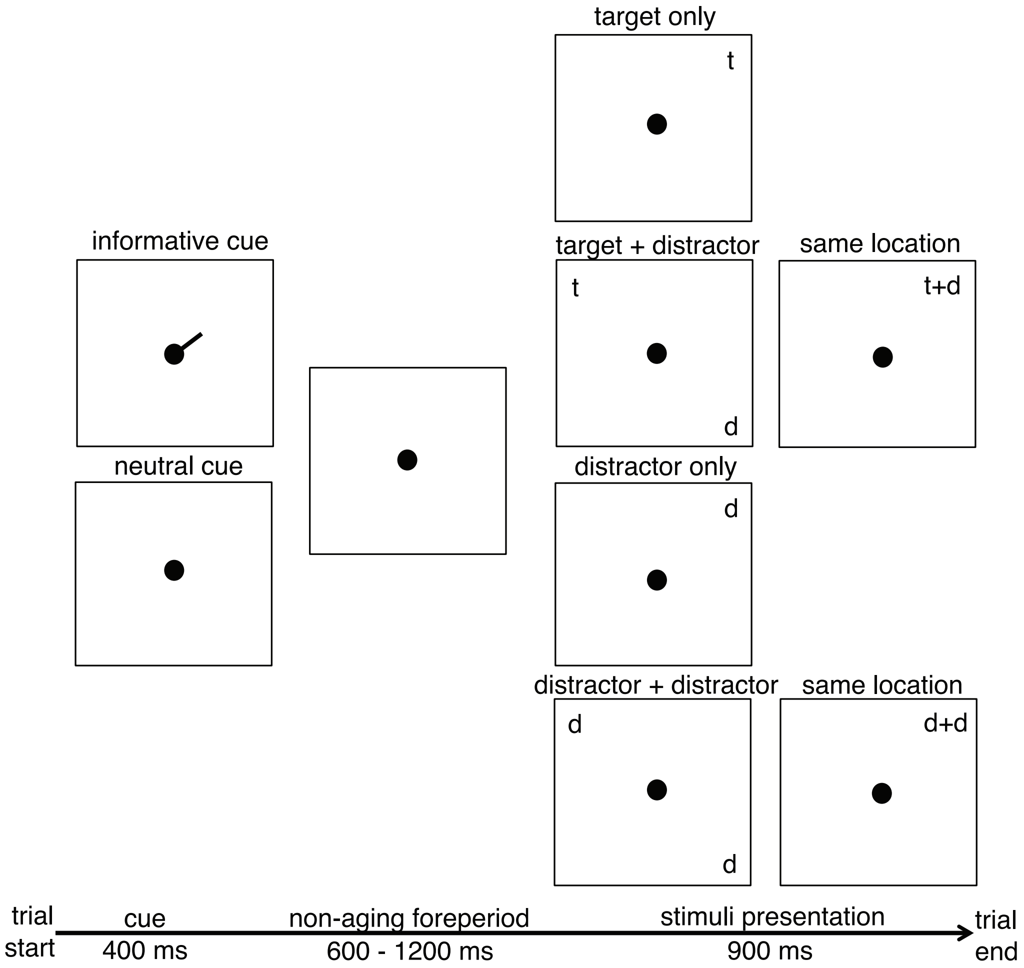

Figure 9. Trial event structure. The figure illustrates the sequence of events in trials where participants either made a simple manual response to the sudden appearance of the target stimulus or foveated it. Each trial started with a change at fixation. Either a partially valid cue, indicating which of four locations was likely to contain either the target or the distractor, or a change in the fixation point alerted the participants that the main stimulus would follow shortly. After a non-aging foreperiod the main display appeared. This could consist of either a target, a distractor, a target and a distractor, or two distractors. Participants were instructed to respond only to the target, either by pressing a button key with their right hand (detection task), or by looking at it (saccadic task).

The stimulus display contained either the target by itself, a distractor by itself, the target and a distractor or two distractors. The target and the distractors were either the outline of a rectangle with a diameter of 2.0° outer frame and 1.7° inner frame, or a circle of 0.8° diameter. When two stimuli appeared, either the target and a distractor or two distractors, one was a rectangle outline, the second a circle. This allowed presenting two stimuli at the same location. The four configurations were presented an equal number of times, thus maximizing the independence between target and distractors, while simultaneously minimizing available cues to target presence. Observers were informed that distractors would appear on most trials, and were instructed to respond only to the target, which appeared in half the trials. The target and distractor were equiluminant and were distinguished by their colour (red and green). Colour equiluminance was established for each participant in a pre-session, using a minimum motion procedure (Anstis & Cavanagh, 1983) which equalized the probability of perceiving clockwise or anti-clockwise motion of two superimposed red and green circular sine waves, by adjusting the luminance of the green phosphor to match that of a maximally bright red one. Half the participants had to respond to a green target and ignore the red distractors, while the other half responded to the red target and ignored the green distractors. In the saccadic task, participants were instructed to fixate the target as soon as it appeared. In the detection task, participants had to press a response key as soon as the target appeared, whilst maintaining their gaze on the fixation point. Fixation was monitored by the eye tracker, and trials where participants broke fixation were identified offline and removed from the analysis.

Participants were tested on five consecutive days, each session lasting around one hour and fifteen minutes. In the first session, participants undertook the procedure to estimate their equiluminance point. Participants were then familiarized with the detection and saccadic tasks following target and distractor cues, over four blocks, each containing one hundred and fifty trials. During training, participants were encouraged to make timely and accurate saccades, or to maintain fixation of the central target in the detection task. The remaining four sessions comprised six blocks each. In each block, participants completed one hundred and fifty trials. In each session, participants were cued either to the target or the distractor's likely location. The task alternated over blocks. Each condition was tested once in a repeated sequence. The order of the sequence was randomized over participants.

Data analysis. Nine hundred trials were collected from each participant on the detection and saccadic task, respectively. Half of the trials contained the target. Eye-movements were analysed off-line using MATLAB™. Saccadic latencies were defined as the period between target onset and onset of the visually evoked saccade. Correct responses were defined as saccades starting within 2° of the central fixation point and landing within 2° of the target. Only the first saccade in a trial was included in the analysis. In the saccadic task, saccadic latencies between 80ms and 900ms were included in the final analysis. In the detection task, responses between 150ms and 900ms were considered to be target evoked responses, and trials containing saccades were excluded. For both the detection and saccadic task, individual oculomotor traces for each trial were visually inspected and trials containing artefacts such as blinks were discarded from further analysis. For each participant and condition, latencies were calculated by averaging 10,000 bootstrapped estimates of the median latency. Overall, 95% of saccadic responses and 96% of manual responses were kept for final analysis.

Results

The aim of the experiments was to determine the effects of endogenous cues and exogenous distractors on covert and overt orienting. We examined how cueing the location of targets and distractors, and distractor presence affected latencies of target related responses. First, we compared the effects of cueing the likely location of the target vs. the distractor. Second, we examined the effects of distractor presence. Finally, we examined sequential effects of target and distractor presence and location on response latencies. All follow-up post-hoc tests were computed using Fisher's Least Significant Difference*s*.

Comparing target versus distractor cueing

A repeated measures ANOVA was used to examine the effects of cued stimulus (target vs. distractor) and validity (valid target, valid distractor, both invalid) using only trials, where the stimulus display contained, at separate locations, the target and a distractor.

Figure 10A and 10B shows the group averaged, median reaction times in the detection task. There was a significant effect of validity $F(2,22)= 13.41$, $p < .001$, $\eta p2 = 0.71$, with faster detection when the target appeared at the cued location, compared to when the distractor appeared at the cued location ($p = .033$) and when neither target or distractor appeared at the cued location ($p < .001$). Detection reaction times were also faster when the distractor appeared at the cued location, than when neither target nor distractor appeared there ($p = .001$). Crucially, the main effect of cued stimulus was not significant $F(1, 11)= 2.962$, $p = .113$, nor its interaction with validity $F(2,22) = 1.939$, $p = .168$, suggesting that any change in attentional set, due to whether the target or distractor location had been cued, did not greatly influence detection latencies.

Figure 10C and 10D shows the overall latencies for the saccadic task. There was a significant effect of validity $F(2, 22) = 15.215$, $p < .001$, $\eta p2 = 0.58$, with faster responses when the target appeared at the cued location, compared to when the distractor appeared at the cued location ($p = .002$), or when neither appeared at the cued location ($p < .001$). Furthermore, responses were also faster when the distractor appeared at the cued location compared to when neither stimulus appeared there ($p = .04$). Again, the main effect of stimulus cued was not significant $F(1, 11) = 2.387$, $p = .151$, nor its interaction with validity $F(2, 22) = 0.43$, $p = .656$.

The detection and saccadic data were combined and analysed using a three-way ANOVA, with the additional factor of task (detection vs. saccadic). The main effect of task was significant $F(1,11) = 104. 405$, $p < .001$, $\eta p2 = 0.90$, with detection reaction times being on average slower than saccadic latencies. Also, the main effect of validity was significant $F(2, 22) = 21.16$, $p < .001$, $\eta p2 = 0.66$. There was a near significant main effect of stimulus cued $F(1,11) = 4.769$, $p = .052$, $\eta p2 = 0.30$ with responses being marginally slower when the cue indicated the likely location of the distractor than the target. The interaction between task and validity $F(2,22) = 0.523$, $p = .60$, task and stimulus cued $F(1,11) = 0.116$, $p = .74$, stimulus cued and validity $F(2,22) = 1.241$, $p = .308$, and the three-way interaction were not significant $F(2,22) = 1.61$, $p = .223$.

Effects of distractor and validity

Next, we examined whether cues affected distractor's interference with covert and overt orienting responses. Figure 11A shows detection reaction times when the target was presented alone or with a distractor (target and distractor at different locations). A three-way repeated measures ANOVA was used to examine the effect of cued stimulus (target vs. distractor), validity (valid target vs. invalid target) and distractor (present vs. absent) on manual detection latencies. There was a significant effect of validity, $F(1, 11) = 44.963$, $p < .001$, $\eta p2 = 0.80$. There was also a main effect of distractor $F(1, 11) = 19.432$, $p < .001$, $\eta p2 = 0.64$, with faster responses on distractor absent than distractor present trials. The main effect of stimulus cued was marginally significant $F(1, 11) = 3.459$, $p = .09$, with faster reaction times following target than distractor cues. The interactions of cued stimulus and validity $F(1, 11) = 0.169$, $p = .689$, validity and distractor presence $F(1,11) = 0.09$, $p = .77$, were not

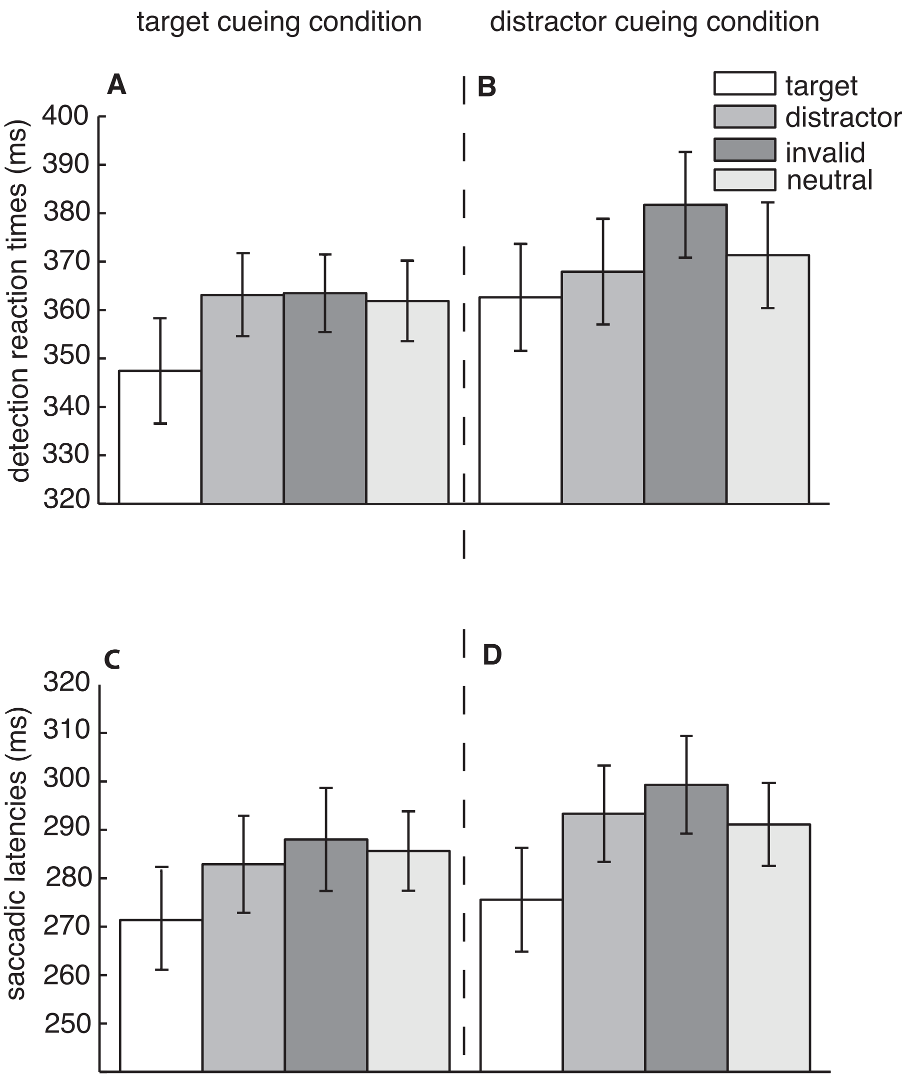

Figure 10. Effects of cued stimulus, target validity and task on response latencies in distractor absent trials. The bar graphs in panel **A** show manual detection reaction times in the target cueing condition, when either the target appeared at the cued location (target), the distractor appeared at the cued location (distractor), no stimuli appeared at the cued location (invalid), or a neutral cue preceded the target (neutral). The bar graphs in Panel **B** shows the same trial-types for manual detection, in the distractor cueing condition. Panel **C** and **D** represents saccadic responses in the target cueing and distractor cueing condition, respectively. Notably, when the target appeared at the location where the distractor was expected, reaction times were briefer than when the target appeared elsewhere or was preceded by a neutral cue. Furthermore, notwithstanding a large difference in overall latencies between detection and saccadic responses, the effects of experimental factors are comparable. Error bars represent standard error of the mean.

significant. The interaction of stimulus cued and distractor presence was marginally significant *F*(1,11) = 3.753, *p* = .079, *ηp2* = 0.25, reaction times differences between distractor present and absent trials when the target location was cued being smaller than when the distractor location was cued. The three-way interaction between stimulus cued, validity and distractor was not significant either *F*(1,11) = 1.767, *p* = .211.

The effect of stimulus cued, validity and distractor presence on saccadic latencies are shown in figure 11B. There was a significant effect of validity *F*(1,11) = 27.913, *p* < .001, *ηp2* = 0.72 and distractor *F*(1, 11) = 4.989, *p* < .047, *ηp2* = 0.031, but no main effect of cued stimulus *F*(1,11) = 1.852, *p* = .201. The interactions of cued stimulus and validity *F*(1,11) = 0.134, *p* = .721, validity and distractor *F*(1,11) = 0.439, *p* = .521, were not significant. The interaction of cued stimulus and distractor *F*(1,11) = 3.454, *p* = .09, *ηp2* = 0.24, was marginally significant with faster latencies on distractor present trials when the target location was cued. The three-way interaction was significant *F*(1,11) = 6.194, *p* = .03, *ηp2* = 0.36. This indicates that during the target cueing condition, distractors slowed responses on valid trials (when the target appeared at the cued location) and trials when the distractor appeared at the cued location. However, the effects of the distractor were remarkably reduced on invalid cued trials; that is, when the target did not appear at the cued location. In the distractor cueing condition, the distractor always increased reaction times.

Detection and saccadic latencies were jointly analysed using a four-way ANOVA, with an additional factor of task. There was a significant effect of task *F*(1,11) = 97.433, *p* < .001, *ηp2* = 0.90, validity *F*(1,11) = 38.067, *p* < .001, *ηp2* = 0.78, and distractor *F*(1,11) = 12.391, *p* < .005, *ηp2* = 0.53, with faster response when overtly orienting to valid targets in the absence of distractors. The main effect of stimulus cued was marginally significant *F*(1,11) = 4.444, *p* = .059, *ηp2* = 0.29, with faster responses following target cues. There was also a significant interaction of cued stimulus by distractor *F*(1,11) = 8.442, *p* = .014, *ηp2* = .43, and a significant three-way interaction of stimulus cued, validity and distractor *F*(1,11) = 5.221, *p* = .043, *ηp2* = 0.32. The latter interaction reflected the fact that distractors did not appreciably affect detection reaction times and saccadic latencies following invalidly cued targets, when the target was cued. In the remainder of the trials, distractors slowed responses down. All the other interactions were not significant and are reported in table 1.

Table 1: Non-significant interactions of task, cued stimulus, validity and distractor.

Effect	*df*	*F*	*P*
T * C	1, 11	0.499	.495
T * V	1, 11	2.151	.17
T * P	1, 11	0.056	.817
C * V	1, 11	0.261	.62
V * P	1, 11	0.083	.778
T * C * V	1, 11	0.01	.923
T * C * P	1, 11	0.01	.921
T * V * P	1, 11	0.346	.568
T * C * V * P	1, 11	0.001	.977

Task is either manual or saccadic task. Cued stimuli is whether the target was cued, or the distractor was cued. Validity refers to if the target stimuli appeared at the cued location or not, independent of cued stimuli. Distractor presence was either distractor present or absent. *df = degrees of freedom. F = F Statistic. p* = p value.

Target and distractor at the same location slow responses

We compared responses in trials where the distractor and target appeared at the same or different locations. We first examined neutrally cued trials using a two-way ANOVA, with factors stimulus cued (target vs. distractor) and location (same vs. different). In the detection task, there was an effect of location $F(1,11) = 6.237$, p = .03, $\eta p2 = 0.36$, with slower responses when target and distractor appeared at the same location. There was no significant effect of stimulus cued $F(1,11) = 0.473$, $p = .506$. The interaction was not also significant $F(1,11) = 0.473$, $p = .506$.

For the saccadic condition, there was an effect of stimulus location $F(1,11) = 7.418$, $p < .02$, $\eta p2 = 0.40$, with slower responses when the target and distractor appeared at the same location. There was no significant effect of cueing condition $F(1, 11) = 0.027$, p = .872. The interaction was also not significant $F(1, 11) = 1.59$, $p = .233$. When we combined data from the two tasks, we found that there was a significant effect of task $F(1, 11) = 61.211$, $p < .001$, $\eta p2 = 0.85$, and location $F(1, 11) = 10.428$, $p = .008$, $\eta p2 = 0.49$. There was no significant effect of stimulus cued $F(1, 11) = 0.337$, $p = .573$. The interaction of task and cued stimulus was not significant $F(1, 11) = 0. 33$, $p = .577$, nor the interaction of task and location $F(1, 11) = 0.168$, $p = .69$. The interaction of cued stimulus and location was marginally significant $F(1, 11) = 4.737$, $p = .052$, $\eta p2 = 0.30$, because responses following target cues were slower than responses following distractor cues only when the target and distractor appeared at different locations (compare neutral trials response timings for neutrally cued trials in figure 10 and figure 12). The three-way interaction was not significant *F*(1, 11) = 0.186, *p* = .675.

We also examined the effect of validity in trials in which the target and distractor appeared at the same location, with a two-way, repeated measures ANOVA. The factors were stimulus cued (target vs. distractor) and validity (valid vs. invalid). In the detection task, there was no effect of stimulus cued *F*(1, 11) = 2.757, *p* = .125, but there was a significant effect of validity *F*(1, 11) = 14.163, *p* = .003, *ηp2* = 0.56 with faster responses to valid than invalid targets. The interaction between cued stimulus and validity was not significant *F*(1, 11) = 0.008, *p* = .930. In the saccadic task, there was no significant effect of stimulus cued *F*(1, 11) = 1.741, *p* = .214. However, there was an effect of validity *F*(1, 11) = 9.106, *p* = .012, *ηp2* = 0.45, with faster responses to valid than invalid targets. The interaction between cued stimulus and validity was not significant *F*(1, 11) = 0.634, *p* = .443.

For the combined manual and saccadic data that was analysed using a 3 way repeated measures ANOVA, there was a significant main effect of task *F*(1, 11) = 81.03, *p* < .001), *ηp2* = 0.88, and validity *F(*1, 11) = 11.871, *p* < .005, *ηp2* = 0.51. There was a marginally significant effect of cued stimulus *F*(1, 11) = 4.074, *p* = .069, with faster responses when the target was cued. The interaction of task and validity was marginally significant *F*(1, 11)= 3.808, *p* = .077, because validity effects were larger in the saccadic than the detection task. The interaction of task and stimulus cued *F*(1,11) = 0.432, *p* = .525, validity and stimulus cued *F*(1, 11) = 0.33, *p* = .577, and response, stimulus cued and validity was not significant *F*(1, 11) = 0.472, *p* = .506.

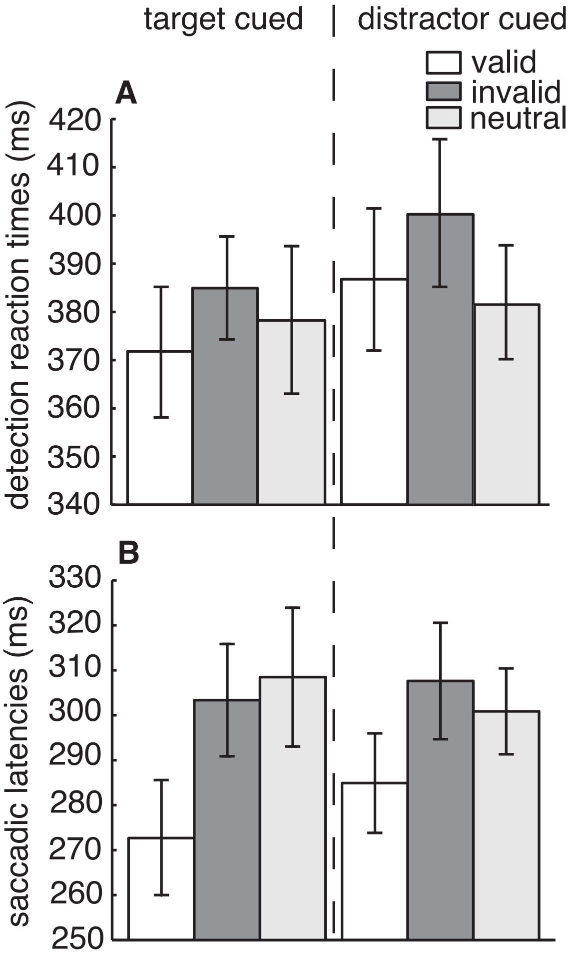

Figure 12. Effects of cued stimulus, cued stimulus validity, and task on response latencies in trials where the target and distractor appear at the same location. Panels **A** and **B** show the group averaged response latencies, in the detection and saccadic task respectively. When the target and distractor appeared at the cued location, response latencies were briefer than when they appeared elsewhere. Following cued indicating the distractor location, there was no advantage in response latencies when the target and distractor appeared at the cued location compared to neutrally cued trials in the detection task. Error bars represent the standard error of the mean.

Memory kernel analysis

An unanticipated aspect is that the timings of the ocular responses are markedly longer than those customarily reported in similar tasks. For example, the latency of saccadic eye movements in choice reaction time tasks is generally around 180 ms (Carpenter and Williams, 1989), on the contrary saccadic latencies in our task were around 270 ms (see figure 11B), even when no distractor was present. Equally, we previously found much faster covert and overt orienting responses in experiments where targets were presented in most trials and in the absence of distractors, suggesting that response latencies in this task may be unusually slow. There are a number of explanations one could put forth.

Firstly, participants may have cautiously adopted a strict criterion to initiate a response, because of uncertainty regarding the presence and location of the target and distractor(s). Therefore, increased detection reaction times and saccadic latencies may simply reflect longer decision times. Alternatively, mixing trials in which the target was present and trials in which the target was absent, may have lead to a decrease in response priming, previously shown to affect response timing in visual search tasks (Maljkovic, & Nakayama, 1994; McPeek, Maljkovic & Nakayama, 1999). We therefore examined sequential effects of target presence, target position, distractor presence, and distractor position on response latencies. Figure 13 shows the detection reaction time and saccadic latency difference between trials preceded by: A) trials containing the target vs. trials not containing the target; B) trials in which the target appeared at the same location vs. trials in which the target appeared at a different location; C) trials in which the distractor appeared vs trials in which it did not, all the trials containing a target; D) trials in which the distractor appeared at the same location or at a different location, all trials containing a target. The effects of sequential position of the preceding trial and task were assessed using a two-way ANOVA, the dependent variable was the reaction time difference between trials preceded by target present vs. target absent trials and so on. We first examined the effects of target presence in the preceding trials on the current trial response latency. There was a near significant effect of task $F(1,11) = 4.322$, $p = .062$, $\eta p2 = 0.28$. There was a significant effect of time, $F(9, 99) = 12.541$, $p < .001$, $\eta p2 = 0.53$, and a significant interaction of task by time $F(9, 99) =11.400$, $p < .001$, $\eta p2 = 0.51$, suggesting that the effects of target presence vs. absence in the trial prior the current trial was different for detection reaction times and saccadic latencies. To examine more closely the effects of previous trials on the current n^{th} trial, a single exponential function was fit to the detection reaction time and saccadic latency differences, starting from to the n-2 up to the n-10 trial. The bootstrapped group median time constant was 2.69 inter trial intervals (ITIs), for the detection reaction times, and 2.26 ITIs, for the saccadic latencies. The difference was not significant, $t(11) =1.00$, $p = .34$. The amplitude of the exponential was 36.78ms, for reaction times and 32.01ms for latencies. The difference was not significant, $t(11) = 0.93$. $p = .37$. Overall the effect of previous trials' target presence on reaction times and latencies was similar, suggesting that the difference between the two was short lived.

An important issue is whether the priming effects of target presence reflect facilitation of target pop-out (Maljkovic & Nakayama, 1994). If so, priming should be greatly diminished when the target appears alone. To examine this we split the data in distractor present and distractor absent trials and return the ANOVA adding distractor presence as a factor. There was no main effect of distractor presence $F(1, 11) = 0.463$, $p = .51$. The interaction of distractor presence and time $F(9, 99)$

= 1.178, *p* = .318, distractor presence and task *F*(1, 11) = 2.036, *p* = .181) and the three-way interaction *F*(9, 99) = 0.424, *p* = .920, were not significant.

Distractor priming effects are illustrated in figure 13B, for trials in which the distractor was present. There was no main effect of task *F*(1, 11) = 2.147, *p* = .171) or time *F*(9, 99) = 1.069, *p* = .392). The interaction of task by time was also not significant *F*(9, 99) = 0.939, *p* = .495), suggesting that the presence or absence of distractors in previous trials did not affect distractor effects in the current trial.

The effects of target position are shown in Figure 13C. Priming effects were smaller than those of target presence, suggesting that priming by target presence did not simply reflect the accumulation of target related spatial information. Task had no significant effect on target position priming *F*(1, 11) = 2.874, *p* = .118, but there was a significant effect of time *F*(9, 99) = 2.593, *p* < .010, *ηp2* = .19, suggesting that when the target location in the preceding trials was repeated in the current one, detection reaction times and saccadic latencies were speeded up. The interaction of task by time was also not significant *F*(9, 99) = 0 .742, *p* < .670. The exponential fits indicated that the time constant was 13.2 ITIs for detection reaction times and 2.28 ITIs for the saccadic latencies. The difference was not significant, *t*(11) = 1.04, *p* = .32. The amplitude was 1.40ms for the detection reaction times and 18.39 ms for the saccadic latencies. The difference was not significant, *t*(11) = -1.08, *p* = .32.

Finally, we examined the priming effects of repeated distractor position, shown in figure 13D. The main effect of task was significant *F*(1, 11) = 4.987. *p* = .047, *ηp2* = 0.31, priming being larger in the saccadic than detection task. The main effect of time was also significant *F*(9, 99) = 8.955, *p* < .001, *ηp2* = 0.44. The interaction of response and time was significant *F*(9, 99) = 8.695, *p* < .001, *ηp2* = 0.44, indicating that the priming effects for the trial immediately preceding the current one were smaller in the detection than saccadic task. The exponential fits indicated that the time constant was 3.22 ITIs for the detection reaction times and 3.07 ITIs for the saccadic latencies. The difference was not significant, *t*(11) = 0.75, *p* = .47. The amplitude was 7.2ms for the detection reaction times and 7.4ms for saccadic latencies. The difference was not significant, *t*(11) = -1.17, *p* = .12,

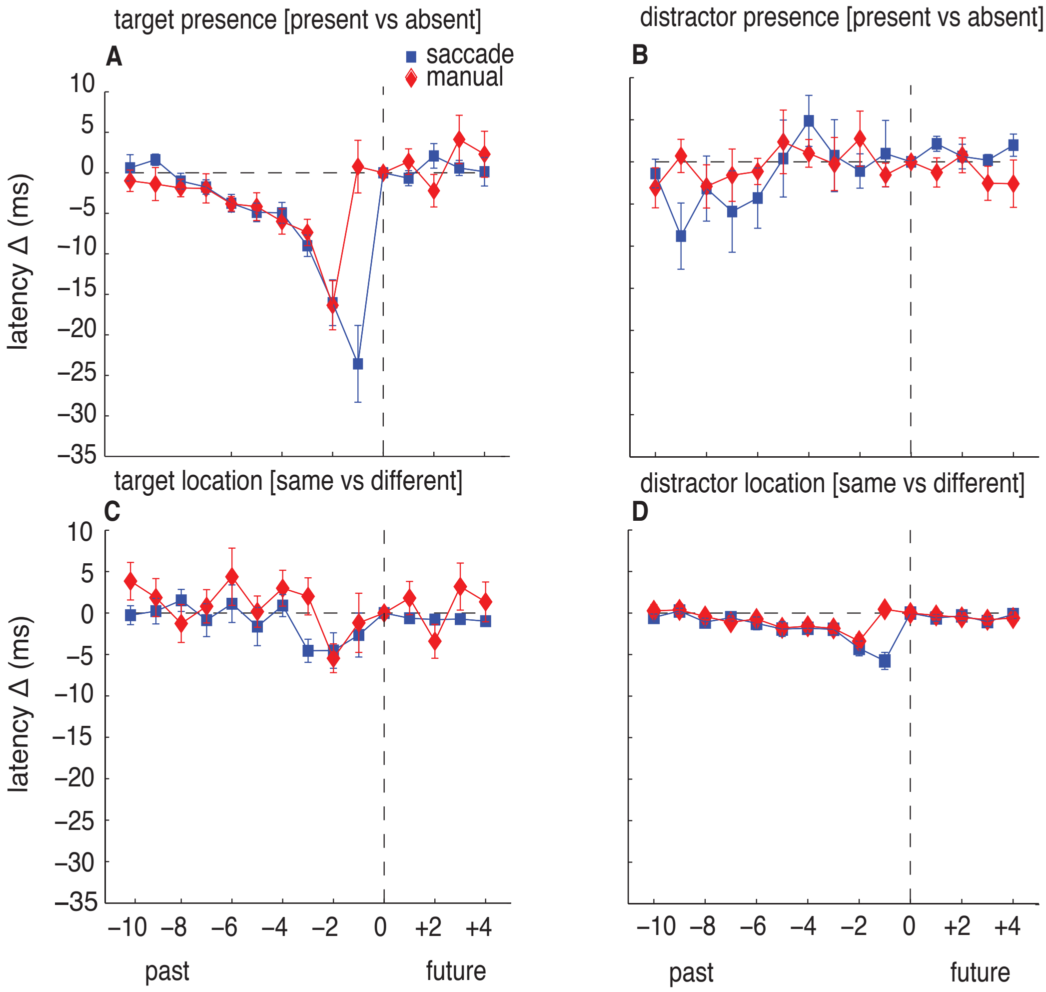

Figure 13. Sequential effects of target presence and location, distractor presence and location, by task on response latencies. Panel **A** shows the effects of target presence in trials preceding by one, two etc. the current one, in the detection and saccadic task respectively. The effects of target presence were very similar in the detection and saccade task, except fro the trial preceding the current one, where no priming effect was found in the detection task. In panel **B** the effects of distractor presence are shown. The effect of repeating the target location are shown in panel **C**, while panel **D** shows the effects of repeated distractor location. Error bars show the standard error of the mean.

Discussion

Endogenous distractor cueing does not result in spatial inhibition

We examined how covert and overt orienting responses, evoked by an eccentric visual target, are influenced by endogenous cues, providing probabilistic information about the likely location of either the target or a task-irrelevant distractor. We found that when the distractor location was cued and the distractor appeared at the cued location, its interference with the target response was diminished compared to when the distractor appeared elsewhere, suggesting that participants used advance information about the distractor location to diminish distractor interference. However, when the target occupied the location where the distractor had been cued to appear, responses were also faster than when the target appeared elsewhere, suggesting that processing of stimuli at the cued location was not suppressed. If this interpretation of the findings is correct, then diminished distractor interference by itself does not imply that distractor processing is suppressed, instead diminished distractor interference may simply reflect more efficient processing of the stimulus at the cued location. This conclusion may also provide a plausible explanation for the puzzling finding that distractor cueing leads to positive preparatory BOLD signals in retinotopic regions, similar to those evoked by target cues (Ruff & Driver, 2006; Serences et al., 2004).

We did find that cueing the target led to faster responses than cueing the distractor, and that when the distractor and the target appeared at the same location this effect was diminished. One explanation for this finding may be that observers started their search at the location containing the stimuli which was cued on that trial (e.g. the cue was informative for target locations), therefore leading to faster responses when the target, rather than the distractor, was cued. However, endogenous orienting to valid targets was not highly selective for the features that distinguished target and distractor, since distractors slowed responses. This clearly stands in contrast with the remarkable selectivity observed in invalidly cued trials discussed below.

Violations of spatial expectations diminish distractor interference

When the target location was invalidly cued, detection reaction times and saccadic latencies were prolonged, compared to when the target was validly cued, a finding widely replicated since its initial demonstration (Posner, 1980). More interestingly, the presence of a distractor did not prolong detection reaction times and saccadic latencies further when the target location was invalidly cued, even though the presence of a distractor delayed the response when a valid target appeared at the cued location, or when the distractor location was cued, either validly or invalidly. The obvious inference from these data is that a highly selective feature search (Folk, Remington & Johnston, 1992; Lamy & Egeth, 2003; Lamy, Carmel, Egeth & Leber, 2006) is initiated following reorienting of attention to an invalid target.

Previous neuroimaging findings provide a simple, if mechanistic interpretation of this result. During search through visual stimuli presented in a rapid sequence, cortical areas in the Temporal-Parietal junction (TPJ) show sustained decrements in baseline BOLD signals (Doricchi et al, 2010; Shulman et al., 2003, 2007). However, following target detection, TPJ shows prominent positive responses (Corbetta & Shulman, 2002), that are greater for invalid than valid targets, at least in the non-dominant hemisphere (Doricchi et al, 2010). Furthermore, the amplitude of the search related deactivation in TPJ predicts whether the observer will correctly detect the target in demanding tasks (Shulman et al., 2007), suggesting that signal decrements improve the efficiency of visual search. Therefore, brain regions involved in reorienting to invalid targets (Corbetta & Shulman, 2002) and the evaluation of target related properties (Hayn and Marois, 2014), are prominently deactivated during the search for the target, presumably because distractor related signals, which would otherwise activate them, are filtered out.

A prediction, based on the imaging and behavioural data, can then be formulated: reorienting does not only initiate a transient attentional shifts, but also a strategy change, which enforces a highly selective feature based search. This strategy change is prompted by the appearance of the search stimulus and is maintained by a specific attentional set. This interpretation is in keeping with the fact that reorienting to an invalid target did result in greatly diminished distractor interference, when the target location was cued, but not when the distractor location was cued. Presumably, when the distractor location was cued, the participants began searching for the non-target feature and therefore could initiate the search for the target only after the one for the distractor had been completed.

Previous behavioural data indicated that parallel search can either be driven by target saliency, in a purely bottom up fashion, or by target defining features, in a top down fashion (Bacon & Egeth, 1994). The fact that distractors slower response timing suggest that feature guided mechanisms were not recruited by default in our paradigm, for reasons that are not further explored here. However, previous evidence suggests that when participants can select the target by either saliency, such as novel onset, or on the basis of a specific target feature, e.g. the stimulus colour, they prefer the former strategy, and adopt the latter only when inappropriate on most trials (Lamy, & Egeth, 2003; Lamy, Carmel, Egeth, & Leber, 2006). Since the target appeared by itself in half of the target present trial, one may speculate that a saliency driven search may have been adopted, leading new onset distractors, presented simultaneously with the target, to capture attention automatically. Nevertheless, our results suggest that the search becomes highly selective after the target appears at an unexpected location. Only then distractors, which do not share the target colour, are efficiently prevented from capturing attention and therefore do not interfere with reorienting to the target.

Alternative interpretations of this finding are less likely. For example, it has been suggested that distractor suppression is engaged only when the sensory load and the attentional demands of the task are increased (Lavie, Hirst, de Fockert, & Viding, 2004). On invalid trials, where the task is made more difficult by a breech of spatial expectations, improved distractor suppression could then be the consequence of the attentional demands placed by reorienting to an invalid target. By itself, this account does not explain why the same degree of distractor suppression was not found when the distractor location was cued, despite response latencies being just as long as when the target location was cued, or longer (Lahav, Makovski & Tsal, 2012; Lahav & Tsal, 2013; Lavie, Hirst, de Fockert, & Viding, 2004; Tsal & Makovski, 2006). Overall, our findings are consistent with the idea that in this task distractor suppression cannot be initiated purely endogenously, but requires an exogenous event, such as the appearance of an invalidly cued target (Corbetta & Shulman, 2002). This conclusion is in keeping with a number of previous studies, which failed to document evidence for distractor suppression, under conditions that require the inhibitory set to be adjusted trial by trial (e.g. Lahav & Tsal, 2013).

Covert and overt orienting show similar cueing effects

Overall, detection reaction times were longer than saccadic latencies, reflecting biomechanical differences between the motor plants used to report target a detection and a saccade. Nevertheless, the effects of endogenous cues and distractors on detection reaction times and saccadic latencies were remarkably similar. The finding that endogenous and exogenous manipulations of attention have similar effects on detection and saccadic latencies has a couple of implications. First, it suggests that both target detection and target evoked saccades require the preliminary deployment of focal attention to the target location, contrary to the suggestion that only the latter does (Bravo & Nakayama, 1992; Maljkovic & Nakayama, 1994; McPeek, Maljkovic & Nakayama, 1999), but in keeping with earlier conceptualizations of the detection task (e.g. Posner, 1980). Moreover, it is consistent with the idea that covert attentional shifts and overt saccadic eye movements largely share the same control processes (Rizzolatti, Riggio, Dascola, &

Umiltà, 1987; Shepherd, Findlay, & Hockey, 1986; Sheliga, Riggio, & Rizzolatti, 1995).

Our finding that saccades are affected by distractors does depart from some earlier observations. Under conditions, which minimize observers' spatial and temporal uncertainty regarding targets and distractors, the appearance of a distractor modifies the distribution of saccadic latencies with a specific spatiotemporal profile (Buonocore & McIntosh, 2013). When the target and the distractor appear in close proximity, saccadic latencies are decreased and saccades land at locations intermediate between target and distractor, suggesting additive interactions between target and distractor evoked signals (Findlay, 1983, 1983). On the other hand, when the target and the distractor appear at locations separated, in the radial direction, by more than 20°, the distribution of saccadic latencies shows a dip at around 60-100ms following the distractor's onset (Ottes, Van Gisbergen & Eggermont, 1984; Walker, Deubel, Schneider & Findlay, 1997; Walker, Kentridge & Findlay, 1995), with a prolongation of the median saccadic latency, suggesting inhibitory interactions between distractor and target evoked signals. Our data indicate that the appearance of the distractor and target at the same location did not result in saccadic latencies briefer than those evoked when target and distractor appeared at different locations. Instead, saccadic latencies to spatially contiguous stimuli were longer than those to targets that were spatially separated from the distractor (compare figure 2B and figure 4B). This lack of averaging effects may reflect competition between sensory, attentional (Desimone & Duncan, 1995) or response related signals when target and distractor appear at the same location. Additionally, distractors delayed saccadic latencies, even though their onset preceded the median responses by more than 200ms, suggesting that distractors influence saccadic latencies over more extensive time windows than those previously associated with saccadic inhibition (Reingold, & Stampe, 2002**).** This prolonged inhibition of saccadic latencies has several potential explanations. For example, the overall slowing in saccadic latencies observed in our paradigm may have also delayed distractors' interference on the selection of the target and responses.

Cumulative effects of orienting and distractors

We found that response latencies, even when the target appeared in isolation, were remarkably increased compared to values reported in previous studies (e.g. Findlay, 1983; Carpenter & Williams, 1995). A number of possible reasons for this departure could be hypothesised. Our task differed from previous, because the observer's uncertainty, regarding the presence, location and timing of the target and distractor, was maximised. Therefore, observers could not use *ad-hoc* strategies and had to rely on general purpose, possibly inefficient, search mechanisms. Alternatively, it is possible that the absence of consistent repetitions of stimulus configuration in subsequent trials, may have lead to a loss of priming effects on the latency of covert and overt orienting responses (Feactau & Munoz, 2002). Indeed, McPeek, Maljkovic, and Nakayama (1999) examined saccadic latencies to a target displayed among distractors. The target's colour was different from the distractor's, thus providing the opportunity for both a saliency and feature driven search. When the colour of the target was the same as in previous trials, observers showed faster saccadic latencies than when the target's colour switched from trial to trial. Moreover, the repetition of the target feature had a cumulative effect, which extended over about seven trials, suggesting that a central integrator, with a long time constant, accumulated information about the target feature. These sequential effects appear to be automatic and impermeable to voluntary influences (Maljkovic & Nakayama, 1996) and have been interpreted as reflecting the facilitation of bottom-up, driven target saliency (Maljkovic & Nakayama, 1994, 1996), which guide attentional selection.

The interpretation that repetition priming improves target pop-out has been disputed (Lamy, Carmel, Egeth, & Leber, 2006). We examined the effects of target and distractor presence and location on detection reaction times and saccadic latencies. There were large effects of target presence on both detection and saccadic responses, with faster responses when previous trials contained a target compared to when they did not. However, these data also indicate that these priming arise in context, which does not match the experimental conditions thought essential by the investigators who made those seminal observations. First, the detection task used here simply required observers to establish whether a highly discriminable target was present, contrary to Maljkovic and Nakayama (1996, 1998 and 2000) who asked their highly trained observers to perform a fine shape discrimination task to ensure that they would attend the target. We found large effects of target repetition, on both detection and saccadic latencies. If this effect arose because of facilitation of target selection, then one may have predicted that saccades would have shown it, since they require the deployment of focal attention, while detection should have not, contrary to the empirical evidence. Therefore, either focal attention was deployed to the target, both in the detection and saccadic tasks, as the similarity of the effects of endogenous attention and distractor capture on the detection and saccadic latencies already indicates, or priming indexes facilitation of a process other than target saliency.

Maljcovich and Nakayama (1994, 1996) argued that priming effects mainly benefit the ability to select salient targets among distractors, where performance is determined by how quickly the observer can establish which feature identifies the target, having found that increasing the number of distractors, which improves the target saliency, when homogenous distractors are used, decreased the effects of previous trials priming. These authors concluded that this interaction provided evidence that previous trial priming and distractor density affect the same low-level processes, which give rise to pop out effects. However, priming effects were observed in our task, regardless of whether the target was presented in isolation or accompanied by a distractor. This finding suggests that priming facilitates target selection not by increasing somehow the saliency of the target, but by speeding up selection *per se*. The idea that sequential effects reflect a facilitation of premotor, selection mechanisms, may also account for the finding that the priming effects of the n-1 trial were much smaller in the detection than the saccadic task (see figure 13A). Since priming effects in the two tasks were otherwise undistinguishable, the finding suggests a short lived, inhibitory signal is generated in the detection task during the response to a target. This inhibitory signal would then end up delaying the response to a target in the following trial and may be related to the need to withhold an overt orienting response in the detection, but not in the saccadic task (Tassinari, Aglioti, Chelazzi, Marzi, & Berlucchi, 1987).

Distractor priming

Not only the target, but also distractors primed subsequent trials. In the presence of a distractor, covert and overt orienting responses were faster when distractors had appeared at the same location as in previous trials. The priming effects of distractor on response latencies were smaller than those associated with target presence and were spatially specific, since they were not observed when distractors occupied different locations in the current and previous trials (see figure 13B). Maljkovic and Nakayama (1996) showed that when targets appeared at locations previously occupied by a distractor, response latencies were increased, suggesting that processing at locations of previous distractors is suppressed. Interestingly, these authors also found that the effects of feature and location priming were independent, suggesting independent featural and spatial implicit memory mechanisms. Our results confirm the presence of priming effects that are both spatially and not spatially specific, although the former are much smaller.

An interesting issue is the neural site where information about the history of previous trials is maintained, which is necessary to give rise to the priming effects we observed. The duration of the cumulative effects, observed up to eight trials prior, suggests that the mechanism responsible for storing information has a long time constant, in the range of 20 to 30 s at least (Maljkovich & Nakayama, 2000). Neural integrators with the required time constants are known to be located in the brainstem and provide a tonic signal, used to maintain steady fixation of eccentric targets following a saccade (Leigh & Zee, 1991). These mechanisms belong to circuits that are also involved in both covert and overt orienting (Hartwich-Young, Nelson, & Sparks, 1990; Krauzlis, Lovejoy, & Zénon, 2013). Consequently it is not unreasonable to put forth the speculative, but tantalizing proposal that the same neural mechanisms involved in the integration of saccadic eye velocity are also used to accumulate signals about target presence, features and position over subsequent trial.

Chapter four

Endogenous orienting is unimpaired in a patient with abnormal saccades following a thalamic stroke

Abstract

Patients with low level, oculomotor impairments can show significant attentional deficits. These results have suggested that any impairment in overt orienting can be followed by a similar impairment in covert orienting. We examined a middle aged stroke patient with a lesion to the medial-dorsal thalamus, who had recently presented with oscillopsia and objective oculomotor deficits, worse for vertical eye movements. The patient showed impaired saccadic kinematics whilst performing a visually guided saccadic task. In particular to targets in the upper and lower visual field. However, saccadic latency was not impaired in comparison to the control group. In a detection task, where highly visible visual targets were preceded by partially valid endogenous cues, the patient exhibited a validity effect not significantly different from controls, whether the targets were horizontally or vertically displaced. Overall these findings are consistent with the view that deficits of overt orienting can present without additional impairments in covert orienting. Implying that processes shared between covert and overt orienting may not include those specifically involved in determining the kinematics of visually evoked saccade and which arise in structures where the oculomotor signal is parcellated into horizontal and vertical components.

The relationship between eye movements and spatial attention has been the focus of much investigation. A number of studies have demonstrated that shifts of attention and gaze are tightly coupled (Craighero & Rizzolatti, 2005; Rizzolatti & Craighero, 1998; Rizzolatti, Riggio, Dascola, & Umiltá, 1987). One influential account of this finding is *premotor theory*, which claims that shifts of spatial attention are dependent on activation of oculomotor circuitry (Rizzolatti et al., 1987).

Evidence supporting the idea that eye movements and attention arise from the same neural circuits comes from a variety of behavioural experiments. One of the most convincing arguments in support of premotor theory is the *meridian effect* (Rizzolatti et al., 1987. This was first demonstrated in a seminal study by Rizzolatti and colleagues (1987), where participants were required to manually respond to targets where the likely location was indicated using a partially valid, symbolic cue. The results showed that participants were slower to respond with a button press when the imperative stimuli appears in the hemifield opposite to where attention has been deployed by the cue. The authors concluded that this finding is not supportive of the position that attention arises from an independent system, as there is no reason why an anatomical landmark such as hemifield should affect a supramodel cognitive process. Instead, the authors claimed that a delay could be accounted for in a scenario where in order where in order for attention to be shifted, the system has to program an eye movement to the required location, as this would account for the effect of anatomical landmarks on orienting times. Consequently, if the target fails to appear in the expected location, then an eye movement must be reprogrammed to the new location. Such a scenario would account for the additional cost of invalidly cueing across hemifields, as a new saccade must be programmed. This and a number of subsequent studies (e.g. Craighero & Rizzolatti, 2005; Sheliga, Riggio, & Rizzolatti, 1994) were used to make the claim that covert shifts of attention, where observers adjust attention without shifting gaze, are dependent on the programming (but not the execution) of an overt shift of attention, namely an eye movement.

The idea that attention and eye movements are coupled in this way has been extremely influential, leading to a large number of behavioural and neuropsychological attempts to delineate both processes. For example, several studies have demonstrated that perception is enhanced at, and around, the location of a planned saccade (Deubel & Schneider, 1996; Schneider & Deubel, 1995) with perceptual facilitation maintained at that location up until the eye movement is initiated (Jonikaitis, Papper, & Deubel, 2011). The general interpretation of this being that enhanced perception means that attention cannot be deviated away from the planned location for a saccade, without a new saccade being programed.

Further support for the close coupling is provided from studies which show eye movements and attention share a common, mechanically defined boundary, in that attention cannot be optimally deployed to spatial locations which cannot be foveated through an eye movement. For example, Craighero, Nascimben, and Fadiga (2004) restrained participants in a headrest, and then used a central cue to indicate the likely location of an upcoming target which would appear in the peripheral vision, but too far for it be directly foveated. Participants showed a reduced validity effect compared to targets which could be foveated, which the authors claimed is evidence than attention and eye movements share similar networks. Other support for this mechanically dependent limitation have been reported in ophthalmic patients. For example, in eight patients with VI cranial nerve palsy affecting one eye, Craighero, Carta, and Fadiga (2001) reported that, when using a central cue in the paretic eye, patients failed to show a cost on invalid cues, suggesting that patients had difficulty covertly orienting attention to locations where they also had disability executing a saccade.

A number of other studies have also reported attentional impairments in the presence of oculomotor disability. For example, patients with progressive supranculear palsy (PSP) a neurodegenerative disorder affecting nuclei in subcortical structures of the brain stem and basal ganglia, often present with opthalmoplegia affecting vertical eye movements more than horizontal movements. A previous investigation of PSP patients (Rafal et al., 1988) reported PSP patient showed an impaired validity effect, when compared to Parkinsonian controls, suggesting that covert and overt orienting signals also converge within deep brain structures. Whilst the implication of these studies suggest that covert and overt orienting appear to share a common, biomechanically defined boundary, others have failed to demonstrate this. Khan and collegues (2009) reported in a single patient optic ataxia after suffering unilateral lesion in the parietal cortex dissociation of saccades and attention. Specifically, the patient was unable to perform a letter discrimination task in the contralateral field, despite being able to execute a saccade to that location, suggesting that attentional orienting was preserved in the presence of oculomotor impairment.

A number of neuroimaging studies have also demonstrated that signals relating to covert and overt orienting travel along common neural pathways. For example, Corbetta et al., (1998) and Nobre et al., (2000) were unable to dissociate eye movements and attention at the cortical level when comparing preparatory activity related to attentional shifts and eye movements. However, whilst imaging signals appear to show virtual overlap between signals associated with covert and overt orienting, single unit recording have demonstrated some degree of dissociation between covert and overt orienting. For example, using a pro and anti-saccade task, Sato and Schall (2003) identified two distinct neuronal populations, which were activated at different epochs whilst the saccade was executed; one population appeared to be engaged by the appearance of a singleton and the other by the need to prepare a saccade. Other studies have also have also reported differences within the FEF among neurons coding for covert vs overt orienting responses (Cohen, Pouget, & Heitz, 2009; Juan et al., 2008).

In the literature it is clear that attention and the oculomotor system are tightly linked, behaviourally and anatomically, although there are instances where both processes can be dissociated. Therefore, here we investigate in a patient who reported a problem executing vertical, but not horizontal, eye movements after suffering a thalamic stroke, to investigate if the structures shared between covert and overt orienting also overlap at the location where horizontal and vertical components of eye movements are parcellated.

Methods

At the time of testing, the patient was a right handed, 47 year old male who had suffered a cryptogenic, thalamic stroke two weeks prior to commencing testing. The patient had taken part in an endurance-sporting event, following which he felt dizzy. The next day he noticed that he was having vertical diplopia and decided to seek medical help. On presenting to the Emergency Department of the local hospital, neurological examination revealed normal mental status with no impairment in orientation or memory. Magnetic resonance imaging revealed a focal lesion in right medial-dorsal thalamus, confined to the reticular thalamus nucleus (TRN) as shown in figure 14.

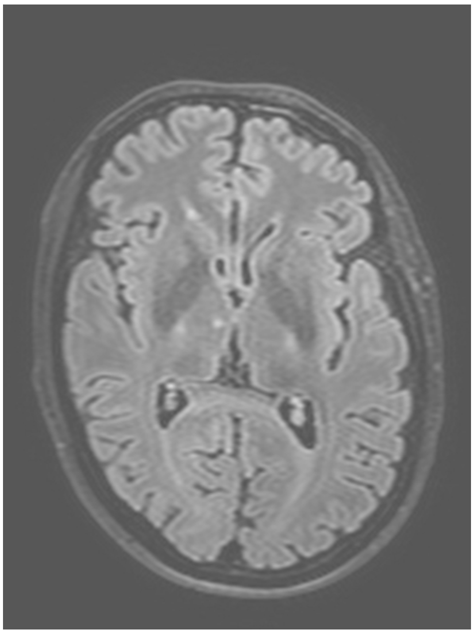

Figure 14 Patient's T1 weighted axial MRI scan showing the lesion in the right, medial-dorsal thalamus.

Controls

We recruited nine age (mean age 46; range 40:53) and gender matched, right handed controls. Controls were recruited from the Bangor University community participant panel. The experimental protocols had been approved by the Ethics Committee at Bangor University, School of Psychology. Participants gave written consent prior to commencing any experimental procedure and received monetary compensation for their time.

Apparatus and procedure

All testing took place in a dark room. Head position was restrained by a chin and forehead rest. Stimuli were generated and displayed using a custom coded MATLAB™ script and a set of procedures which allow precise timing of the display and synchronization with the eye-tracker (Brainard, 1997; Cornelissen et al., 2002; Pelli, 1997). Visual stimuli were presented at a distance of 57 cm from the observer, on a 19" Viewsonic G90fB Graphics Series Monitor, set at a 1024 x 768 resolution and a 60 Hz refresh rate. Eye movements were recorded using an infrared camera based Eyelink CL 1000 system (SR Research, Mississauga, Canada), set at a 1000 Hz sampling rate. Calibration took place at the start of each block, using a 3 point calibration and validation procedure. Calibration was considered successful when the error was < 1° of visual angle.

In experiment 1 (figure 15) each trial began when the central fixation point (0.2°) turned from black to red (0.8°) for 400ms. The fixation point was visible throughout the trial. This was followed by a non-aging foreperiod lasting between 600 and 1200 ms. Its duration, namely the stimulus onset asynchrony (SOA) was obtained by sampling the following exponential distribution with replacement:

$$p(\mathrm{SOA}) = e^{-\frac{\mathrm{SOA}-0.6s}{\tau}} \text{ iff } 0.6\mathrm{s}<\mathrm{SOA}<1.2\mathrm{s}$$

else

$$p(\mathrm{SOA}) = 0$$

where τ = 0.2 s.

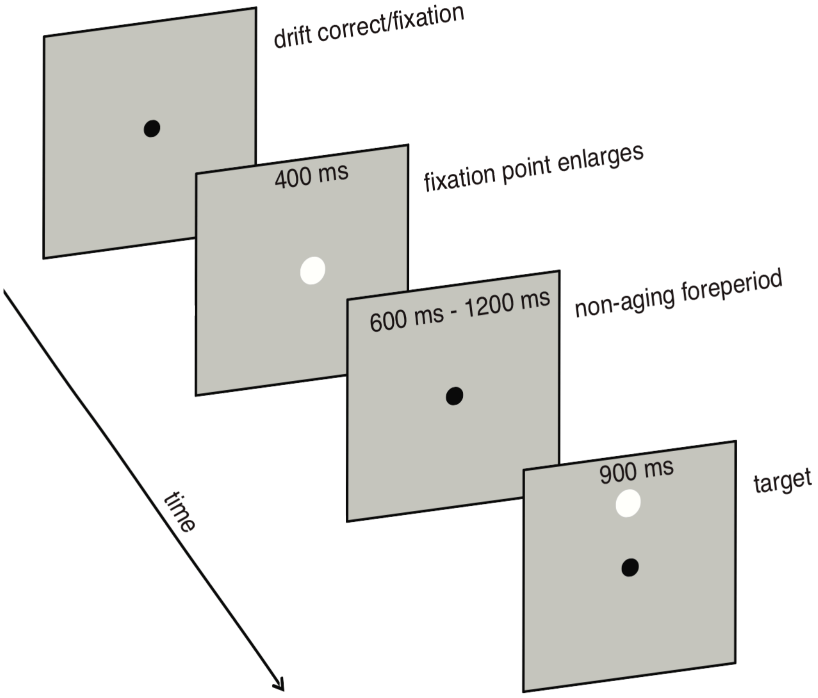

Figure 15. Saccadic localisation paradigm. Trial started with a drift correct, followed by an enlargement of the central fixation point for 400ms. Finally, after a non-aging foreperiod between 600 – 1200ms, the target was presented for 900ms. Participants were instructed to make timely and accurate saccades to the stimuli.

A bright, highly salient circular target appeared on 95% of trials. The target had a Gaussian luminance profile with a standard deviation of 0.25°, and appeared at an eccentricity of 7° from a central fixation square, along either the vertical or horizontal meridian. The background luminance was 12.75 cd/m^2 and the peak target luminance was 62.4 cd/m^2. Participants were required to execute a saccade whenever the target appeared on the screen. The location where the target could appear was equiprobable. The target remained visible for 900ms. An auditory tone indicated the end of the trial and prompted the participant to press the spacebar to initiate a new trial, and simultaneously performing a drift correct.

In experiment 2 (figure 16), all parameters were the same as in experiment 1, except at the start of each trial, there was a white, 0.8° long line abutting the fixation point (0.2°) which was removed after 400ms. The line functioned as a probabilistic cue which accurately indicated the target location 75% of the time.

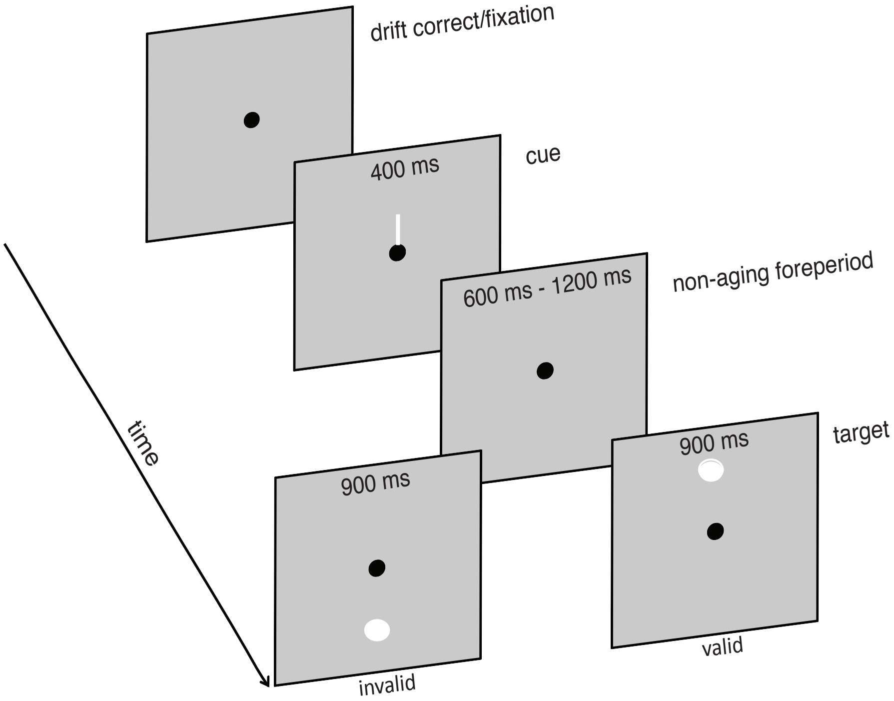

Figure 16. Central cueing paradigm. Trial started with a drift correct, following by the presentation of the cue for 400ms. Then followed a non-aging foreperiod between 600 – 1200ms, following by the presentation of a target for 900ms. Participants were instructed to make a button press quickly and accurately whilst maintaining fixation on the centre point.

Eye movement and response analysis.

Data for both tasks was collected over two sessions for all participants. In both experiments, latencies for each participant and condition were calculated by averaging 10,000 bootstrapped estimates of the median latency. In the first experiment where participants were required to saccade to a highly visible target, we collected a total of 450 trials over two sessions. Saccadic latency was defined as the period between target onset and initiation of the saccade and only the first saccade made during a trial was analysed. Saccadic latencies briefer than 80ms and longer 900ms, or 3.5 times away from individual participant means were excluded from further analysis. Correct responses were defined as saccades starting within 2° of the central fixation point. Visual traces were inspected and trials were only included if the saccade was over 1° in length and executed in the general direction of the target. A flexible criterion was chosen in light of the patient’s reported difficulty making eye movements. Overall in the first experiment, 95% were used for the patient and 93% trials were used for the control group.

In the second experiment, participants were required to make a manual response to the target whilst maintaining fixation on the central point. Reaction times shorter than 150 ms or greater than 900 ms, or 3.5 times away from individual participant means were excluded from further analysis. Finally, oculomotor traces for each individual trial were examined, and trials containing artefacts such as blinks or saccadic responses to the target were discarded. Overall, 93% of the patients trials and 89% of the control groups trials were used for final analysis.

Results

Experiment 1

To examine saccadic performance we had the participants execute simple reflexive saccades to a highly visible luminance target that could appear in one of four locations, either left, right, above or below an the central fixation square, at an eccentricity of 7°. The target was presented at the four locations in a randomized order. The saccadic latency, amplitude, peak velocity duration were estimated trial by trial. Saccadic latency is the time between the onset of the visual target and the onset of the visually guided saccade.

The median saccadic latencies to targets appearing in each of the four locations for the patient's responses and those of the controls are presented in figure 17. As evident in the graph, the patient's saccadic latencies were well within the 95% confidence intervals of the control group, suggesting that the time taken by the patient to determine the location of the target and the saccades is not different from that of the controls.

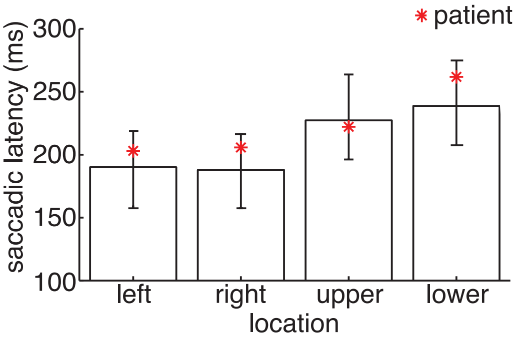

Figure 17. Saccadic latencies to targets located in the four quadrants. The bar graphs show the latencies of the control group with 95% confidence intervals. The red stars represent the patient's saccadic latencies. Notably the graph shows that the patient's latencies are within the 95% confidence intervals plotted by the error bars, and accordingly are not significantly different from the control group.

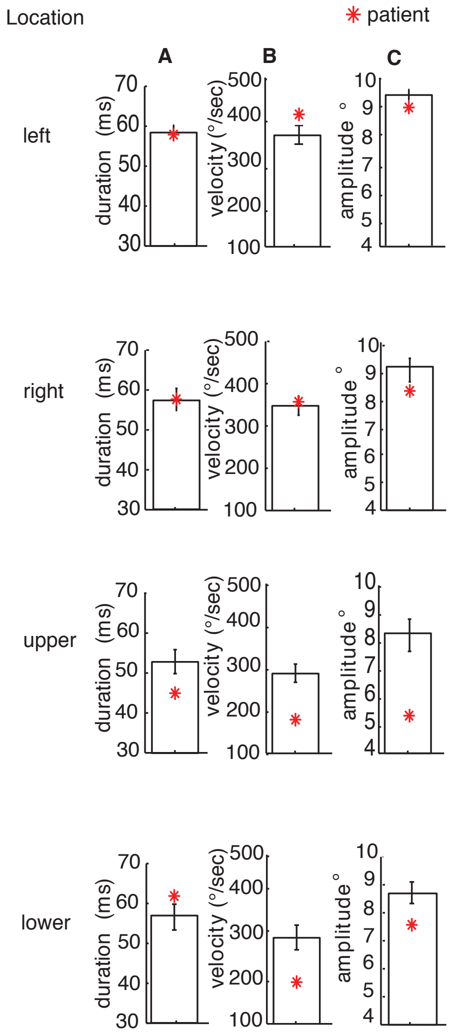

Figure 18. Bar graphs show in **A.** saccadic duration, in **B.** saccadic velocity, in **C.** saccadic amplitude. The bar graphs represent the control groups averaged median latency with 95% confidence intervals. The red star plots the patient's data. As can be seen from the graphs, there is general widespread disruption of the patients saccadic kinematics to all locations. Particularly affected are responses to targets appearing in the upper and lower locations.

Looking at the graphed kinematics (figure 18A to 18C), it is clear that the patient showed abnormal saccadic kinematics compared to the controls. This was the case when the target appeared in all four locations. The patient's saccadic *amplitude* falls beyond the 95% confidence intervals of the control group (figure 18C), to all target locations.

The largest departure from the performance observed in the control group was found when targets appeared in the upper and the lower visual field. The duration of saccades to targets appearing in the upper and lower visual field all falls outside the control group 95% confidence intervals. Saccades to targets appearing in the upper visual field have a shorter duration than saccades to targets appearing in the lower visual field. The peak velocity for saccades to targets in the upper and lower visual field was also below the 95% confidence intervals of the control group. Interestingly, the velocity for saccades executed to targets appearing in the left visual field are above the 95% confidence intervals of the control group, suggesting faster ballistic movements to targets at that location. Overall the results from this task suggest that the latencies of visually evoked saccades are not specifically disrupted in the patient. Nevertheless, the patient shows a slowing and hypometric saccades especially to targets placed above and below fixation.

Discussion

The impairment of oculmotor movement reported in the first experiment is clear evidence of oculomotor disruption. Whilst the overall reduced amplitude suggests the dysfunction is widespread to all locations within the visual field, it appears that the disruption is most severe in the upper and then lower visual field. Disruption of these parameters can also indicate fatigue (Miles, 1929), however here we observed location specific effects. Therefore it is unlikely fatigue, if a contributing factor, is the sole factor, and the results reflect an impairment of oculomotility.

However, it is of note that saccadic latencies were unimpaired. The time taken to program a saccade in response to the onset of a target, the saccadic latency, is often used as a proxy of spatial decision making (e.g. Carpenter & Williams, 1995; Glimcher, 2003), although it also includes an element of attentional orienting (Walker et al., 1995). The normal results of the patient would suggest that his ability to program a saccade is not impaired to the point that performance is noticeably different from controls. Consequently, we may not expect to see an effect of this lesion on attentional orienting.

Experiment 2

In experiment 1, we found that the patient's ability to make a saccade to a highly visible target was impaired when compared to age-matched controls. We next assessed his performance using a simple cueing paradigm using a centrally presented cue (see figure 19). In this task, the participants were required to report as quickly as possible the appearance of a highly visible target. The target could appear in the same four locations used in the previous experiment. The trial structure was as follows. At the start of each trial participants were presented with central fixation point, and a central cue abutting the fixation point would appear for 400ms. The cue correctly indicated the location of the target 75% of the time. We expected that if the patient had an impairment with attentional orienting, this would be demonstrated in the way of an impaired validity effect when compared with controls.

The data for the cueing data is presented in figure 19A-C. The patient's reaction times for valid (figure 19A) and invalidly cued trials (figure 19B) are within the 95% confidence intervals of the control group.

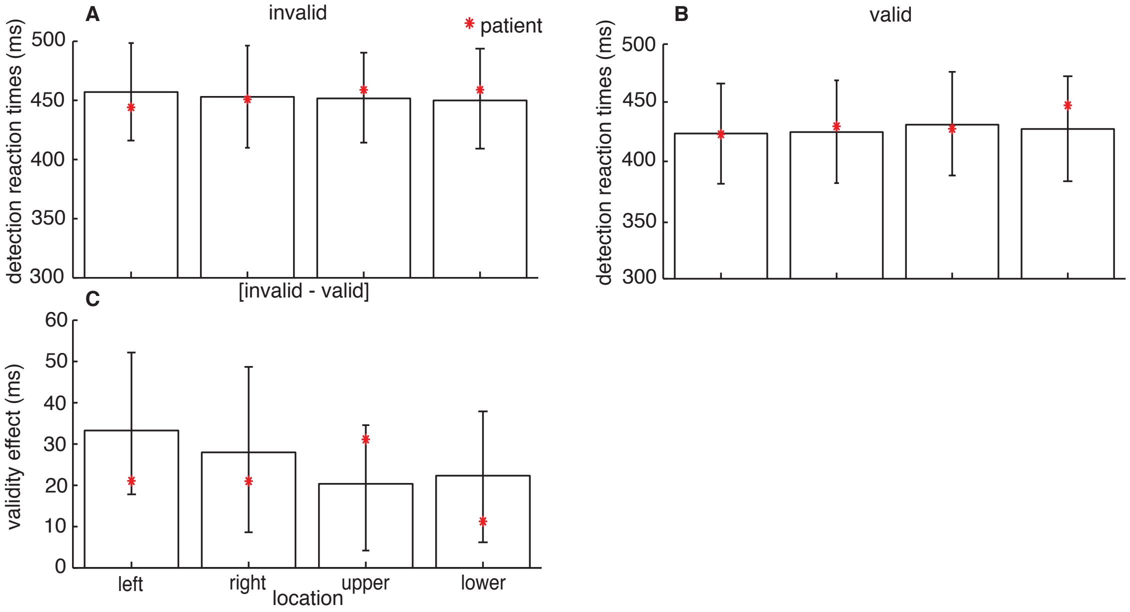

Figure 19. Detection reaction times in the covert orienting, central cueing task. The bar graphs show the averaged median reaction times of the control group with 95% confidence intervals. The red star plots the patient's median reaction times. **A.** Shows invalid reaction times. **B.** Shows valid reaction times. **C**. Shows the validity effect which was calculated by subtracting valid from invalid reaction times. As is clearly evidence from the figures, the patient's performance is within the 95% confidence intervals of the control group, indicating that attentional orienting was not significantly impaired in the patient. Error bars represent 95% confidence intervals.

We also calculated validity effects for each of the four locations (figure 19C) by subtracting valid response reaction times from invalid response reaction times to provide a measure of spatial orienting. As can be seen by the figure, the patient's performance did not differ from the control group at any of the locations. To further investigate if there was a specific effect to horizontal and vertical orienting, we calculated a validity effect specifically those locations. The patient's validity effect for the horizontal component (median = 22.78ms) was within the 95% confidence boundaries of the control group (group averaged medians (29.47ms, 95% CI: 13.05; 48.20 ms). The patient's validity effect for the vertical component (median = 21.05ms) was also within the confidence boundaries of the control group (group averaged medians = 21.05ms, 95% CI: 6.77ms; 27.03ms). Overall these results indicate the patients ability to orientate attention as directed through a central cue was not significantly different compared to the control group.

Discussion

The central cueing paradigm used in experiment 2 is a widely used paradigm for investigating attentional orienting (Posner, 1980). The data suggest that the patient reaction times in valid and invalid trials, and the magnitude of the validity effect, were not different from those observed in the control group. Therefore, the results presented here suggests that in this instance attentional orienting was not impaired. The implications of this will be discussed in the general discussion.

General discussion

We assessed the relation between covert and overt orienting in a patient with a focal lesion in the medial-dorsal thalamus. When the patient had to generate visually evoked saccades to targets appearing unpredictably at one of four cardinal positions, he demonstrated kinematic abnormalities which generalized across all gaze directions. Furthermore, these were most noticeable when targets appeared in the upper and lower visual field. On the other hand, saccadic latencies were not obviously slower in the patient compared to age matched healthy controls. In a separate task, we assessed the effects of partially valid endogenous cues on detection reaction times, where the likely target location was indicated by a central arrow cue. The patient showed no obvious decrement in reaction time speed whether orienting to a valid or reorienting to an invalidly cued target, suggesting that disengaging and moving attention covertly was not affected by his neurological deficits.

These results are at odds with previously published data, which indicate that congenital and acquired oculomotor impairments result in parallel decrements of exogenously driven covert orienting. These previous finding were interpreted as providing support for the premotor theory of attention, namely the idea that attentional orienting requires the same neural machinery that is recruited when moving one’s eyes (Rizzolatti et al., 1987)**.** If so, then our result would be inconsistent with that theory. On the other hand an alternative interpretation of the premotor theory is that saccadic programming and saccadic execution represent separate phases of the processes involved in overt orienting response (Smith & Schenk, 2012). According to this view, despite the oculomotor impairments, the lack of diminished attentional orienting in the presence of normal saccadic latencies is not all that surprising.

However, whilst this account is consistent with our findings, several studies have demonstrated impaired covert orienting in individuals with oculomotor impairments due to peripheral abnormalities of the oculomotor plant. Craighero et al.,(2001) found that validity effects following central cues were diminished in patients with peripheral sixth nerve palsy when the cued location laid in the field of action of the paralyzed lateral rectus muscle. Similarly Gabay, Henik, and Gradstein (2010) demonstrated in three patients with Duane Retraction Syndrome, a disorder characterized by impaired eye abduction, that while endogenous cueing resulted in validity effects similar to those found in controls, cueing resulted in a reversal of the validity effects when targets appeared in the field of diminished oculomotor range. Oddly this effect was driven entirely by an increase in reaction times on valid trials, but there was no obvious effect on invalid trials, whether the target appeared on the side of diminished oculomotor range or the opposite one. In a preceding study, an ophthalmologic patient with congenital hypoplasia of the extraocular muscles, demonstrated also abnormalities in covert orienting impairment, with diminished validity effects following exogenous cues, but increased validity effects following endogenous cues (Smith et al., 2001). These findings were interpreted as indicating that the attentional capture is diminished when normal overt orienting response cannot be generated. The reason why only reflexive, but not endogenously driven shifts of attention were affected in this patient was not investigated further.

Probably the work most relevant to the present findings is a study comparing covert orienting in patients with parkinsonism and progressive supranuclear palsy (PSP; Rafal et al., 1988). The crucial difference between the two patients groups, relevant to the hypothesis of the study, is that while patient with parkinsonism show a generalized deficit in initiating saccades in all directions, patients with PSP show a specific and prominent impairment performing vertical saccades especially in the downward directions. PSP patients had smaller validity effects when the targets were presented above or below the fixation point than when they were presented left and right of the fixation point. This was the case both when the target was cued exogenously or endogenously. The authors concluded that the ability PSP patients to covertly attend targets along the vertical meridian was less than targets along the horizontal meridian, thus replicating the overt orienting problem. However this interpretation does not account for the fact that the validity effects in patients were vastly greater than those encountered in healthy controls suggesting that patients did not have diminished covert orienting. Overall, here we empirically demonstrate intact attentional orienting in the presence of impaired upper and lower saccadic eye movements, suggesting that covert and overt orienting signals are not converged at the point where saccadic signals are parcellated by their horizontal and vertical components.

Chapter 5

Discussion

In **chapter one,** we reviewed the literature on visual attention and highlighted three key issues for further investigation within this body of work. First we asked if probabilistic expectations influence a ballistic, binary process where attention is either committed to a location over a number of trials matching the cue; or if expectations influence an information theoretical, decision making process. The second question the inhibitory mechanisms of spatial attention, and if they are sensitive to top-down expectations. The final problem was the relationship between attention and eye movements, with some theories claiming attention and eye movements are one and the same, and competing accounts that propose attention and eye movements are tightly coupled, but ultimately distinct systems. In **chapter two**, we investigated if attentional accounts or information theoretical accounts could better explain the effects of target probability on covert and overt responses. The data we present shows that for both covert and overt orienting, the effects of target probability were largely the same, with the notable exception of a larger validity effect for central cues in overt response condition. Furthermore, this data is not adequately described by attentional accounts or information theoretical accounts. In **chapter three** we investigated predictions that central cues could be used to endogenously inhibit a spatial location where a distractor is expected to appear, as this is at odds with reports in the literature that central cues invoke automatic orienting. Here we presented data illustrating that central cueing a distractor containing location led to facilitation and not inhibition of the cued location. The effects of cueing the distractor location and the effects of the distractor were same for covert and overt responses. We did however find a difference for covert and overt responses in the priming effect of target and distractor stimuli, with the priming effect nulled for the immediately preceding trial in the manual response task. In **Chapter four** we investigated attentional orienting in a single patient who presented with saccadic disruption after a stroke resulting in lesion in the medial-dorsal thalamus. Based on data obtained in the previous experiments, and literature demonstrating a coupling between attention and eye movements, we expected to see an accompanying attentional impairment because of the ocular disruption, however this was not the case.

Taken together these findings indicate that the relationship between top-down expectations and exogenous effects on covert and overt attention is extremely complex. Subtle manipulation of expectations can result in drastically different behavioural outcomes, which none of the major theories presented within this thesis are currently able to adequately capture the presented results. In the next section, we shall discuss the overall implications of the presented results, before discussing limitations and future avenues of research.

The effects of expectations are largest when expectations are breached

An overall theme of the data in this thesis is that the largest effects of expectations on covert and overt orienting appear to be captured when expectations are breached. This was presented in chapter II (figures 6), were we found that the largest effects of spatially blocking the cued location are found when targets appeared in low probability locations, rather than high or neutral probability locations and then in chapter III, as the distractor was suppressed on invalidly cued, target cueing trials (figure 11). These data suggest that the expectations specifically engage processes when expectations are breached. Accounts for this finding have included habituation to recurring stimuli (Sokolov, 1963) or that the interruption of expectations invokes circuitry specialized for examining novel and unexpected stimuli (e.g. Corbetta & Shulmen, 2002; Pavlov, 1927), or the reorientation of attention to the new stimuli containing location (Laberge, 1973). Indeed, a number of studies have reported a stimulus driven system, which is sensitive for orienting to sudden, unexpected stimuli (e.g. Shulman et al., 2010).

Central cues do not initiate endogenous spatial inhibition

The data presented in the second chapter (figures 10, 11, 12) suggests that centrally cueing the location of a distractor resulted in facilitation not inhibition of the cued location is harmonious with claims that attempts at active inhibition can, surprisingly, lead to increased priority of the to-be-inhibited stimulus (Lahav et al., 2012; Tsal & Makovski, 2006). There are several explanations for this. On one hand, these findings are inline with predictions that attempts at active inhibition leads to increased activation of the stimuli in memory, which results in facilitation rather than inhibition of the stimulus intended to be ignored. By contrast, another explanation is that the automatic orienting effects associated with central cues (Hietanen et al., 2006) could mean they are simply not suited to communicating information intended to encourage spatial inhibition (indeed the validity effect for neutral cues reported in chapter two may also reflect an automatic orienting effect). Indeed, previous reports that spatial inhibition can arise from using symbolic cues to cue a location are at odds with the finding that such cues result in automatic orienting of attention to the cued location. One explanation is that distractor cueing negates the effects of distractors on motor processes, rather than orienting processes. As previous studies have used a duel choice response method (e.g.

Munneke et al., 2008) or have investigated the effect of distractor cueing on motor processes such as saccadic trajectories (Van der Stigchel & Theeuwes, 2006). Although some claim that saccadic deviation from distractor stimuli is evidence of spatial inhibition (Sheliga, Riggio,& Rizzolatti,1994). Alternatively, the system may simply opt not to inhibit spatial locations when there is a chance, however small, that a relevant stimuli may appear in the distractor expected location, thus our finding may reflect an adaptive response strategy.

Whilst the central cue failed to invoke spatial inhibition, our data showed evidence of non-spatially specific distractor suppression. Specifically, we found that the effect of the distractor was nullified during invalidly cued trials, when the purpose of the cue was to indicate the location of the target, but not for trials when the role of the cue was to encourage spatial inhibition by indicating the location of the task-irrelevant distractor. This suggests that the overall search strategy was defined according to the purpose of the cue, possibly leading to co-activation of the signals associated with filtering irrelevant distractors and the signals associated with re-orienting (Shulmen et al., 2007).

The memory kernel analysis (figure 13) revealed reaction-times were slightly faster when the distractor appeared in a previously occupied location and the benefit for persisted for ~7 trials. The analysis also found that reaction times were faster when the target had previously been presented one of the previous 7 trials. These findings imply that prior events are tracked in the way of a tonic signal which is spatially specific for the location of the distractor stimuli, and spatially and event (when it appears vs. has not appeared) for the target stimuli.

The effects of expectations on covert and overt orienting are largely the same

A central question to this thesis regards the nature of the relationship between eye movements and attention. Is the nature of this relationship one where attention and eye movements are tightly coupled, but inherently different systems? Or is this relationship one where attention, or the increased processing priority of a stimulus, is a byproduct of a planned ocular movement to the stimulus? We chose to investigate this behaviourally in chapters two and three, by comparing the effect of manipulating observer expectations on saccadic and manual responses in healthy young adults. When we were unable to discrimination between the two response types using this method, we decided to augment the first two behavioural studies with a neuropsychological investigation of the relationship between the two processes using a patient who presented oculomotor problems.

The patterns of the behavioural data presented in chapters II and III showed that the effects of expectations on covert and overt responses were largely the same, although there were a number of notable discrepancies. The first departure was the finding of saccadic anisotropies reported in chapter two. It has been claimed that this represents an orienting effect (Zhou & King, 2002), however that we failed to demonstrate this effect in the manual version of the task, indicates that mechanism responsible for this appears not to influence simple detection responses in the same manner. One potential explanation of this finding, is that these affects arise during the motor execution stage of a saccade, which has previously been argued as distinct from programming (Smith & Schenk). Consequently, these differences are not evidence against premotor theory (e.g. Smith & Schenk, 2012). However, the original explanation of premotor theory proposed that the involvement of motor specific structures, such as ocular muscles, took place during covert orienting (Rizzolati et al., 1987) therefore such an argument is somewhat invalid.

The next difference was also presented in experiment two where we found a larger validity effect for saccadic responses compared to manual responses (figure 7), which was due to cue validity modulating the proportion of express saccades. This finding is harmonious with reports that failed to find express responses for manual response tasks and suggests that central cues can activate ocular specific pathway. The final departure we reported was the absence of the priming effect in the previous trial shown in figure 13. One possible explanation for this finding, is that this inhibition reflects the lingering effects of cancelling a previously programmed eye movement, as has been proposed to occur in covert orienting tasks (Rizzolatti et al., 1987). However aside from the previous trial, the effects reported in that analysis are identical, which perfectly illustrates the idea that eye movements and attention are coupled by shared computational processes.

In **experiment three** we further interrogated the relationship between attention and eye movements by investigating if there was evidence of an attentional impairment in a single patient who presented with upward, hypometric saccades after suffering a lesion in the medial-dorsal thalamus. Based on the behavioural results of experiment one and two, we would expected that the impairment in saccades to be accompanied by an attention impairment. Instead the data showed that whilst there was overall ocular disruption, with the largest disturbance in the upper and lower visual field, there was no evidence of impaired covert orienting. This finding supports previous reports that there are ocular specific and attention specific structures within the brain (Smith & Schenk, 2012), and specifically our finding indicates that this includes brainstem structures where horizontal and vertical aspects of eye movements are parcellated.

Implications for theories of attention and eye movements

Aside from some minor deviations, one of which - the manual response inhibition seen the memory kernel analysis - can still be connected to ocular processes, the behavioural results of this study are overall supportive of claims that covert and overt orienting share a single computational process. However the results presented in chapter IV are in line with claims that the signals for attention and eye movements are also isolated within certain structures. When the results presented in this thesis are considered together, the grand implication is that attention is unlikely to be the product of the ocular system as proposed by premotor theory (Rizzolatti et al., 1987). Nor is the converse explanation adequate, that attention and eye movements are two unrelated processes, as such a stance is not supported by the literature, because whilst attention can be deployed independently of eye movements (e.g. Helmholtz, 1867), saccadic movements typically require attention to be deployed at the planned saccadic location (Duebal & Schneider, 1996). Instead our findings are supportive of the perspective that covert and overt orienting are coupled by a single computational system as(Duebal & Scheider, 1996) but are ultimately distinct processes, as proposed by VAM. Since this viewpoint could account for similar patterns of behavioural findings across covert and overt orienting; indicative of a shared computational mechanism processing expectations. Whilst also accounting for the finding of unimpaired covert orienting in the presence of oculomotor disruption, which is indicative of distinct systems.

In evolutionary terms, the notion that a single attentional resource is a shared asset across different perceptual modalities makes intuitive sense, due to limited cortical space and therefore it would be a waste of resources to have several systems with a common role – to orientate towards goal-relevant, visual stimuli. Less tantalizing, is the concept of a data processing system crucial for all aspects of our survival, which is interrupted each time the eye moves (Schneider, 1995). So where does leave premotor theory? Whilst the strictest interpretation of premotor theory clearly fails to hold up against the data presented in this thesis (and when examining the wider literature), it still provides an extremely useful platform from which to probe the relationship between eye movements and attention. Indeed, as this thesis has shown, simple paradigms can be easily adapted to investigate both processes, which provide easily comparable data. Less useful however, is the use of premotor theory as an explanatory account. Instead, the VAM model described at the beginning of this thesis is significantly better at capturing the results presented within this thesis: namely that action and attention are distinct processes, which are reconciled through a shared mechanism.

Limitations and future studies

A number of interesting issues arose from the data presented in this thesis, which should be the subject of future investigations. One theme of the date is that much of the behavioural effects of expectations are observed when they are breached. Consequently, an interesting avenue of research could be to investigate what happens when expectations are met, using methods that may provide more sensitive measures than reaction-time tasks. One line of investigation could be to use electrophysiological techniques. For example, whilst the behavioural difference for high probability and equiprobable targets were less than the difference between low probability compared to high/equiprobable targets (chapter two), electrophysiological investigations could reveal differences not observable through reaction time based experiments. One candidate for investigation could be event related potential positive 300, the P300, which has been proposed as related to attentional expectations (e.g. Polich, 2004). This would also be particularly useful to follow-up the paradigm presented in chapter III, where we found no differences inn participant cue across cueing conditions, despite each of the two cues being reliable for different stimuli. Therefore an electrophysiological study could delineate different computational processes, which cannot be captured with purely behavioural experiments.

Another thought-provoking question arises from the priming effects presented in chapter three, regarding where this tonic signal is stored. A likely structure could be the superior colliculus, as previous studies have shown this structure is sensitive to tracking previous events (Basso & Wurtz, 1998). Therefore future studies could investigate if activity within this structure, is correlated with the magnitude for the priming effect, by adapting our paradigm for use with functional magnetic imaging. Similarly, future studies on expectations could also apply the memory kernel analysis to ascertain precisely how much of a behavioural effect is the product of priming; rather than the result of strategic, top-down responses. One final interesting issue that arises from this analysis is if this effect is crossmodal. A future behavioural study could address this by mixing manual and saccadic response trials within blocks, and then perform MKA analysis using the alternative response type as the history trial. The benefit of such an approach would be direct evidence of a shared computational process between attention and eye movements.

We failed to demonstrate evidence of endogenously deployed inhibition in chapter three. One interpretation is that attempts at active suppression result in an attentional *white bear effect*, leading to facilitation of the distractor containing stimuli due to associated automatic orienting effects. Alternatively, it may be that central cues are simply not suited to communicating information intended to encourage in spatial inhibition. Therefore future studies should employ other means of biasing expectation of distractor stimulus, such as spatially blocking the distractor stimulus.

The final limitation discussed here relates to the patient case study reported in chapter four. Whilst we were able to delineate ocular and attentional processes using two different paradigms, it would have useful to have applied the methodological theme used in chapters II and III, and had the patient perform both saccadic and detection versions of the target localization and cueing task. Consequently, future patient studies probing premotor theory should continue to use the single patient study due to it being more sensitive than group studies where lesion subtleties can be lost within group variance, but they should compare different response measures on the same task. Unfortunately in this instance we were unable to recall the patient back due to logistical difficulties on the patient's side.

Future studies investigating the relationship between attention and eye movements could extend research to investigate the extent to which attention is coupled to other motor modalities. Indeed the two prominent theories which claim eye movements and attention are related, both claim that this relationship extends to all motoric actions. Such a program of study could easily adapt the methodological theme adopted within this thesis of setting up paradigms in ways that different modalities of responses can be directly compared.

Appropriateness of the methodology

Another question that is pertinent for this discussion is the adequacy of the methodological method employed within this body of research. One of the key themes was the comparison of covert and overt response methods. We decided to directly compare manual and saccadic responses as this would allow us to adequately compare how saccades and manual detection (considered to index covert orienting) computed expectations, with the intention of seeing if we could disassociate attention and eye movements by observing different patterns of behavioural results. One criticism of this method is that it could be considered to be less sensitive than methods which have attempted to delineate attention from eye movements by spatially dissociating the two processes (e.g. Kowler et al., 1995) or investigating how manipulating attentional demands affect eye movements. However, it is already well documented that attention is involved in eye movements, thus we wanted to probe the two systems with the main aim to of identifying differences in computational processes. That we found subtle differences between covert and overt orienting in chapters one and two, clearly supports this decision.

Closing statement

This body of research makes a number of contributions to the literature discussed in the opening chapter. **One**, the evidence presented here indicates that the facilitatory aspects of attention are extremely sensitive to expectations, particularly when they are breached. **Two**, the inhibitory mechanisms however seem less easy to manipulate using prior expectations, or at least they are not as intuitive as one would expect: namely as they did not use the cued information to inhibition a spatial location, rather they changed the search strategy, but not in a way that was non-spatially selective, rather event selective, when the target was invalidly cued. **Three,** the memory kernel analysis indicated that the events on a trial can influence expectations for a considerable number of future trials, thus attentional orienting is sensitive to endogenous effects. Finally, **four**, the behavioural results covert and overt orienting share a common, computational mechanism; however the results of the patient study fail to demonstrate a casual relationship between these two mechanisms. Overall these results, their implications, and the potential ways in which they could be followed up with future research confirms that attention is still no less of a challenging and exciting topic than it was for early researchers of the field.

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