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Dimension-specific effects of endogenous and exogenous spatial cueing : indication for integration of spatial and feature-based attention

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**Dimension-specific effects of endogenous and exogenous spatial cueing:
Indication for integration of spatial and feature-based attention.**

Katherine E. Burnett

A thesis submitted to Bangor University
for the degree of
Doctor of Philosophy
2012

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Acknowledgements

There are many people to whom I owe a great deal for their help, support and encouragement throughout the course of my PhD, indeed, throughout my time in Bangor.

Many thanks to my supervisors: Thanks to Dr. Ayelet Sapir for allowing me the freedom to take this research in the direction I wanted, for respecting my decisions, and for supporting me when I made mistakes. Thanks to Dr. Giovanni d'Avossa for his interest in my project, and his willingness to offer programming expertise and theoretical input. Thanks also to Prof. Steve Tipper for making review meetings something to look forward to! I'd also like to thank the members of the lab, in particular Alex Close, with whom I've shared an office since we both started our research.

My PhD has afforded me the luxury of international travel in order to present my work at conferences and attend training workshops in Lausanne, Switzerland; Maastricht, The Netherlands; Naples, Florida; and Chicago, Illinois. I have been very lucky to have these opportunities, as they allowed me to meet and visit friends, and to discover new places. Thank you, BrandeEEEE, for always being in a different city but being the same incredible friend. Thank you, the Kustus family, for welcoming me into your home: my home away from home. Thank you, Biddy Andrews, for letting me drag you on a 30hr train journey to Texas, to a honky tonk bar, to shop for cowboy boots, and for listening to country music the whole time ... and for enjoying it!

I have made some wonderful friends in Bangor. Some have already left, but their constant support and friendship still means a lot to me: "Katy from the Isle of

Man,” “Izzy Beans Sloss,” and “Aye-ler Watson,” I love you guys. Thanks also to my friends across North Wales who provided important escapes from the stress and pressure of completing this thesis! Pam handed in her PhD thesis just as I started my PhD, and I’d like to thank her for every time she’s listened to me, encouraged me, and reassured me over the years.

In the last year of my PhD, I’ve been fortunate to make some new friends who are really close to my heart. Thank you, Anna Beres, for making me laugh, for making me pancakes, and for taking the time to listen to me. Thank you, Vicky Lovett, for always lending an ear, and for being a sensitive and caring friend. Thank you, Sharon Nelis, for the tremendous support and kindness you’ve shown me. You made me smile at times when I really needed it, and I’ve always enjoyed spending time in your company. I will miss you.

Those alongside me during my PhD have contributed hugely to my enjoyment of my time here. Book group/board games (particularly those that do not require lying or stealth) night/Apprentice night has brightened up my week. Biddy Andrews, Julie Kerai, Lowri Hadden, Wendy Adams and Thandi Gilder have made me laugh and seen me cry, and I consider myself very lucky to have got to know them during the course of our studies. I am extremely lucky to have been part of a fantastic department, and I’ve thoroughly enjoyed the working environment in the School of Psychology.

Finally, to my Mum, Dad, brother Adam, and all my family, thank you for your support and love.

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Abstract

The experiments in this thesis were designed to examine the consequences of endogenous and exogenous spatial cueing in a dual-task set-up. The first experiments, presented in Chapters 2 and 3, explored whether spatial attention generalises across dimensions in the same location. Chapters 4, 5, and 6 contain a second series of experiments using exogenous cues, in which cue properties were manipulated.

A dual-task set-up was used in all studies in this thesis, with a display of four random dot kinematograms containing motion and colour features. In order to examine whether endogenous attention may be spatially oriented to only one feature dimension, a central cue was presented that was 70% valid for the location of only one task. Both tasks showed validity effects, but the task for which the cue was informative showed larger attentional modulation. This suggests that spatial attention is not a single 'spotlight' but can be biased in favour of expected features. There was also asymmetry in the tasks, whereby the validity effect was modulated for motion, but comparable for colour regardless of the task for which the cue was informative. This asymmetry was also evident when using uninformative exogenous cues preceding the same tasks. Peripheral luminance and colour cues affected the validity effects for the motion and colour tasks differently, suggesting that the relationship between cue properties and proceeding stimuli modulates attentional effects. The size of a frame cue leads to different attentional effects on tasks of different sizes.

These experiments make a considerable contribution to the spatial attention literature, by showing that spatial attention may be biased either by cue properties or cue information, suggesting that spatial attention and feature-based attention may interact. They also provide further evidence that motion is better represented than colour in visual attention.

Chapter 1. Literature Review

Attention Overview

As organisms, we are constantly surrounded by countless stimuli, from which to construct our internal world and behave accordingly. Our brains are tremendously powerful but cannot process every stimulus around us in every millisecond of our days. Therefore, the brain must be able to select those stimuli that are important to us, and ignore those which are irrelevant. Attention is a mechanism that allows the brain to select stimuli that warrant further processing and disregard others (James, 1890).

In order to identify stimuli that are important for our goals and survival, attention can be captured by salient stimuli, or directed voluntarily based on probability weightings about likely locations or features of an expected stimulus. Salient stimuli, such as sudden new object onsets, lead to a stimulus-driven, or bottom-up, effect known as orienting of exogenous attention. Top-down intentions can lead to orienting of endogenous attention, driven by goals and prior information, such as the probability of a target appearing in a certain location. The manner in which attention is oriented leads to distinctive behavioural effects, with some researchers suggesting that endogenous attention and exogenous attention are separate, independent mechanisms (e.g. Berger, Henik, & Rafal, 2005). Regardless of these differences, both mechanisms lead to similar effects in that performance is improved for attended compared to unattended locations or dimensions.

Attention improves performance on different tasks, using both supra-threshold and threshold stimuli, in which participants are asked to detect or discriminate some aspect of the stimulus. One such stimulus is the random-dot

kinematogram (RDK). RDKs are windows containing a number of individual dots. Each dot moves in a given direction for a certain length of time before being re-plotted randomly within the window. Translating a proportion of the dots in the same given direction creates coherent motion. Attention affects the threshold at which participants are able to accurately report perceptual features, such that the threshold to correctly report motion direction is lower when attended (e.g. White & Carrasco, 2011).

Two means of selecting task-relevant stimuli have been studied extensively; attention to location, and attention to non-spatial features or dimensions. Attention can be directed in space with (overt attention) or without (covert attention) eye movements. Feature-based attention is widely accepted to select based on either dimensions (e.g. shape, colour, motion) or features (e.g. square, red, upward motion) that are defined as non-spatial. Research suggests that these two systems are independent (e.g., Egner et al., 2008; Fecteau, Korjoukov, & Roelfsema, 2009; Patzwahl & Treue, 2009; Sàenz, Boynton, & Koch, 2006; Schenkluhn, Ruff, Heinen, & Chambers, 2008; Serences & Boynton, 2007; Treue & Martínez-Trujillo, 1999), though there are some authors who propose that location is actually a feature of a target, so that spatial attention is a sub-type of an attention system built on feature processing (Patzwahl & Treue, 2009).

This chapter contains a discussion of literature that examined spatial and feature-based attention, both in isolation and conjunction, in order to review evidence for independence or interaction of the two mechanisms. The distinctions between endogenous and exogenous spatial attention are also considered.

Spatial Attention

One way in which attention selects stimuli for further processing is by location. In an early study, Eriksen and Collins (1969) displayed six letters in a clock array, and participants were required to report the identity of a target letter that was indicated using an arrowhead or symbolic number in the centre. The authors noted that performance increased when the letter was indicated prior to it appearing. They attribute this to time taken to orient attention to the cued location. However, the cue always indicated the letter to report, so the authors did not compare accuracy to conditions in which the location was not known.

Shaw and Shaw (1977) extended these findings by using blocks in which set locations were assigned a probability of containing the target. Therefore, the authors could examine accuracy of reporting the target letter when it appeared in a likely location compared to an unlikely location. Participants maintained this representation of the likely location across numerous trials, and results suggest that attention improved performance at the probable location. These early works advanced thinking of location as a means of attentional selection.

Posner cueing paradigm.

Perhaps the most influential contribution for location as a means of attention selection is the Posner cueing paradigm (Posner, Nissen, & Ogden, 1978). In the original Posner paradigm, a schematic of which is shown in Figure 1.1, two possible target locations were used, to the left and right of fixation. Participants made speeded responses to a target presented in one of the possible locations. The target detection task was preceded by a central cue at fixation; either a plus sign providing no spatial information, or an arrow that informed participants which location the

target was more likely to appear at. Reaction time (RT) was compared in three conditions: neutral, in which case no spatial information was provided and the target was equally likely on either side (50%); valid, in which the target appeared at the cued location (80%); and invalid, in which the target appeared at the uncued location (20%). RT to targets following a valid cue was significantly faster than to targets following neutral cues, and RT to targets following invalid cues was significantly slower than to targets following neutral cues. Therefore, valid cues were associated with a performance benefit and invalid cues were associated with a performance cost. The authors conclude that prior knowledge of spatial position aids performance, implying a shift of attention to the likely location.

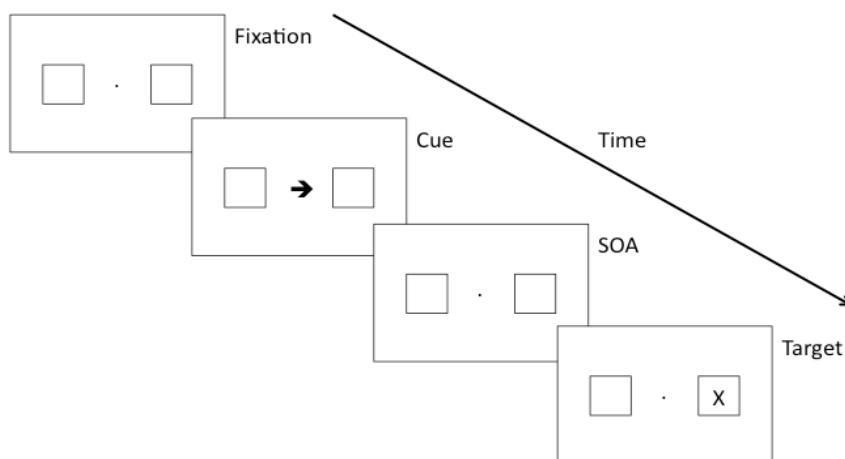


Figure 1.1. Illustration of the Posner cueing paradigm. Trials begin with a period of fixation, followed by a spatial cue, in this case an arrow. The cue holds a certain probability that the location it indicates will contain the target. After another period of fixation, a target appears in one of the two placeholders, and participants make a response. The trial shown is a valid trial.

This same effect has been observed with increased possible target locations. For example, Posner, Snyder, and Davidson (1980) used four locations, two either side of fixation at eccentricities of 8° (near) and 24° (far). The cued location was 79% likely to contain the target, with the other locations 7% each. A clear benefit when the target appeared at the cued location, and a cost when it appeared at the uncued location, were observed. Moreover, the authors identify the difference in performance on valid and invalid trials as a measure of attention allocation due to expectancy. Additional research has corroborated this finding, demonstrating that accuracy and sensitivity also show a validity effect (Giordano, McElree, & Carrasco, 2009; Jonides, 1980; Posner et al., 1978).

Cue reliability.

The Posner cueing paradigm has been extended by manipulation of the usefulness of the cue. In order to inform participants to orient voluntary attention, central cues have attached probability values, which indicate how likely it is that the target will appear in the cued location. The usefulness of a cue is often known as cue validity, referencing how often the cue indicates the correct, or valid, target location. Throughout this thesis, the probability value attached to a cue will be referred to as cue reliability.

Jonides (1980) investigated performance following central cues with different associated cue reliabilities. Letters were arranged in an eight location circular display, and participants were asked to respond accurately and quickly to which target (L or R) was present. A central pre-cue was neutral, or 70%, 50% or 30% reliable, in separate sessions. The RT and accuracy measures both showed a cue type (valid, invalid or neutral) by cue reliability interaction, due to an increase in

validity effect as cue reliability increased. As validity effect is a measure of cue utilisation, Jonides suggests that the higher the reliability of a cue, the more we use it.

Further research into cue utilisation in endogenous attention has also used varied cue reliabilities (Eriksen & Yeh, 1985; Giordano et al., 2009; Madden, 1992; Vossel, Theil, & Fink, 2006). Giordano et al. (2009) asked participants to discriminate the orientation of a target Gabor stimulus, following a central cue of 12% (chance), 33%, 50%, 66% or 100% reliability in separate sessions. Both the difference in sensitivity (d'), and the difference in RT at the valid versus invalid locations increased with cue reliability. Taken together, these results confirm the suggestion of Jonides that cue utilisation increases with cue usefulness.

Imaging research has also corroborated the behavioural data (Vossel et al., 2006). By mixing 60% and 90% reliable cues on a target detection task, the authors showed behaviourally, through the validity effect, that it was possible to utilise cues differentially even when they are not blocked by reliability. Blood-oxygen level dependent (BOLD) activation in the right parietal and frontal lobes showed modulation related to cue reliability, suggesting a neural basis for the difference in validity effects seen in behavioural studies.

Estimating cue usefulness.

Eriksen and Yeh (1985) showed that the proportion of trials in which attention was focussed to the cued location could be directly predicted from the associated cue probabilities. They used primary and secondary cue reliabilities for four possible target locations, so that the cue indicated the target location either 40%, 70% or 100% of the time. When the cue was 40% valid for the primary

location, it was also 40% likely in the secondary (diametrically opposite) location. When the cue was 70% valid for the primary location, it was 10% valid for the secondary location, equating to the target being equally likely in the remaining three locations. They found that as the primary cue reliability increased, RT decreased, supporting the idea that cue reliability informs attentional orienting. Importantly, they also found that using a 40% valid cue meant participants would focus attention at the cued location on 40% of trials.

However, Madden (1992) used linear regression analysis, and found that the proportion of focussed attention trials in the best fitting model was consistently higher than that predicted by cue reliability. This was especially true of lower reliability cues. This overestimation of the usefulness of low reliability cues has also been seen when using symbolic cues, such as arrowheads, that are uninformative about the location of an upcoming target. Even though these cues do not provide any spatial information, participants still show greater performance at cued than uncued locations (Gibson & Bryant, 2005). Furthermore, larger validity effects were observed when participants were required to identify whether the symbol was a bar or an arrow on a go or no go task. This suggests that processing the cue increased cue use, which again bolsters the argument that these are voluntary attention effects.

Models of spatial attention.

Several models of spatial attention have been proposed, based on the assumption that attention has limited capacity (Cheal & Gregory, 1997; Eriksen & Yeh, 1985; LaBerge & Brown, 1989; Posner, 1980; Shaw & Shaw, 1997). Estes and Taylor (1966) used a visual search task, and showed that accuracy decreased and RT was slower as the number of letters in a display increased. This was attributed to an

attentional mechanism of *serial search*. The authors suggest that attention operates serially, checking each location for a possible target before moving on to the next, so that the more items in the display, the longer visual search takes.

Treisman (Treisman & Gelade 1980; Treisman, 1988) suggests that individual features, such as colour or motion direction, are processed in parallel and do not require attention in order to be recognised. Consequently, when a target differs from distractor objects in a visual scene on only one dimension, such as colour, it can be easily located without the need for attention. However, in order to combine features into objects, Treisman proposes that attention is necessary – known as feature integration theory. Therefore, when a target is defined by a combination of features, and differs from some distractors on one dimension but from others on a different dimension, attention is vital in order to identify the target. Whereas feature search is not influenced by the number of distractors present, RT to detect a conjunction target increases as set size increases, suggesting that each stimulus is attended in serial until the target is found or all stimuli have been processed.

Two-stage models of spatial attention separate visual search into two processes (Bergen & Julesz, 1983; Folk & Egeth, 1989; Hoffman, 1979). A parallel assessment of all locations is preattentive and is then followed by serial search of likely locations. Bergen and Julesz (1983) support this hypothesis by showing that in the case of a target (L) detection task, varying the number of dissimilar distractors (+) did not reduce accuracy, as these targets would “pop-out”. However, when the distractors were similar (T), increasing the number of distractors led to a decline in accuracy.

Theeuwes, Kramer, and Atchley (1999) suggest that there is an attentional component even with pop-out targets, which is in contrast to the two-stage model.

With both endogenous and non-informative exogenous cues, they were able to show a validity effect on a simple pop-out detection task. If pop-out targets were identified in stage one in parallel, as suggested in the two-stage model, attentional effects would not have been found. These results are therefore inconsistent with a two-stage model.

Jonides (1983) proposed a different model, the *two-process model*. The major proposal of the model is that attention is first directed to the cued location. If the target is not present at the cued location, then attention is spread and the remaining locations are processed in parallel. In the absence of a spatial cue, attention remains spread and processes all locations in parallel (Jonides, 1980).

Many models include specific predictions about the nature of directing spatial attention. Proponents of the *spotlight theory* recommend that spatial attention is a focussed beam, which enhances stimuli within its bounds (Posner et al., 1980).

LaBerge (1983) presented five letter words or non-words, and attention was manipulated by the participants' task, either a single (central) letter or whole word task. A probe then appeared in any of the five letter positions, and RT to discriminate the probe was measured in each task condition. Following the central letter task, discrimination was faster for central probes and slower for peripheral probes, in a V shape curve. The pattern was not the same following the whole word task, with RT not significantly different across probe positions. LaBerge attributes this pattern to the spotlight width. When the spotlight had been contracted to complete the single letter task, RT to the probe was slower outside of the bounds of attention. However, when the spotlight was wider in order to take in the whole word, probe RTs were equal because they were all within the bounds of the spotlight.

Alternative models have followed from the spotlight analogy. Eriksen and Yeh (1985) proposed the *zoom lens* model of attention, which advocates one attention system that expands or contracts for optimal attention resources. Focussing the lens directs the attentional resources to a small area, whereas expanding the lens spreads attentional resources over a wider area. This would allow for both the parallel processing or close attentional focus of Jonides' (1983) two-process model, but as one integrated system.

One prediction of the zoom lens model is that if attention were spread over a larger area, the attentional effects would be weaker than when attention was focussed on a small area. Using an eight-letter circular array, Eriksen and St James (1986) cued one, two or three contiguous locations with four stimulus onset asynchronies (SOAs; -50ms, 50ms, 100ms, 200ms). A target letter always appeared within the cued area, and RT to identify the letter was measured in each trial. The larger the cued area was, the slower RTs were. This suggests that the spread of attention over bigger areas 'dilutes' its effects, supporting a model of a zoom lens.

N. G. Müller, Bartelt, Donner, Villringer, and Brandt (2003) tested the zoom lens model using fMRI. The authors applied the principles of retinotopy; neurons in visual cortical areas are organised relative to the visual space they process (Sereno et al., 1995), and attention has been shown to modulate the response of cells corresponding to the attended location (Tootell et al., 1998). N. G. Müller et al. hypothesised that attention operating through a zoom lens, generates two predictions. Firstly, when attention is spread over a larger area, the response of a larger area of visual cortex should be activated. Secondly, limited resources spread over a larger area should render the amplitude of response smaller than when resources are focussed on a smaller region. Participants were endogenously cued to

one, two or all four possible target locations, and asked to report target presence or absence in each trial. Behaviourally, N. G. Müller et al. replicated the results of Eriksen and St James (1986); performance was higher on small cued trials, and lower for medium and large cued trials. The imaging data showed a significantly larger extent of activation as the cued area increased, alongside a significant decrease in BOLD amplitude as the area increased. Therefore, the results support the zoom lens model of spatial attention.

A competing model of spatial attention is *gradient theory*. Rather than a beam or lens, gradient theory supposes that attention is distributed throughout visual space differentially depending on task demands (Madden, 1992). Henderson (1991) suggests that attention has a focus and diminishes radially from this centre, so that attention gradually decreases as it gets further from the focal point. In a target discrimination experiment, Henderson found that the validity effect was larger following small cues than large cues, and that the costs of an invalid cue were greater for small cues than large cues. Henderson explained that to focus attention on a smaller area removes resources from more distant areas, whereas to focus on a larger area leaves a more distributed attentional field.

Endogenous and exogenous shifts of attention.

The shift of spatial attention can be either endogenous, from within participants following information or experience, or exogenous, automatic and stimulus-driven. Exogenous attention is attracted by peripheral cues in, or adjacent to, a spatial location, whereas endogenous attention is oriented following centrally presented cues indicating a spatial location. Central cues are often arrows or lines, oriented towards the location to be attended, but some researchers use learned

colour or number associations. These systems have been studied both in isolation and in opposition in order to examine their natures and assess their relationship.

In some of the early work examining exogenous and endogenous cueing, Jonides (1981) identified four different characteristics of exogenous and endogenous attention. Firstly, both cue types were examined under increasing levels of load. Higher cognitive loads led to a reduction in endogenous cueing effects but did not have an influence on exogenous cueing effects, suggesting that orienting endogenous attention is effortful and requires cognitive resources, whereas exogenous attention is automatic. Neuroimaging data support the view that endogenous attention is more effortful, as activation was more extensive for endogenous attention than exogenous attention, suggesting the recruitment of more resources (Rosen et al., 1999).

Secondly, Jonides' experiments provide evidence that endogenous cues can be ignored but exogenous cues cannot. This assertion has been repeatedly reinforced by experiments in which exogenous cues are non-informative yet yield large validity effects (e.g. Berger et al, 2005; Berlucchi, Chelazzi, & Tassinari, 2000; Jonides, 1981; Prinzmetal, Zvinyatskovskiy, Gutierrez, & Dilem, 2009). Thirdly, manipulating the expectancy of a cue showed that exogenous cues always capture attention, but endogenous cueing effects are only observed if the cue is expected, or if there is sufficient time to process it. Finally, the effects of exogenous attention are larger than those of endogenous attention, also replicated by H. J. Müller and Humphreys (1991).

Further research has highlighted two further contrasts between endogenous and exogenous attention. Firstly, the profile of each mechanism differs across time, and, secondly, endogenous attention is more flexible than exogenous attention.

Timecourse.

The respective timecourses of endogenous and exogenous attention show different patterns. Endogenous attentional effects peak at around 300 ms after cue onset (Cheal & Lyon, 1991) and can be sustained for long periods of time (Silver, Ress, & Heeger, 2007). This reflects the intentional component of endogenous attention.

When attention is automatically oriented following an exogenous cue, the greatest benefit comes around 100ms after the cue and the effect is transient, indicating its reflexive nature (Cheal & Lyon, 1991; Nakayama & Mackeben, 1989). Increases in performance at the cued location are replaced by deficits after around 300ms (Posner & Cohen, 1984), an effect known as inhibition of return (IOR). This later suppression has been explained as a mechanism that prevents capture by a stimulus that has already been attended, in order to examine alternative spatial locations (Itti & Koch, 2001). Again, this explanation re-affirms the lack of voluntary control over exogenous attention, and suggests a system that allows for efficient search under automatic conditions.

Flexibility.

Endogenous attention has been found to be a more flexible mechanism than exogenous attention, and can alter its operation based on the stimuli and task demands. Yeshurun and Carrasco (1998) found that exogenous cues led to a decrement in performance at eccentricities where perception of targets would be impaired by a resolution increase, and an improvement at eccentricities where resolution increases would enhance perception of targets. They proposed that exogenous attention always increases resolution at a cued location, regardless of

whether task performance would be impaired, suggesting that its effects are automatic. Conversely, following endogenous cues, there was only an increase in resolution at eccentricities where an increase would benefit performance, and no resolution increase where performance would be impaired (Yeshurun & Carrasco, 2008). This suggests that endogenous attention is a more flexible mechanism that can alter its effects based on the stimuli and task demands.

Are endogenous attention and exogenous attention independent systems?

The distinctions between endogenous and exogenous attention have led to investigations into whether they are separate mechanisms (Berger et al., 2005; Berlucchi et al., 2000; Briand & Klein, 1987; Friedrich, Egly, Rafal, & Beck, 1998; H. J. Müller & Humphreys, 1991; H. J. Müller & Rabbitt, 1989; Prinzmetal et al., 2009; Reuter-Lorenz & Fendrich, 1992; Warner, Juola, & Koshino, 1990). In a key study, Briand and Klein (1987) investigated the effects of endogenous and exogenous cues on a letter detection task under both feature and conjunction conditions. Cue types led to different attentional effects, in which exogenous attention had a stronger effect on conjunction than feature search, but the effects of endogenous attention were similar for each. The authors suggest that the differences in attentional effects in response to central and peripheral cues are evidence that endogenous and exogenous attention are not part of the same system.

Following studies used both endogenous and exogenous cues within trials to compare their effects. H. J. Müller and Rabbitt (1989) compared endogenous and exogenous cues in a letter orientation task. Following an endogenous cue, peripheral flashes occurred at either cued or uncued locations. The flashes always captured attention, but this capture was modulated by endogenous attention. H. J. Müller and

Humphreys (1991) proposed that endogenous and exogenous are separate attention systems with an asymmetric relationship, in which exogenous attention leads to higher inhibition on endogenous attention than endogenous attention on exogenous attention. They offer that different levels of endogenous cue reliability might increase the inhibition of exogenous attention, whereas exogenous attention is “all or none.”

The finding that endogenous attention modifies the effects of exogenous attention has also been revealed with attentional capture effects. Yantis and Jonides (1990) and Theeuwes (1991) showed that by limiting the size of a voluntarily attended region, this eliminates capture by salient stimuli appearing outside the focus of attention. Furthermore, after practice, participants are able to direct endogenous attention to an alternative location following an exogenous cue (Warner et al., 1990).

In a recent study, endogenous and exogenous cues were presented on each trial, with multiple SOAs (Berger et al., 2005). The effects of these cues did not interact on a simple RT task, with each cue resulting in its typical pattern of responses across the timecourses examined. Exogenous facilitation and IOR were independent of the location at which endogenous attention was focussed and endogenous facilitation was present regardless of the location of the exogenous cue. Berlucchi et al. (2000) also found that IOR could not be overcome by endogenous orienting, suggesting independent effects of endogenous and exogenous attention mechanisms. However, in the Berger et al. (2005) study, when the task difficulty was increased, the cueing effects interacted, so that smaller effects were observed for one cue type if the other cue type indicated a contradicting location. The authors suggest that exogenous and endogenous attention rely on separate mechanisms, but share

common resources. When task demands are low, the effects are independent even when the spatial cues are opposing, but when task demands are high, the systems compete for resources leading to an interaction. Further, the authors suggest that the systems are mutually inhibitory, so that endogenous attention may interfere with the effects of exogenous attention (Theeuwes, 1991; Yantis & Jonides, 1990) and also that exogenous attention may interfere with the effects of endogenous attention (H. J. Müller & Humphreys, 1991).

Neural similarities of endogenous and exogenous attention.

Endogenous and exogenous attention, as reviewed above, show different effects on behaviour and it is proposed that they are independent systems (e.g. Berger et al., 2005). Analysis of ERPs implied that different mechanisms are involved in endogenous and exogenous attention (Hopfinger & Ries, 2005). Nevertheless, imaging experiments highlight mainly common areas involved in both endogenous and exogenous attention, even when behavioural results show distinct patterns (Kim et al., 1999; Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005; Nobre, Sebestyan, Gitelman, Mesalun, Frackowiak, & Frith, 1997; Peelen, Heslenfeld, & Theeuwes, 2004; Rosen et al., 1999). For example, Peelen et al. (2004) used a simple RT task preceded by either endogenous or exogenous cues, both with an SOA of 550ms. A typical pattern emerged for both cue types, such that following endogenous cues there was facilitation for targets appearing at the cued location but following exogenous cues there was inhibition. fMRI analysis revealed a difference between cue types only in the right middle temporal gyrus, which the authors attribute to stimulus-evoked activation due to the neutral exogenous cue. All further

comparisons were non-significant, so the authors concluded that the same network controls endogenous attention and exogenous attention.

Target enhancement and noise suppression in spatial attention.

The ways in which endogenous and exogenous attention increase processing power at attended locations have been debated in the literature. Many accounts are based on the idea of biased competition, whereby all stimuli are competing for visual processing, and attention can bias this in favour of salient or relevant stimuli. Increasing the resources devoted to targets, thereby enhancing information about important stimuli, may drive this bias. Conversely, the stimuli that are competing with the target may be suppressed, reducing the noise that may interfere with processing important stimuli. Target enhancement and noise suppression could both allow attentional selection and are not necessarily mutually exclusive. Indeed, there is some research to suggest that both mechanisms may work together under some conditions (Lu & Doshier, 2000).

Awh and Pashler (2000) presented a digit discrimination task under conditions in which many distractors were present, and under conditions in which no distractors were present. Using an exogenous cue, the difference in performance for cued and uncued locations was much larger when distractors were present than when there were no distractors, emphasising the role of noise suppression in exogenous cueing. However, the authors commented that not all of their results could be explained by noise suppression alone, because even when no distractors were presented, there was a cueing effect. This suggests a role of target enhancement as well as noise suppression in exogenous attention, also shown in research by Dobkins and Bosworth (2001) and Lu and Doshier (2000).

On the contrary, Lu and Doshier (2000) only found evidence to support a noise suppression theory of endogenous attention. A more recent endogenous experiment by Lu, Lesmes, and Doshier (2002) varied the amount of noise present in an orientation discrimination task at the cued location. Cueing benefits were greater under high noise conditions, evidence that endogenous attention operates by suppressing noise. There were small attentional effects in low noise conditions, which also suggest a role for target enhancement in endogenous attention. Evidence from fMRI (Kastner, Pinsk, DeWeerd, Desimone, & Ungerleider, 1999; Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004) also suggests the presence of both mechanisms in preparation for a target in endogenous attention paradigms.

In summary, both modes of attention show facilitation, and asymmetrical performance at attended and unattended locations. Furthermore, the overlap in neural regions indicates some similarities between the systems, and there are conditions in which both endogenous and exogenous attention show similar utilisation of mechanisms of target enhancement and noise suppression.

Saliency and priority maps.

Attention is oriented based on salient events and the goals of the observer, through exogenous and endogenous mechanisms. It has been proposed that attention is directed using information plotted on an internal map (e.g. Itti & Koch, 2001; Koch & Ullman, 1985; Treisman, 1988). The *saliency map* is a spatial atlas, onto which the locations of salient stimuli are plotted from bottom-up visual processes. This map is then used to deploy attention to the most salient location. Yantis and Jonides (1990) suggest that a salient cue, such as a new onset, would be encoded onto a saliency map. This in turn would influence attentional orienting by

increasing the salience associated with the cued location. Importantly, the saliency map contains locations that are tagged based on the salience of the visual event, entirely independent of the dimension (Itti & Koch, 2001; Li, 2002; Ullman & Koch, 1985).

Research into attentional orienting frequently incorporates the influence of top-down goals. The effects of highly reliable endogenous cues (e.g. Jonides, 1980) suggest that the observer's strategy contributes to the deployment of attention. The *priority map* therefore encompasses top-down goals and visual salience in plotting behaviourally-relevant locations (Bundesen, 1990; Fecteau & Munoz, 2006; Serences & Yantis, 2006; Yantis & Hillstrom, 1994).

Feature-Based Attention

Attentional selection may also be deployed to non-spatial dimensions, such as colour, motion, or form/shape (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990, 1991). This has been shown through research on directing attention to a dimension, for example colour or orientation (Found & H. J. Müller, 1996; Maljkovic & Nakayama, 1994; H. J. Müller, Heller, & Ziegler, 1995; H. J. Müller, Reimann, & Krummenacher, 2003), or directing attention to a specific feature within a dimension, for example a particular direction of motion (Kamitani & Tong, 2006; Sekular & Ball, 1977; Serences & Boynton, 2007; White & Carrasco, 2011) or a particular colour (Sàenz, Buraças, & Boynton, 2002, 2003).

Bottom-up: Dimensional weighting.

There has been evidence for the influence of bottom-up processes on feature-based attention using visual search tasks, in which participants must report the

presence or absence of a feature singleton target (Found & H. J. Müller, 1996; Maljkovic & Nakayama, 1994; H. J. Müller, 1995). Maljkovic and Nakayama (1994) used a visual search task in which the target was defined by being a colour singleton, and participants responded to whether the left or right side of the target was missing. Participants were faster to respond when the defining colour was the same as previous trials than when it was different. This priming effect lasted up to 30 seconds, and multiple repeated trials show increased priming effects. The authors propose that this effect is entirely automatic, as participants could not willfully suppress the priming effect. H. J. Müller et al. (1995) showed similar results, and explained that when the defining dimension of the target is identified, that dimension becomes weighted, and this weighting persists to the following trial. If the target dimension is the same on the following trial, this will be identified more quickly, but if it is different then a cost will occur due to shifting the weighting to a different dimension.

Top-down: Feature cueing.

Top-down feature information has been shown to modulate attentional capture when no spatial information is provided (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994; Theeuwes, 1991). This suggests that top-down attentional guidance can utilise knowledge of specific features (Bichot & Schall, 2002; Treisman & Sato, 1990; Wolfe, Cave, & Franzel, 1989).

In order to evoke top-down feature-based attention, authors have used symbolic cues to inform participants to attend to a particular feature of a target (Sàenz et al., 2002; White & Carrasco, 2011), or manipulated top-down information about the likely feature or dimension of a target in visual search tasks (H. J. Müller et

al., 1995; H. J. Müller et al., 2003; Sekuler & Ball, 1977). For example, Sàenz et al. (2002) and White and Carrasco (2011) used a colour change at fixation to inform participants to alternate which dimension of the stimulus they were attending.

H. J. Müller et al. (1995) used a singleton visual search task and manipulated the probability of the defining dimension of the target. Trials were blocked by the likely defining dimension (orientation or colour) of the singleton target, and participants were faster to respond when the target differed to distractors along the likely dimension than the unlikely dimension. The same pattern is seen when participants are informed trial-by-trial of the likely defining dimension of the singleton (H. J. Müller et al., 2003).

Interestingly, the same paradigm has been used for feature-cueing, and the results do not show the same pattern. H. J. Müller et al. (2003) cued participants with either a dimension (orientation or colour) or feature (left, right; blue, red). For orientation, a feature cue led to benefits that were dimension-specific, not feature-specific, such that orientation targets had shorter response latencies than colour targets, but there was no difference between left and right orientations (H. J. Müller et al., 2003). The authors suggest that top-down control in visual search is exerted on dimensions rather than features. Colour may be an exception to this as feature-specific effects are seen (see Found & H. J. Müller, 1996; Maljkovic & Nakayama, 1994; H. J. Müller et al., 2003; Folk & Remington, 1998), but it has been suggested that colour may be organised slightly differently into sub-dimensions.

H. J. Müller and colleagues (H. J. Müller et al., 1995; H. J. Müller et al., 2003) investigated the effects of top-down control on dimensional weighting. Though cueing the likely dimension or feature led to a validity effect and reduced stimulus-driven processes, it did not eliminate the inter-trial dimension effects. Thus, top-

down control and stimulus-driven effects can both influence visual search for feature singletons.

Imaging feature-based attention.

Imaging studies investigating feature-based attention have taken advantage of the organisation of visual cortex, in which specialised areas process different stimulus dimensions (Livingstone & Hubel, 1988; Sereno et al., 1995; Zeki, Watson, Lueck, Friston, Kennard, & Frackowiak, 1991). Corbetta et al. (1991) used a single stimulus, and provided evidence that attending to a particular dimension, rather than dividing attention between dimensions, increased participants' ability to discriminate stimulus changes. This was coupled with an indication that attending to different dimensions led to activation in different regions of visual cortex.

Particular focus has been on area V4, which is specialised for colour vision, and area V5, also known as MT, which is specialised for moving stimuli (Zeki et al., 1991). In fMRI experiments, these areas both show modulation due to attention (V4: Corbetta et al., 1991; MT: Büchel, Josephs, Rees, Turner, Frith, & Friston, 1998; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997). Thus, attending to a particular dimension modulates neural activity. Furthermore, this modulation can be seen when participants are preparing to attend to either the colour or motion in a stimulus (Chawla, Rees, & Friston, 1999), in the absence of colour or motion stimulation.

Recently, researchers have shown that attending to a feature within a particular dimension modulates neural activity. Classification methods in fMRI have shown that the pattern of activation in visual cortex reveals which of two different overlapping orientations (Kamitani & Tong, 2005) or motion directions (Kamitani &

Tong, 2006; Serences & Boynton, 2007) is being attended. Thus, attending both features and dimensions can modulate activity in visual cortex.

Feature-similarity gain model.

The effects of feature-based attention have been shown to extend across visual space. Thus, while spatial attention selects by location, feature-based attention selects on the basis of non-spatial attributes. Treue and Martinez-Trujillo (1999) used single cell techniques to compare neural responses when nonhuman primates attended to a preferred or anti-preferred direction of motion outside of the cell's receptive field. The two directions of motion were presented in overlapping dot populations at the same location, yet neural responses were greater when the preferred direction was attended than when the anti-preferred direction was attended. As stimuli were not presented in the cell's receptive field, this suggests that attention can select based on non-spatial features. The authors propose the *feature-similarity gain model*, in which sensory neurons can be regulated according to behaviourally relevant attributes, such as location (receptive field) and feature (direction of motion). In this model, the regulation based on feature is independent of location, and therefore the authors suggest that feature-based attention would modulate responses in cells tuned to the target feature regardless of spatial selectivity.

Two studies from Sàenz et al. (2002, 2003) provide evidence from humans consistent with the feature-similarity gain model. In an fMRI experiment (Sàenz et al., 2002), participants attended an aperture containing two overlapping dot populations - one moving upwards and one moving downwards - and a single population of dots moving in one direction was presented in the other hemifield.

Every 20 seconds, participants shifted attention between the two overlapping dot populations so that in the unattended location, attention alternated between the same and a different direction. The same idea was repeated with colour, so that the attended location contained a red and a green population of dots, but the unattended location only contained a single colour of dots. Activity in early visual areas corresponding to the ignored hemifield was higher when participants were attending the same feature (direction or colour) in the attended aperture than when the features were different. This suggests that attention to feature spreads across the visual field. Further behavioural evidence supports the idea of a spatially global feature-based attention account (Sàenz et al., 2003), even when the feature is irrelevant for the task (White and Carrasco, 2011).

In an fMRI experiment, Serences and Boynton (2007) employed pattern classification methods to examine the spread of feature-based attention. Participants viewed RDKs that contained two overlapping dot populations. On some trials, only one RDK was presented, on either the left or right of fixation, and on some trials an RDK was presented in both hemifields. Participants were cued as to which direction of dots to attend in either the left or right hemifield, and responded to any change in speed in the attended dots. As predicted by previous research, at the attended location, the attended direction was accurately decoded. Two further conditions of interest were examined. Firstly, the direction of attended dots was accurately decoded in the unattended RDK, indicating that the direction of motion was attended across visual space, not solely in the spatially attended RDK. Secondly, the accuracy of decoding was high for the unattended location even when no RDK was presented. This implies that feature-based attention affects baseline responses, and suggests that all areas of visual space will show the spread of feature-based attention, even in

the absence of visual stimulation. Taken together, the above research provides strong evidence that feature-based attention spreads across visual space regardless of the focus of spatial attention.

Target enhancement and noise suppression in feature-based attention.

The proposed methods of increasing processing for attended features are based on the idea of biased competition, in which all visual stimuli are in competition for processing, and attention biases this competition in favour of relevant or salient stimuli. This bias may be in the form of enhancing the features to be attended, or suppressing stimuli that may interfere with processing the target.

Single cell recording studies provide evidence to support a suppression account. Moran and Desimone (1985) used an effective stimulus, a red bar, presented either horizontally or vertically within the cell's receptive field, which elicited a high response. A second, ineffective, stimulus did not elicit a response when presented within the receptive field. When the animal attended to the effective stimulus, the cell response was unchanged regardless of whether the ineffective stimulus was presented within or outside the receptive field. If the animal was attending to the ineffective stimulus, and both stimuli were presented within the receptive field, the elicited response diminished significantly. Therefore, attending to the ineffective stimulus had a suppressive effect on the response elicited by the effective stimulus.

Conversely, White and Carrasco (2011), compared performance on a coherent motion localisation task depending on whether the direction of motion was matched or mismatched with a primary stimulus. There was a benefit when motion direction in the primary and secondary tasks was the same. However, no cost was

observed when mismatched motion directions were compared to a neutral condition. Hence, feature-based attention led to enhancement of the cued direction, and no suppression of the uncued direction.

However, much research suggests that both enhancement and suppression contribute to the attentional effects. Treue and Martinez-Trujillo (1999) demonstrate that attention enhances the responses of neurons to the preferred direction, and suppresses the responses of neurons to the anti-preferred direction. Thus, the difference in responses for these neurons is larger than the enhancement or suppression effects alone.

A behavioural paradigm also indicates the contribution of both enhancement and suppression to feature-based attention. The *negative priming* effect is demonstrated when participants are shown two overlapping objects, one of which is attended (e.g. Tipper, 1985). When the unattended object is probed, naming latencies are longer than those for a non-presented object, suggesting that the object was suppressed during the attention period. Using the same paradigm, naming latencies for a probe that was attended are shorter, indicating facilitation of the attended object.

In summary, there is evidence to substantiate both enhancement and suppression mechanisms in feature-based attention. This support comes from both neural and behavioural studies.

Are Spatial and Feature-Based Attention Independent Systems?

Spatial attention, as the name suggests, is based on the premise that attention selects based on location, whereas feature-based attention selects based on non-spatial attributes. This distinction has led to the view that these are independent

mechanisms (e.g., Brignani, Lapsien, & Nobre, 2010; Egner et al., 2008; Fecteau et al., 2009; Patzwahl & Treue, 2009; Sàenz et al., 2006; Schenkluhn et al., 2008; Serences & Boynton, 2007; Treue & Martínez-Trujillo, 1999) and that both spatial and feature information are adept at informing deployment of attention (Adams & Chambers, 2012).

If spatial attention and feature-based attention are independent systems, the effects of each should be evident in isolation. Using endogenous cueing, Egner et al. (2008) demonstrated that the effects of feature and spatial cues are independent. The cue reliability for the location and feature of an upcoming target were varied orthogonally, and the authors found that each had independent effects, such that participants were able to utilise spatial and feature-based attentional mechanisms additively. Research into bottom-up priming effects has also suggested that the effects of repeating features and repeating locations can be disentangled (Maljkovic & Nakayama, 1994, 1996).

A large amount of research supports global effects of feature-based attention (Sàenz et al., 2002, 2003; Serences & Boynton, 2007; White & Carrasco, 2011). As feature-based attention spreads across visual space, it is necessarily independent of spatial attention. Conversely, it is pertinent to ask whether spatial attention generalises to all dimensions or features at the attended location.

One of the key papers that addressed this issue used exogenous spatial cues with one of two tasks on each trial: orientation discrimination or letter identity discrimination (Remington & Folk, 2001). Both tasks required a choice of two responses, mapped to the same two response keys. At the beginning of each trial, participants were informed which of the two tasks they were to perform on the target. Four stimuli were presented on each trial, and the target was a coloured,

tilted L or T. Two were vertical white E or F distractors, which shared no features with the target, and the final stimulus was a similar distractor (foil). The foil was not a coloured letter, but it was a tilted T or L. Thus, the response made to the target could be compatible or incompatible with the response to the irrelevant dimension of the target, as well as with the relevant and irrelevant dimensions of the foil.

The spatial cue indicated one of the four letters at equal probability, and the compatibility effects were compared depending on the cue condition. When the target was cued, the compatibility of the irrelevant dimension influenced the response latencies to the relevant target dimension. This suggests that both dimensions were selected at the target location.

However, the results from the compatibility of the dimensions of the foil do not show such a clear pattern. When the foil was cued, only the relevant dimension showed compatibility effects – the irrelevant dimension did not interfere with response latencies to the target. This result suggests that at the cued location, only the dimension that is relevant to the task is attended, and spatial attention does not generalise across all dimensions at that location. The authors suggest that this pattern of results shows a dissociation between attention and selection.

There is further behavioural evidence for integration of spatial and feature-based attention (Cepeda, Cave, Bichot, & Kim, 1998; Cohen & Magen, 1999; Cohen & Shoup, 1997, 2000; Kravitz & Behrmann, 2011). Cepeda et al. (1998) examined processing using a probe detection task following a letter identification task.

Participants reported the letter that was a colour singleton; for some participants this was a red letter among green distractors, and for the other participants this was a green letter among red letters. Probes that appeared at locations previously occupied by distractors had longer response latencies than those appearing at a

location previously occupied by the target, or blank locations. The authors suggest that there is a feature-driven spatial attention, such that locations that did not contain target features were suppressed.

The Current Thesis

The experiments presented in this thesis address pertinent questions arising from the literature review. Firstly, the interaction of spatial and feature-based attention is examined in Chapters 2 and 3, which investigated whether endogenous attention generalises to all dimensions following a spatial cue. These experiments used a dual-task procedure, in which both dimensions were task-relevant yet a spatial cue was only predictive for the location of one dimension. Secondly, the influence of bottom-up processing was examined in Chapters 4, 5, and 6, by manipulating physical properties of an exogenous cue. Two tasks of different dimensions and spatial extent were presented following exogenous cues of different sizes (Chapters 4 & 5) or different dimensions (Chapter 6). This series of experiments address the role of dimension in spatial attention, in both endogenous and exogenous attention.

All experiments were behavioural investigations, in which participants completed a dual task. Four RDKs were presented, one in each quadrant of the screen. In every experiment, participants reported the direction of motion in the coherently-moving RDK. The second task was either red dot probe localisation or colour discrimination.

The dual task design allowed for the measurement of two responses, a strong advantage when examining the generalisation of spatial attention across dimensions, and controlled for the influence of task set. The design also afforded the

manipulation of cueing properties or information such that subtle changes were easily made to compare across different attentional conditions.

The tasks chosen allowed the investigation of attentional effects on different properties. However, some differences between tasks may have modulated some of the attentional effects observed. These differences are discussed in the empirical chapters and the general discussion.

Throughout this thesis, participants were excluded from group analysis based on a lack of cue-related effects, as follows. In the endogenous experiments, participants were excluded if they did not show a validity effect for the task for which the cue was useful, because this presumably demonstrated that they were not using the cue correctly. In the exogenous experiments, participants were excluded if they did not show a validity effect for either task, because presumably the cue did not capture their attention. The decision to exclude these participants was made in order to ensure that the included participants had followed task instructions, and the cues had led to orientation of attention. However, this exclusion criteria may be inappropriate as only participants who demonstrated cueing effects were selected, inflating attentional effects and potentially biasing data. This issue will be further explained at the end of the thesis.

Chapter 2. Endogenous Cueing I: Motion Discrimination and Probe Detection

Faster and more accurate responses are found for targets in the attended location compared to targets in unattended locations (e.g., Berger et al., 2005; Carrasco, Ling, & Read, 2004; Cheal & Lyon, 1991; Jonides, 1980, 1981; Posner, 1980). Indeed, the term *spatial attention* reflects the assumption that attending to a location improves the perceptual quality of, decisions regarding, or motor responses to all features at the attended location (e.g. the *spotlight theory* Posner et al., 1980; LaBerge, 1983; and the *zoom lens model* Eriksen & St. James, 1986; Eriksen & Yeh, 1985; N. G. Müller et al., 2003). Evidence for this comes from two main lines of research: studies of location as the means of selection, and investigations into the processing of irrelevant stimuli at the attended location.

Perceptual performance improves with the proximity of the stimulus to a location that was cued or previously occupied by a task-relevant target (e.g. LaBerge, 1983; Rizzolatti, Riggio, Dascola, & Umiltà, 1987). This performance benefit is also seen for probe stimuli that do not share a dimension with the target stimulus. For instance, Kim and Cave (1995) used a probe to assess attention distribution following a visual search task. They found that both RT and accuracy were improved if the probe appeared at the target location compared to locations occupied by distractors. This suggests that once attention is allocated, all stimuli at that location show a benefit, regardless of dimension.

The second set of evidence is based on the observation that the task-irrelevant dimensions of the stimulus can interfere with processing of the task-relevant stimulus dimensions, such as in the Stroop effect (Stroop, 1935) and negative priming (e.g. Neill, 1977; Tipper, 1985; Tipper, 2001). This is further

supported by the observation that the closer a distractor is presented to the target, the more performance is impaired (Eriksen & Hoffman, 1973; Eriksen & St. James, 1986), suggesting that proximal distractors are falling within a location-based attentional field.

The assumption that spatial attention facilitates all stimuli in the attended location also implies that spatial attention and feature-based attention are separate and independent processes. This has been widely supported in numerous studies (e.g., Egner et al., 2008; Fecteau et al., 2009; Patzwahl & Treue, 2009; Stoppel et al., 2007; Treue & Martínez-Trujillo, 1999). In a recent study, Fecteau et al. (2009) compared feature and spatial biases in a letter search task. Rather than using cueing, biases were introduced by increasing the probability of an alphabetic target appearing in a particular colour (feature) or at a particular location (spatial). They found that both biases improved performance, but whereas the colour bias was only useful for the associated letter, the location bias assisted in discrimination for all targets appearing there. Thus, spatial and feature-based attention are separate and have independent effects. Furthermore, this supports the idea that spatial attention improves performance for all stimuli at the attended location.

In contrast to the above findings, a few studies found that one can selectively control which dimension of the object to pay attention to and which one to ignore within the selected cued location (Cohen & Magen, 1999; Cohen & Shoup, 1997, 2000; Remington & Folk, 2001). Remington and Folk (2001) used an exogenous cue to indicate the location of the target, a similar distractor (foil) or a neutral character. They measured compatibility effects on the RT to identify one feature of the target. Only the task-relevant dimension of the foil interfered with the target response, while the dimension that was irrelevant to the task had no effect on the target. The

authors suggested that only the task-relevant dimensions of the stimulus at the attended location are being processed, while the irrelevant dimension occupying the same spatial location can be ignored.

In the current study the effects of spatial cueing were examined under dual task conditions, by presenting two stimuli that both required a response and are therefore both task-relevant. The reliability of a spatial cue was manipulated independently for each stimulus. While the cue was predictive of the location of one stimulus, it was uninformative as to the location of the second. If attention improves processing of all task-relevant dimensions (stimuli) at the cued location, then cueing benefits should be observed for both tasks. However, if the information in the spatial cue is faithfully reflected in the allocation of attention, then a cueing effect should only be observed for the dimension whose location was informatively cued.

Experiment 1.

The effect of a spatial probabilistic cue on a dual task was investigated using two distinct stimuli and a single endogenous cue. The cue was 70% valid for one task, motion direction discrimination, but was non-informative for the second task, colour probe localisation.

Method.

Participants.

Six participants (four female) were tested repeatedly in this experiment. Three were practiced observers (including the author), and three were naïve participants, recruited from the School of Psychology, Bangor University. The naïve participants received monetary compensation for their time. All participants had

normal or corrected-to-normal visual acuity. The Ethics Board of the School of Psychology, Bangor University approved all the experiments.

Stimuli and apparatus.

Stimuli were created using Matlab 7.6 with Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997) and generated by an Apple Mac Pro 1.1 computer. Stimuli were displayed on a LaCie Electron 22blue IV CRT screen, with a refresh rate of 60Hz. Head position was restrained by a chin rest at a distance of 70cm from the monitor. The stimuli were shown against a black background, and participants were in a dark environment.

A pre-cue was used in each trial. The spatial cue was a 0.5° line, oriented towards one of the four quadrants of the screen. The neutral cue consisted of a colour change at fixation and provided only temporal information.

The stimuli were circular random-dot kinematograms (RDKs), of 10° diameter. Each RDK contained 100 randomly moving white dots, 0.2° in diameter. Each dot had a lifetime of two frames, with the location of its first frame determined by sampling a uniform distribution. The random movement, *dynamic noise*, was created by displacing the dot in a random direction within the aperture at a speed of $8.5^\circ/\text{s}$.

In the target RDK, the first 100ms of presentation was dynamic noise, followed by a 200ms period of *coherent motion*. During coherent motion, a certain proportion of the dots were displaced systematically in a given direction, either up, down, left or right, at the same speed ($8.5^\circ/\text{s}$) as the dynamic noise. The final 100ms of presentation was, again, a period of dynamic noise.

Simultaneously, a probe was presented in half of the trials. The probe was defined by a colour and size change of one of the RDK dots, which turned red and became slightly larger (0.26° visual angle for practiced observers, 0.3° for naïve participants).

Design.

On 70% of the trials the cue indicated the location of the coherent motion, while on the remaining 30% of the trials the coherent motion had an equal chance of being displayed at any of the uncued locations. Sixty-four of the 416 trials were neutrally cued. Neutrally and spatially cued trials were interleaved randomly. The colour probe was present in 50% of the trials. The probe was equally likely to appear at each of the four locations. The spatial cue provided no information regarding the probe location. Accuracies in discriminating the direction of coherent motion and probe localisation were measured.

Procedure.

Each participant completed 2496 trials, across five sessions of approximately one hour. Firstly, participants practiced the motion task, with feedback, on a staircase procedure. No spatial information was provided during practice trials. Naïve participants had at least two hours of training on this task before beginning experimental trials. All participants also completed 150 training trials at the beginning of each experimental session. The proportion of coherently moving dots was set at the level where participants were 60% accurate on the training trials for each session.

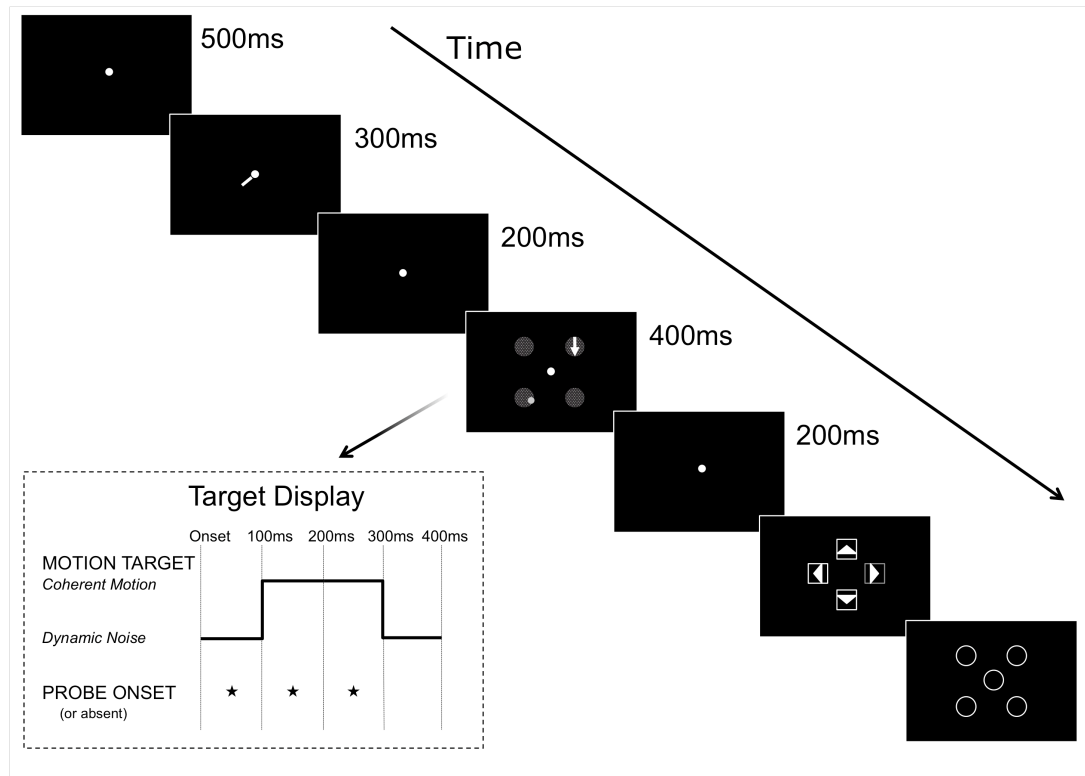


Figure 2.1. Procedure for simultaneous motion discrimination and probe localisation task, not to scale. Invalidly cued motion, probe present at cued location. Arrow on target display represents direction of motion and was not displayed. The white dot represents location of the red dot probe. Inset box shows timings during the target display.

The structure of each trial is displayed in Figure 2.1. A white square marker, subtending 0.1° was visible at the centre of the screen throughout each trial. Eye movements were not recorded, but participants were told to maintain fixation on this point and that moving their eyes would make the tasks more difficult. At the beginning of each trial, the fixation marker was presented for 500ms, followed by the addition of an endogenous line cue that was visible for 300ms. Participants were informed of the cue reliability. The target display appeared 200ms after cue offset, and lasted 400ms. Three RDKs contained dynamic noise and one contained coherent

motion. In 50% of trials a probe was presented for 100ms, and was equally likely to appear in any of the four locations. The probe appeared 150ms after target display onset for naïve participants, therefore 50ms after the onset of coherent motion. For the practiced observers, three probe onset times were used; 50ms, 150ms (the same as naïve participants) and 250ms after the onset of the target display.

At the end of each trial the participants were asked to indicate the direction of motion by selecting one of the four direction arrows. The following screen outlined the four locations and a central circle, and the participants selected the location where the probe had appeared, or in the case of an absent probe trial, the central circle (see Figure 2.1).

Results and discussion.

Percentage accuracy was calculated for probe localisation by dividing the number of hits by the number of probe present trials in each condition. Motion accuracy was calculated across all trials.

Since only probe present trials were used to compute probe accuracy, the validity effect for motion discrimination (accuracy on valid trials minus accuracy on invalid trials) was compared between probe present and probe absent trials. A paired t-test showed no significant difference in the magnitude of the validity effect in motion discrimination whether the probe was present or absent, $t(5) = 0.07$, $p = .95$. Therefore, all trials were included in further analyses of the motion discrimination data.

As there were three probe onset times for the practiced observers, and only one onset time for the naïve participants, a Chi-Square analysis was used to verify that performance was independent of the probe onset time. Two of the participants

showed no effect of onset times (practiced observer 1: $\chi^2(2) = 3.86, p = .15$; practiced observer 2: $\chi^2(2) = 1.18, p = .42$), while one showed a significant effect, $\chi^2(2) = 6.32, p < .05, V = .07$. For this reason, only trials with a probe onset time of 150ms (the same as naïve participants) were included in the group analysis for practiced observer 3.

Table 2.1.

Mean Accuracy (%) for Motion Discrimination and Probe Localisation Tasks on Valid and Invalid Trials for Experiment 1.

Task	Valid		Invalid	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion	71.50 (9.18)	[61.86, 81.14]	62.83 (8.61)	[53.80, 71.87]
Probe	50.33 (18.85)	[30.55, 70.12]	47.33 (16.40)	[30.12, 64.55]

Note. CI = confidence interval.

Next, the main analysis was performed. Motion discrimination and probe localisation data were entered into a group analysis, and mean accuracies are shown in Table 2.1. The validity effects for motion discrimination and probe localisation are shown in Figure 2.2.

The data were normalised by taking the arcsine of the square root of the proportion of accurate responses, a standard transformation for proportional data, which normalises the data and stabilises the variance (Sokal & Rohlf, 1981). Data were then analysed in a 2 (task: motion, probe) x 2 (validity: valid, invalid) repeated measures ANOVA. There was a significant main effect of task, $F(1, 5) = 11.80, p = .019, \eta_p^2 = .70$, since accuracy was higher on the motion task than the probe task. There was a main effect of validity, $F(1, 5) = 21.78, p = .005, \eta_p^2 = .81$, however there was no significant interaction, $F(1, 5) = 3.65, p = .11, \eta_p^2 = .42$. Planned t tests showed

a significant validity effect for the motion task, $t(5) = 4.16$, $p = .009$, but not for the probe task, $t(5) = 1.51$, $p = .19$.

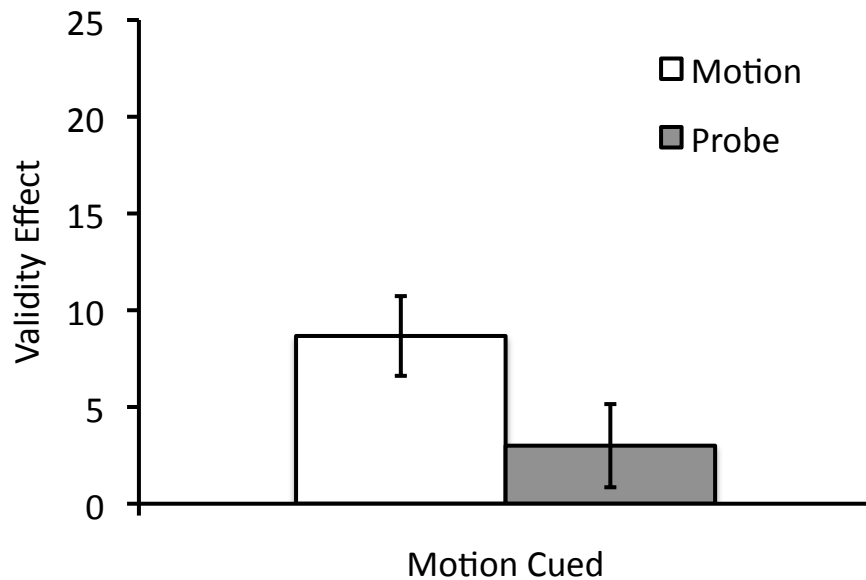


Figure 2.2. Validity effect in the motion discrimination task (white bars) and the probe localisation task (grey bars) in Experiment 1. Error bars represent ± 1 standard error of the mean. The validity effect was calculated by subtracting the percentage accuracy on invalid trials from the percentage accuracy on valid trials.

If spatial cueing draws attention to all task-relevant perceptual features at the cued location then similar performance benefits should be observed in both tasks. However, Experiment 1 shows a validity effect for the motion discrimination task, but not for the probe localisation task. There is, therefore an indication that participants biased their attention at the cued location towards the stimulus dimension whose location was predicted by the cue. However, the interaction between task and validity was not significant, meaning that the conclusions that can be drawn from these results are restricted. The lack of interaction here is likely due

to the small number of participants, and this limitation will be addressed in Experiment 3.

However, accuracy for the motion task was much larger than for the probe task. This may indicate that the task for which the cue was informative, the motion task, was prioritised. In this case, participants may have used the cue to complete the motion discrimination task, and then subsequently attempted to localise the probe. To examine further the specificity of spatial cueing effects, and to rule out the possibility that cueing simply does not affect the colour localisation task, in the next experiment the probe location was cued with a 70% valid cue that was not predictive for the location of coherent motion.

Experiment 2.

In Experiment 2, we tested the conclusion that attention can be selectively oriented to those stimuli or dimensions whose location is predicted by the cue. Hence, the cue reliabilities were switched for the two tasks.

Method.

Participants.

Eleven participants were recruited using the online participant panel at the School of Psychology, Bangor University. They received course credits for participation. None of the participants had taken part in Experiment 1. All participants had normal or corrected-to-normal vision.

Design, stimuli, and procedure.

The cue reliability for coherent motion was 25%, while it was 70% for the probe location, in trials in which the probe was present. Otherwise, the display was similar to that of Experiment 1, apart from the following small modifications: 1) the RDKs were displayed from the beginning of the trial. 2) The distance of the center of each RDK from the fixation point was increased to 14° in order to encourage cue utilisation. 3) The dots' maximum lifetime was increased to three frames to reduce motion discrimination training.

Each participant completed 416 trials. The maximum length of a session was 90 minutes, including approximately 45 minutes of motion discrimination training using a staircase procedure.

Results and discussion.

Accuracy was calculated in the same way as Experiment 1. Motion discrimination accuracy was not significantly different across probe present and probe absent trials, $t(10) = 0.78, p = .45$, so all trials were included in the analysis of the effects of cue validity on motion discrimination accuracy. Mean accuracies on valid and invalid trials are displayed in Table 2.2.

The validity effects are shown in Figure 2.3, and results were analysed in a 2 (task: motion, probe) x 2 (validity: valid, invalid) repeated measures ANOVA. There was a significant effect of task, $F(1, 10) = 6.34, p = .031, \eta_p^2 = .39$, indicating that participants had higher accuracy on the motion task than the probe task. As expected, there was a main effect of validity, $F(1, 10) = 9.22, p = .013, \eta_p^2 = .48$, but this did not interact with task, $F(1, 10) = 0.85, p = .38, \eta_p^2 = .078$. Planned t tests indicated a significant validity effect for both motion, $t(10) = 2.78, p = .020$, and

probe, $t(10) = 2.32, p = .043$. Unlike Experiment 1, there were validity effects for both tasks following the predictive cue for the colour probe.

Table 2.2.

Mean Accuracy (%) for Motion Discrimination and Probe Localisation Tasks on Valid and Invalid Trials for Experiment 2.

Task	Valid		Invalid	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion	72.64 (13.84)	[63.34, 81.94]	68.45 (11.95)	[60.42, 76.48]
Probe	64.45 (12.65)	[55.95, 72.95]	56.00 (15.45)	[45.62, 66.38]

Note. CI = confidence interval.

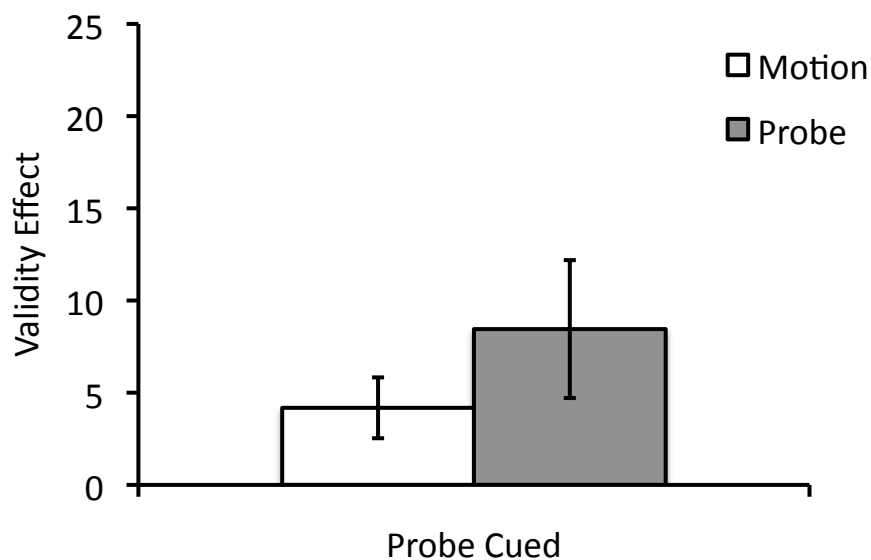


Figure 2.3. Validity effect in the motion discrimination task (white bars) and the probe localisation task (grey bars) in Experiment 2. Error bars represent ± 1 standard error of the mean. The validity effect was calculated by subtracting the percentage accuracy on invalid trials from the percentage accuracy on valid trials.

Comparison of Experiments 1 and 2.

When examined together, the results from Experiments 1 and 2 seem to show a pattern of modulation of validity effect based on the predictive value of the cue. Though the interaction of task and validity did not reach significance in either experiment, visual inspection of the figures suggests an effect of cue usefulness. Therefore, a 2 (experiment: motion cued, probe cued) x 2 (task: motion, probe) x 2 (validity: valid, invalid) mixed ANOVA was conducted with cue condition as a between groups factor and task and validity as within subjects factors. Performance was equivalent across experiments, $F(1, 15) = 1.76, p = .20, \eta_p^2 = .11$, and there were no interactions with task, $F(1, 15) = 0.90, p = .36, \eta_p^2 = .057$, or validity, $F(1, 15) = 0.02, p = .89, \eta_p^2 = .001$. As expected, there were main effects of validity, $F(1, 15) = 16.54, p = .001, \eta_p^2 = .52$, and task, $F(1, 15) = 16.55, p = .001, \eta_p^2 = .53$. Task and validity did not interact, $F(1, 15) = 0.31, p = .59, \eta_p^2 = .020$, but there was a near-significant interaction of Task x Validity x Experiment, $F(1, 15) = 3.10, p = .099, \eta_p^2 = .17$, suggesting that there was a trend towards modulation of the validity effect for each task based on cue reliability. This interaction will be examined further in Experiment 3.

Experiment 3.

The data from Experiments 1 and 2 suggest that participants are able to utilise the information in a spatial cue in order to optimise performance. This was observed in the modulation of the cueing effects depending on the task for which the cue was informative. In Experiment 3, the previous two experiments were run within subjects, in order to examine the interaction between cue information and task validity effects. By adopting a within subjects design, it is possible to investigate

whether participants are able to selectively bias attention to the dimension for which the cue was informative.

Method.

Participants.

Twenty-three naïve participants (17 female) from Bangor University were recruited through the online participant panel or via advert and were either awarded course credits or paid for their participation. None had taken part in the previous cueing experiments, and all had normal or corrected to normal vision.

Design and stimuli.

These were the same as in the previous experiment; with the exception that the RDKs were not present until after the cue period, as in Experiment 1, and that the size of the red dot was set separately for each participant. The probe size was determined using a staircase procedure for each participant in the same way as the motion task, in an attempt to reduce variability in the probe task.

Procedure.

Participants were tested in two sessions on non-consecutive days; one session for each cue condition: The first session lasted two hours including training and the second session lasted one hour. Each participant completed 416 trials in both cue conditions. In the first session, participants completed 200 training trials on the motion coherence threshold program, and 200 training trials on the probe size program. In session one, participants were randomly allocated to begin with either the motion or probe cue condition.

When participants returned for their second session, they completed 80 trials each of the motion and probe training programs and difficulty levels were adjusted accordingly. They then completed the second experimental block, the opposite of the cueing condition they had completed in session one.

Results and discussion.

Accuracy was calculated in the same way as the experiments above. Six participants (6 females) were excluded because the cue failed to elicit a validity effect for the task for which it was reliable in one or both cueing conditions, suggesting that the cue was not effective in drawing attention in these participants. The accuracies for the motion and probe tasks on valid and invalid trials are shown in Table 2.3, and the validity effects are plotted in Figure 2.4.

Table 2.3.

Mean Accuracy (%) for Motion Discrimination and Probe Localisation Tasks on Valid and Invalid Trials in Experiment 3.

Task	Valid		Invalid	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion cue				
Motion	77.18 (6.59)	[73.79, 80.56]	58.18 (14.48)	[50.73, 65.62]
Probe	79.35 (8.75)	[74.85, 83.85]	68.88 (10.27)	[63.60, 74.16]
Probe cue				
Motion	70.18 (9.79)	[65.14, 75.21]	61.00 (12.11)	[54.77, 67.23]
Probe	81.18 (6.34)	[77.92, 84.43]	65.76 (13.93)	[58.60, 72.92]

Note. CI = confidence interval.

Results were analysed in a 2 (cue condition: motion, probe) x 2 (task: motion, probe) x 2 (validity: valid, invalid) repeated measures ANOVA. This yielded a significant validity effect, $F(1, 16) = 40.18, p < .001, \eta_p^2 = .72$, as expected based on the selection of participants who showed cueing effects. There was also a significant effect of task, as probe localisation was completed more accurately than motion discrimination, $F(1, 16) = 7.39, p = .013, \eta_p^2 = .25$. Crucially, there was a Cue Condition x Task x Validity interaction, $F(1, 16) = 10.71, p = .005, \eta_p^2 = .40$, suggesting that the validity effects for the two tasks were different following the two cues. The remaining comparisons were all non-significant ($F < 1$).

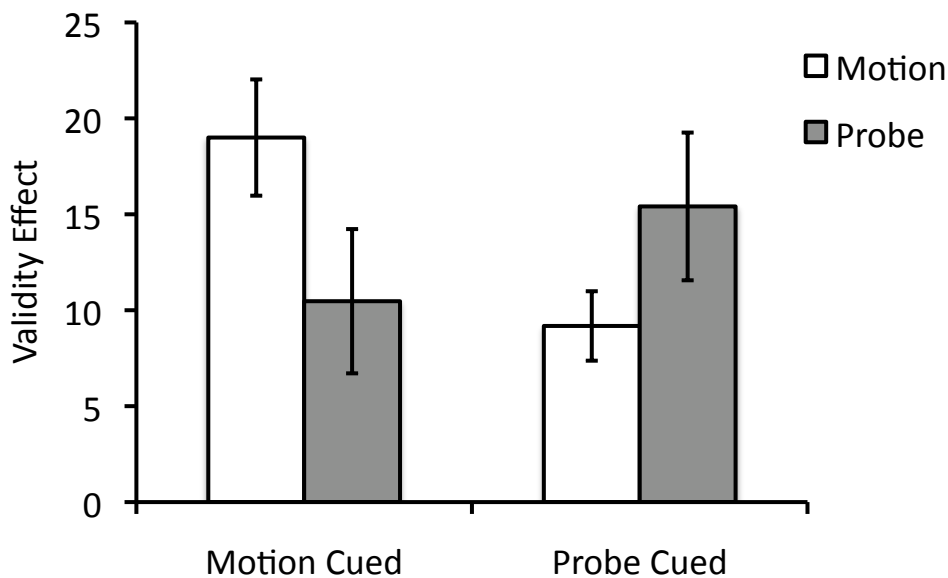


Figure 2.4. Validity effect in the motion discrimination task (white bars) and the probe localisation task (grey bars) in Experiment 3. Error bars represent +/- 1 standard error of the mean. The validity effect was calculated by subtracting the percentage accuracy on invalid trials from the percentage accuracy on valid trials.

In order to examine this interaction, two separate ANOVAs were conducted for the two tasks, with cue condition (motion, probe) and validity (valid, invalid) as factors. For the motion task, there was a significant interaction between cue condition and validity, $F(1, 16) = 12.92, p = .002, \eta_p^2 = .45$, as the validity effect was larger following the cue that was reliable for coherent motion ($M = 19.00, SD = 12.50$), than following a cue that was reliable for the location of the probe ($M = 9.18, SD = 7.44$), suggesting that attention was modulated by the usefulness of the cue. For the probe task, there was a significant validity effect, $F(1, 16) = 15.73, p = .001, \eta_p^2 = .50$, as valid trials were more accurate than invalid trials, indicating that the cue elicited an attentional effect. There was no interaction of cue condition with validity, $F(1, 16) = 1.81, p = .20, \eta_p^2 = .10$, suggesting that the validity effect was not different in the two cue conditions.

The results in the motion cued condition show a statistically different pattern to those in Experiment 1. In Experiment 1, the cue was useful for the motion discrimination task and not the probe localisation task, and there was a validity effect for motion but no validity effect for probe. Here, there are validity effects for both tasks. There are only minimal differences between the experiments. Aside from a difference in the number of trials completed, the dots had a longer lifetime in Experiment 3 than Experiment 1, and the probe size was set using a staircase training procedure in Experiment 3, whereas it was the same size for all participants in Experiment 1. These changes were introduced to reduce training for the motion task, and to reduce variance and increase accuracy for probe detection.

The results were compared in a 2 (experiment: Experiment 1, motion cued condition of Experiment 3) x 2 (task: motion, probe) x 2 (validity: valid, invalid) mixed ANOVA. There was a main effect of experiment, $F(1, 21) = 14.12, p = .001, \eta_p^2$

= .40, suggesting that accuracies were larger in Experiment 3 than Experiment 1, and an interaction of Experiment x Validity, indicating that the validity effects were larger in Experiment 3 than Experiment 1. Crucially, there was no Experiment x Task x Validity interaction, meaning that the pattern of results observed was similar for the two experiments. It is not certain why the probe validity effect was absent in Experiment 1 when it was present in Experiment 3, but it may be due to a difference in the size of the validity effects in the two experiments and is likely related to statistical power given the small number of participants in Experiment 1.

When comparing across the tasks, there is a clear modulation of the validity effect based on the task for which the cue is reliable. Therefore, using a spatial cue that is reliable for the location of only one target stimulus leads to biasing of attentional effects. Similar effects have been shown in exogenous attention and in flanker compatibility tasks, in which only the relevant dimensions of distractor stimuli are attended (e.g. Cohen & Shoup, 1997; Remington & Folk, 2001). However, in the present tasks, both stimulus dimensions are relevant, so these biases should be eliminated.

Chapter Discussion

The current chapter investigated whether the effects of endogenous spatial attention are similar for all task-relevant stimuli at the cued location. When the spatial cue was only predictive for the location of one stimulus, that stimulus showed a larger validity effect. Contrary to predictions based on a previous literature, spatial cueing effects were significantly smaller for the task for which the cue was uninformative, despite the fact that both stimuli were task-relevant. The finding challenges the assumption that spatial attention is a single entity that can be

oriented or distributed, as proposed in previous models (Eriksen & Hoffman, 1973; Eriksen & St James, 1986; Eriksen & Yeh, 1985; Hoffman, 1979; Jonides, 1983; LaBerge, 1983; Madden, 1992; N. G. Müller et al., 2003; Posner et al., 1980) and research (Egner et al., 2008; Fecteau et al., 2009; Patzwahl & Treue, 2009; Treue & Martínez-Trujillo, 1999).

The results in this chapter can be compared with those of Remington and Folk (2001), who found that observers could restrict processing of attended stimuli to the task-relevant dimension, while ignoring the irrelevant dimensions. However, the experiments in this chapter were designed such that both dimensions were task-relevant, and a similar pattern is found: Processing of task-relevant dimensions is more enhanced at the cued location for stimuli whose location is predicted by the cue. Therefore, cue information about the likely location of specific dimensions can be exploited, but there is no evidence that the dimension for which the cue is uninformative is suppressed or ignored at the cued location.

The effect of likely dimension at the cued location speaks to the debate of a dichotomous model of attention, in which spatial and feature attention are separate. A large body of empirical evidence supports the idea that spatial and feature-based attention are distinct mechanisms, and more specifically that while spatial attention generalises across non-spatial dimensions, the effects of feature attention are spatially non-selective (e.g. Fecteau et al., 2009; Sàenz et al., 2002, 2003). Additionally, others have reported that the effects of spatial and feature cueing, on physiological measures of neural activity, are additive (e.g., Egner et al., 2008; Patzwahl & Treue, 2009; Treue & Martínez-Trujillo, 1999). For example, in an imaging study, Egner et al. (2008) used probabilistic cues, which predicted independently the upcoming target's location and colour. It was found that the

effects on the BOLD response of varying the reliability of the spatial cue did not interact with the effects of varying the validity of the feature cue. The authors concluded that spatial and feature cueing engage independent attentional processes. However, the study design required that spatial and feature cues be utilised independently in order to optimise performance, and therefore could not determine whether the BOLD effects reflected the task demands or the organisation of attention. There are circumstances, as in this chapter, in which optimal performance requires the integration of spatial and non-spatial information for selection and thus provide the conditions to test the hypothesis that feature and spatial attention are independent.

Recent functional imaging work (Jehee, Brady, & Tong, 2011) has provided initial physiological evidence that spatial cueing may selectively enhance task-relevant stimulus dimensions. Two tilted Gabor stimuli were presented either side of a central fixation point, and a spatial cue informed participants of which Gabor to attend. Participants performed either an orientation, contrast, or colour task at the attended location. Therefore, participants were attending a particular feature at one location in the visual field. Voxel-wise patterns of visually evoked BOLD response were shown to be informative of the attended target's feature only when the feature belonged to a task-relevant dimension. For example, when participants performed an orientation discrimination, the orientation decoding accuracy was higher for the attended location than the unattended location. However, when performing a contrast discrimination, the orientation decoding accuracy was no different at attended and unattended locations. In other words, the effects of spatial attention did not generalise to task-irrelevant stimuli, indicating that spatial and feature-based attention work in conjunction.

It is proposed that attentional affects motion and colour processing differently at the cued location, based on the reliability of the cue for the given dimension. However, there are a number of differences between the two tasks used above. Firstly, the motion task required discrimination and the colour task required detection and localisation, and it may be that higher-order attentional processes deal differently with these tasks. Moreover, the spatial extent of the target stimuli was different: The motion task filled the entire RDK window and would be best completed by integrating local motion signals, whereas the probe task required detecting a single red dot, and integration of signals would hamper performance in this task. Therefore, rather than biasing attention by colour or motion, there may have been differences between the stimuli that led to strategic differences in how they were completed. A third difference between the tasks is that the red dot probe was never a coherently moving dot. This may have meant that the stimuli were interpreted as distinct objects (Duncan, 1984; Egly et al., 1994), and that the difference in validity effects was due to object attention. These potential confounds are addressed and discussed in Chapter 3.

In conclusion, the experiments in this chapter demonstrate that the effects of spatial attention are not necessarily similar for all stimuli at the cued location. Furthermore, the design of these experiments provides the conditions in which to test the independence of spatial and feature-based attention. Participants are able to bias attention to a likely dimension at the cued location, suggesting that they are able to integrate spatial and feature-based attention.

Chapter 3. Endogenous Cueing II: Motion Discrimination and Colour Discrimination

The experiments presented in Chapter 2 suggest that spatial attention does not generalise equally to all stimuli at a cued location. When using a spatial cue to indicate the likely location of one task in a dual-task experiment, both tasks showed typical spatial cueing effects, but these were modulated by the information in the cue. Participants were able to bias attention towards the likely dimension at the cued location, suggesting that spatial attention is not oriented as one entity as a spotlight (e.g. Posner et al., 1980) or zoom lens (e.g. Eriksen & St. James, 1986; Eriksen & Yeh, 1985), which enhances everything at the attended location equally.

These effects were demonstrated in Chapter 2 using a motion discrimination task and a probe localisation task, showing a clear pattern of modulation. The experiments in Chapter 3 were designed to test the conclusion that spatial attention can be biased towards different dimensions at the same location.

The following experiments were designed in the same way as the previous experiments, with a dual-task set up in which one task was reliably cued. The colour task was a colour change of a proportion of RDK dots, and participants reported whether the dots changed to red or green, such that both tasks span an entire RDK and both require discrimination. The change in the colour task allows assessment of whether the ability to bias spatial attention in the experiments in Chapter 2 was reliant on task differences between motion discrimination and probe localisation.

Experiment 4.

The following experiments were designed to test whether if one task is reliably spatially cued, a second task will show equal attentional effects. Participants were required to discriminate the direction of coherent motion in one RDK and whether the dots in one RDK changed to red or green. In Experiment 4, the cue was 70% valid for the location of coherent motion but uninformative for the colour change.

Method.

Participants.

Twenty-one naïve participants (15 females) from Bangor University took part. They were selected using the online participation panel, received course credits for their time and had normal or corrected to normal vision.

Stimuli.

Stimuli were created as in the previous experiments with the following changes: All the dots were orange and instead of a red dot probe, in one of the four RDKs, the dots changed to either red or green for 100ms. An equiluminance procedure was run to find the subjective ratio for green compared to red for each participant. Following this, in the training and the experiment, red was set at [255 0 0] and green set as the equiluminant [0 (255*ratio from the equiluminance program) 0]. Following piloting, these colours were then mixed slightly (80% of the original colour with 20% of the opposing colour) to increase difficulty of the discrimination task. Mixing the red and green RGB values together created the

orange shade that was equal in luminance to both the red and the green and was the colour of all dots other than the red or green colour discrimination dots.

The number of motion and colour discrimination dots was determined using staircase coherence programs. The threshold at which participants were 60% correct at each discrimination task was selected for use in the experiment. Colour change dots were selected from the RDK dots independently of the coherent motion dots, so that if both tasks appeared at the same location, colour change dots included both translating dots and randomly moving dots. Similarly, coherently moving dots contained both orange and colour change dots.

Design.

On 70% of the trials the cue indicated the location of the coherent motion, while on the remaining 30% of the trials the coherent motion had an equal chance of being displayed at any of the uncued locations. Sixty-four of the 416 trials were neutrally cued. The colour change was equally likely to appear at each of the four locations, and the spatial cue provided no information regarding the colour change location. Accuracy in discriminating the direction of coherent motion and colour change were measured.

Procedure.

A session lasted two hours and each participant completed 416 trials of the experiment. Participants first completed an equiluminance procedure, in which a freely-available script was modified, based on the minimum motion luminance measurement procedure (Cavanagh, MacLeod, & Anstis, 1987). Briefly, the stimulus consisted of a complex, annular grating comprising two counter-flickering,

superimposed visual patterns. The first component contained two spatially offset cosine waves, defined respectively over red and green phosphors only, such that where one phosphor peaked, the other troughed. The amplitude of the luminance profile of one phosphor was kept constant, while the second was varied across trials. The second component was a grey level, sinewave grating in quadrature phase with the colour gratings, across both space and time. When the two components were superimposed, the annulus appeared to rotate either clockwise or anti-clockwise unless the luminance of the two phosphors was matched. This rotatory motion was driven by the luminance difference in the two phosphors; when the luminance of the red was larger than the green, the annulus appeared to rotate clockwise, whereas if green was larger than red the annulus appeared to rotate anticlockwise. Participants reported the direction of motion as clockwise or anticlockwise, and responses were used to compute a cumulative probability function. The ratio of red to green luminance at which participants were equally likely to report clockwise and anticlockwise motion was the point of equiluminance. In the first block of trials, well-spaced luminance ratios were used. Subsequent blocks used decreasing increments of luminance values to focus in on the equiluminance point.

Participants then completed 350 trials on the motion coherence training program, and 200 trials of colour discrimination, both on staircase procedures. In the motion training program, half the trials were neutrally cued - fixation colour change – and half were preceded by a 100% valid spatial cue, while in the colour training, half the trials were neutrally cued, and half were preceded by a non-informative spatial cue. The difference in the reliability of the cue during the training was to simulate the experiment, in which the cue is valid for the motion but non-informative for the colour. The neutral trials were used to set the number of dots for

motion discrimination and colour discrimination in the experiment, at the level at which participants were 60% correct.

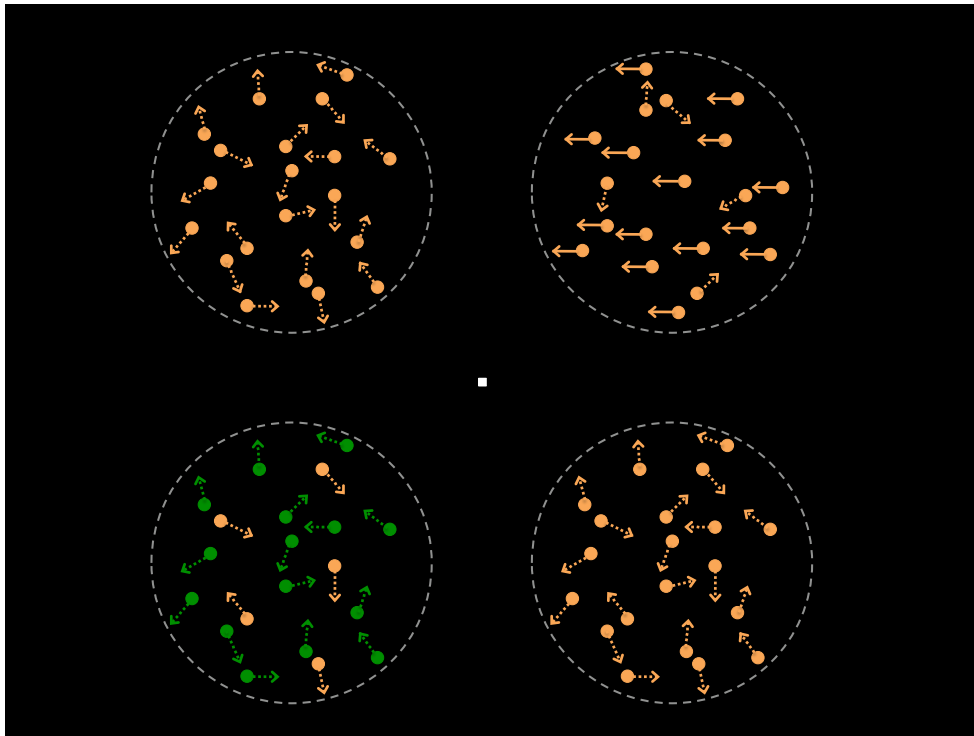


Figure 3.1. Target display in Experiment 4. RDK dots were orange. In one RDK, the dots changed to red or green for 100ms, as shown in the bottom left. In one RDK, the dots translated either up, down, left, or right, as shown in the top right.

The target display is shown in Figure 3.1, and the timing and structure were the same as that of the experiments in Chapter 2. The two tasks could be in different RDKs (as shown in Figure 3.1) or the same RDK. The participants were aware that the colour change dots were equally likely to be red or green. Participants were instructed to report both the direction of coherent motion and the colour of the colour change dots at the end of the trial.

Results.

Two participants who showed no validity effect for either task were excluded, as this indicated that they had not used the cue to orient their attention. A further participant was excluded because performance was at chance for red targets.

Accuracy on motion discrimination was obtained in the same way as in the previous experiments, and scores were arcsine corrected before group analysis. For the colour discrimination task, percent correct scores were also arcsine corrected.

Accuracy did not differ across the red and green trials, $t(17) = -1.74, p = .10$.

Accuracies for both tasks on valid and invalid trials are shown in Table 3.1.

Table 3.1.

Mean Accuracy (%) for Motion Discrimination and Colour Discrimination Tasks on Valid and Invalid Trials for Experiment 4.

Task	Valid		Invalid	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion	76.67 (8.57)	[72.40, 80.93]	62.39 (10.15)	[57.34, 67.44]
Colour	82.72 (6.39)	[79.54, 85.90]	75.17 (8.14)	[71.12, 79.21]

Note. CI = confidence interval.

The validity effects for both tasks can be seen in Figure 3.2. The results were analysed in a 2 (task: motion, colour) x 2 (validity: valid, invalid) repeated measures ANOVA. There was a main effect of task, as participants were more accurate at the colour task than the motion task, $F(1, 17) = 42.28, p < .001, \eta_p^2 = .71$. There was, as expected based on the selection of participants who showed cueing effects, a main effect of validity, $F(1, 17) = 28.92, p < .001, \eta_p^2 = .63$, as responses to stimuli on valid

trials were more accurate than on invalid trials. There was also a significant interaction of Task x Validity, $F(1, 17) = 6.81, p = .018, \eta_p^2 = .29$, indicating that the validity effect for the motion task was larger than for the colour task. Planned t tests confirmed validity effects for the motion task, $t(17) = 5.64, p < .001$, and the colour task, $t(17) = 3.93, p = .001$.

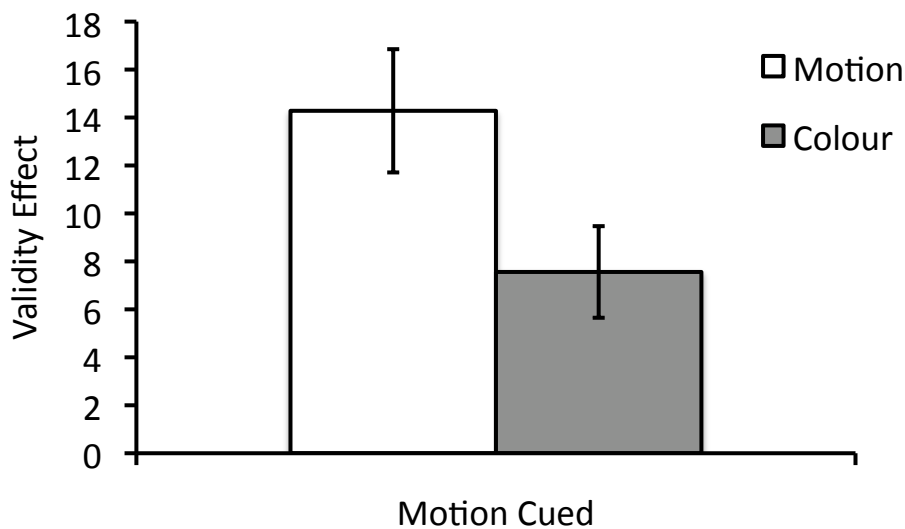


Figure 3.2. Validity effect in the motion discrimination task (white bars) and the colour discrimination task (grey bars) in Experiment 4. Error bars represent ± 1 standard error of the mean. The validity effect was calculated by subtracting the percentage accuracy on invalid trials from the percentage accuracy on valid trials.

Discussion.

Following a 70% valid cue for the location of coherent motion, there was a validity effect for both motion discrimination and colour discrimination. Though both tasks showed a clear validity effect, the magnitude of these effects differed: The motion validity was larger than the colour validity effect. As the motion task was the task that the cue was informative for, this suggests that attention modulated

performance in this task to a greater degree than the colour task. These results are in agreement with the conclusion from Chapter 2 that spatial attention can be biased by dimension.

The pattern of results from Experiment 1 is mirrored here, even with a different colour task. In Experiment 1, the motion task was discrimination of a threshold motion stimulus, whereas the colour task was localisation of a red dot probe. In Experiment 4, the colour task was altered so that both tasks required discrimination of stimuli that were thresholded. If the results in Experiment 1 were due to differences in task demands (discrimination versus detection), the validity effects in Experiment 4 should have been similar for the two tasks as both required discrimination. However, there is modulation of the validity effects based on the information in the cue, suggesting that the effects are due to differences in allocation of attention to dimensions, not task differences.

A second difference between the motion and probe in Experiment 1 was that the two tasks were of different sizes; the coherent motion filled the entire RDK, but the probe was a single red dot. Therefore, the optimal attentional strategy may have been different for the two tasks, as motion discrimination would be most accurately completed by summing local motion signals from across the RDK and this same strategy would be detrimental to probe detection and localisation. As the cue was useful for the location of coherent motion, participants may have prepared to sum signals rather than detect the probe. In Experiment 4, both tasks were represented across the RDK in a proportion of the dots, and there is still a larger cueing benefit for the motion task than the colour task, hence it is unlikely that the attentional modulation was due to the spatial extent of the task.

The colour task change in Experiment 4 also counters another possible explanation for the attentional modulation of cueing effects in the first set of experiments. When the colour task was a single red dot probe, this was always restricted to be one of the non-coherently moving dots, so that even when both tasks appeared at the same location, the probe was never one of the translating dots. Thus the dots were drawn from separate populations and may have been perceived as distinct objects. Proponents of object-based attention report that attention generalises across all features of an object once it has been selected (Duncan, 1984; Egly, Driver, & Rafal, 1994), as supported by the work of Remington and Folk (2001), who found that the irrelevant dimension of a target led to a compatibility effect. The colour change dots in Experiment 4, however, were drawn from both coherently moving and non-coherently moving dots when both tasks appeared at the same location. Thus, the motion and colour discrimination tasks were not completed on separate objects. The results show the pattern expected if participants are able to bias spatial attention towards a likely dimension at the cued location, and the design counters an object-based explanation.

Experiment 5.

Though both tasks in Experiment 4 showed a validity effect, this was higher for motion than probe. The same experiment was repeated but with the cue 70% valid for the colour change location and uninformative for the coherent motion location, in order to test the conclusion that participants can bias attention towards a likely dimension at a spatially-cued location.

Method.

Participants.

Twenty naïve participants (13 females) from Bangor University were recruited using the online participation panel and received course credits for their time. All had normal or corrected to normal vision. None had taken part in the previous cueing experiments.

Stimuli and design.

These were the same as in the previous experiment, with the exception that the cue was now 70% predictive for the colour change location and provided no information about the location of the coherent motion.

Procedure.

Participants began with the same equiluminance procedure as in the previous experiment, and this was used to calculate the red-green ratio in the colour change dots, and the orange colour for the remaining dots.

Participants then completed training trials on both the motion and colour tasks. For the coherent motion, half of the trials were neutrally cued (fixation colour change) and half were preceded by a non-informative line cue. For the colour change task, half the trials were neutrally cued and half the trials were preceded by a 100% valid cue. This was for participants to practice using the cue. The neutral trials were used to set the number of dots to translate or change colour in the experiment, by calculating the level at which participants were 60% correct.

Results and discussion.

Two participants who showed no validity effect for either task were excluded, as this indicated that the cue had not been effective in directing their attention. A third participant was excluded as she told the experimenter that she had chosen to ignore the cue throughout the experiment.

Accuracy on motion discrimination was obtained in the same way as in the previous experiments, and scores were arcsine corrected before group analysis. For the colour discrimination task, percent correct scores were also arcsine corrected.

Accuracy did not differ across the red and green trials, $t(19) = -1.16, p = .26$.

Accuracies for both tasks on valid and invalid trials are shown in Table 3.2.

Table 3.2.

Mean Accuracy (%) for Motion Discrimination and Colour Discrimination Tasks on Valid and Invalid Trials for Experiment 5.

Task	Valid		Invalid	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion	76.29 (7.77)	[72.30, 80.29]	72.18 (4.81)	[69.70, 74.65]
Colour	76.59 (6.85)	[73.07, 80.11]	70.47 (7.26)	[66.74, 74.20]

Note. CI = confidence interval.

The validity effects for both tasks can be seen in Figure 3.3. Results were analysed using a 2 (task: motion, colour) x 2 (validity: valid, invalid) repeated measures ANOVA. There was no effect of task, $F(1, 16) = 0.08, p = .78, \eta_p^2 = .005$, so performance in both tasks was equivalent. There was, as expected based on the selection of participants who showed cueing effects, a main effect of validity, $F(1, 16)$

= 33.04, $p < .001$, $\eta_p^2 = .67$. There was no Task x Validity interaction, $F(1, 16) = 0.53$, $p = .48$, $\eta_p^2 = .032$, suggesting that the validity effects were not significantly different across the two tasks. Planned t tests indicated significant validity effects for the motion task, $t(19) = 2.86$, $p = .010$, and the colour task, $t(19) = 5.06$, $p < .001$.

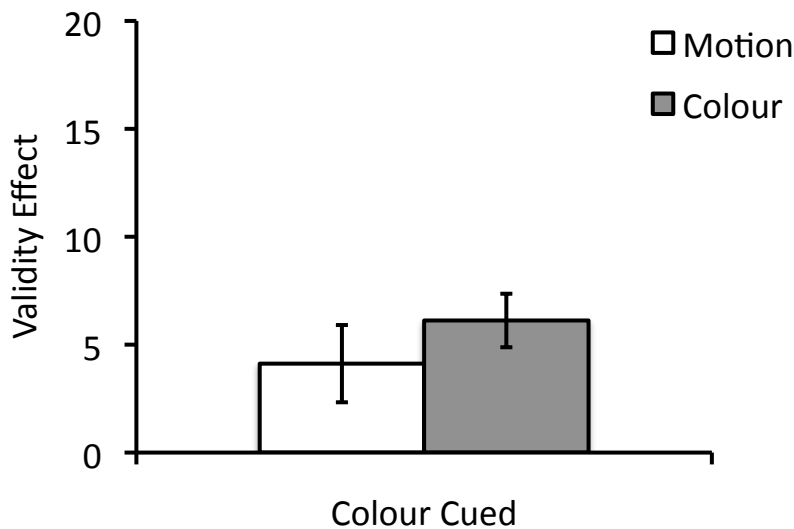


Figure 3.3. Validity effect in the motion discrimination task (white bars) and the colour discrimination task (grey bars) in Experiment 5. Error bars represent +/- 1 standard error of the mean. The validity effect was calculated by subtracting the percentage accuracy on invalid trials from the percentage accuracy on valid trials.

Cueing the colour task with an informative cue led to validity effects for both the colour and the motion tasks. Unlike Experiment 4, the difference in magnitude of these effects is not evident here; the colour validity effect does not appear as qualitatively larger than the motion validity effect.

Experiment 6.

The previous two experiments were run within-subjects, in order to investigate the differences in magnitude on the coherent motion and colour change tasks. This allows for comparison across experiments to examine the interactions of cue reliability and attentional effects.

Method.

Participants.

Nineteen naïve participants (15 female) from Bangor University were recruited through the online participant panel and awarded course credits for their participation. All had normal or corrected to normal vision. Five participants who had completed Experiment 5 responded to the invitation to take part in a follow-up so both of their sessions are included in this experiment; no others had taken part in our previous cueing experiments.

Design and stimuli.

These were the same as in the previous two experiments.

Procedure.

Participants were tested in two sessions on non-consecutive days; one session for each cue condition. The first session lasted two hours and the second session lasted one hour. In the first session, the equiluminance ratio was calculated for each participant using the procedure described previously. Participants then completed 350 practice trials on the motion coherence threshold program, and 200

practice trials on the colour coherence threshold program. In session one, participants did either the motion or colour cue condition.

When participants returned for their second session, they completed 80 trials each of the motion and colour training programs and thresholds were adjusted accordingly. The same equiluminance value was used as in session one. They then completed the second experimental block, the opposite of the one they did in session one.

Results and discussion.

Three participants were excluded, because they failed to show a validity effect for the reliably cued task in both cue conditions, indicating that the cue was not effective in directing their attention. Accuracies for both tasks on valid and invalid trials are shown in Table 3.3.

Table 3.3.

Mean Accuracy (%) for Motion Discrimination and Colour Discrimination Tasks on Valid and Invalid Trials for Experiment 6.

Task	Valid		Invalid	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion cue				
Motion	81.50 (7.50)	[77.50, 85.50]	70.13 (8.63)	[65.53, 74.72]
Colour	77.00 (7.70)	[72.90, 81.10]	72.13 (6.05)	[68.90, 75.35]
Colour cue				
Motion	78.75 (6.62)	[75.22, 82.28]	73.00 (8.96)	[68.23, 77.77]
Colour	78.00 (4.56)	[75.57, 80.43]	72.56 (7.99)	[68.30, 76.82]

Note. CI = confidence interval.

Figure 3.4 shows the validity effects for each task. Results were analysed in a 2 (cue condition: motion, colour) x 2 (task: motion, colour) x 2 (validity: valid, invalid) repeated measures ANOVA. There was a significant validity effect, $F(1, 15) = 60.15, p < .001, \eta_p^2 = .80$, as expected based on the selection of participants who showed cueing effects. There was also a Task x Validity interaction, $F(1, 15) = 6.03, p = .027, \eta_p^2 = .29$ and Cue Condition x Validity approached significance, $F(1, 15) = 4.08, p = .062, \eta_p^2 = .21$, driven by the larger validity effect for motion when motion was cued. However, this effect did not yield a significant Cue Condition x Task x Validity interaction, $F(1, 15) = 1.46, p = .25, \eta_p^2 = .089$. All further comparisons were non-significant ($F < 1$).

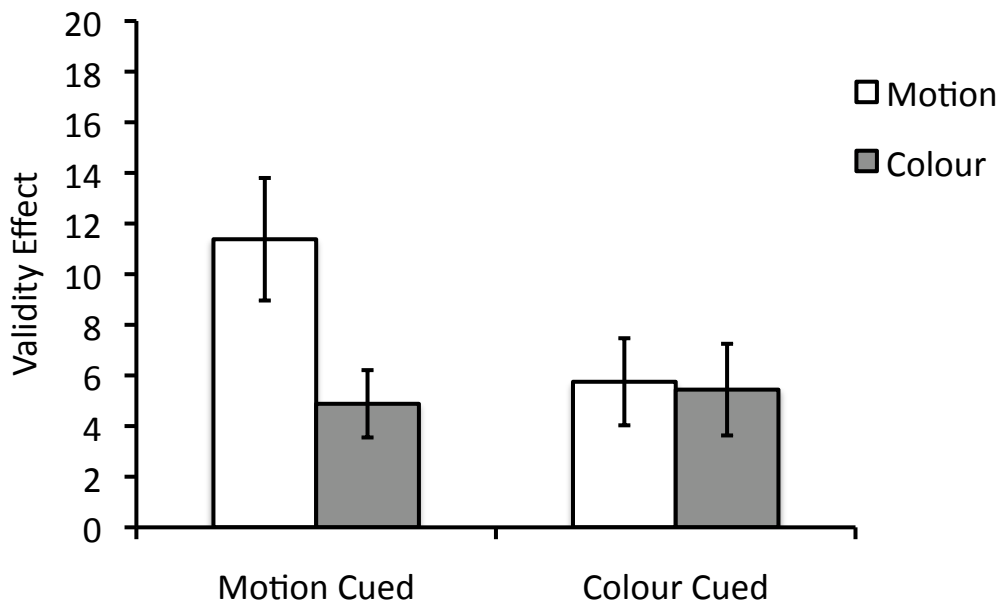


Figure 3.4. Results from Experiment 6, within participants. Validity effects on the motion and colour discrimination tasks following a cue that was either useful for motion or colour. Error bars represent +/- 1 standard error of the mean.

A 2 (cue condition: motion, colour) x 2 (validity: valid, invalid) repeated measures ANOVA was also conducted for each task. For the motion task, there was a main effect of validity, $F(1, 15) = 45.16, p < .001, \eta_p^2 = .75$. The Cue Condition x Validity interaction approached significance, $F(1, 15) = 3.43, p = .084, \eta_p^2 = .19$, suggesting that the validity effects in the motion task depended on whether the cue was useful for the task. For the colour task, there was a main effect of validity, $F(1, 15) = 27.83, p < .001, \eta_p^2 = .65$, but no Cue Condition x Validity interaction, $F < 1$.

When participants are presented with cues that are informative for one task and not another, they do have the ability to implement this information. This is evidenced in the validity effects being modulated by cue information even when the tasks and stimuli are well-matched. However, this effect is asymmetric: the validity effect for motion discrimination was modulated, but colour discrimination was not.

Chapter Discussion

The current study was designed to extend investigation into whether the effects of endogenous spatial attention are similar for all task-relevant stimuli at the cued location. The two stimuli were matched across spatial extent and both tasks were forced-choice discrimination. When the spatial cue was only predictive for the location of the coherent motion, the motion task showed a larger validity effect. Therefore, this extends the work in the previous chapter: Spatial cueing effects do not fully-generalise to the task for which the cue was uninformative, despite the fact that both stimuli were task-relevant. The second outcome from these experiments is the finding that motion and colour stimuli show an asymmetry in attentional effects. The validity effect for the motion task was modulated by cue information, but the

validity effect for the colour task was not. These two conclusions will be discussed in turn.

The results from this chapter extend the findings in Chapter 2, in that participants are able to bias spatial attention towards a dimension that is likely to appear at the cued location. The results in these experiments show that this is also the case when the colour task is a discrimination task that fills the entire window. This demonstrates that spatial attention is not a single spotlight (e.g. Posner et al., 1980) or zoom lens (e.g. Eriksen & Hoffman, 1973; Eriksen & St James, 1986) that generalises to all dimensions at the attended location. Instead, the results suggest an interaction between spatial and feature-based attention, consistent with the findings of Cohen and colleagues (Cohen & Magen, 1999; Cohen & Shoup, 1997, 2000) and Remington and Folk (2001), and supported by the structural organisation of visual cortex.

The results provide compelling evidence that participants are able to exploit specific cue information, but there is also an asymmetry. The validity effect for the motion task was modulated by the usefulness of the cue, whereas the validity effect for the colour task was equal regardless of the cue condition. Furthermore, the motion validity effect was larger than the colour validity effect following a cue predictive for the location of the motion task, yet the validity effects for colour and motion were equal when the cue was predictive for the location of the colour task. This asymmetry suggests a larger role for attention in motion processing than colour processing. Supporting evidence for this account comes from examination of visual processing pathways in the brain, and from imaging investigations of higher-order attentional mechanisms.

Two routes of visual processing have been studied, ventral and dorsal, (Ungerleider & Mishkin, 1982), and dubbed 'what' and 'where' (Ungerleider & Haxby, 1994; Ungerleider & Mishkin, 1982). The ventral pathway is concerned with object-based visual attributes such as colour, and the dorsal pathway has a role in motion and location (Ungerleider & Haxby, 1994; Ungerleider & Mishkin, 1982). It has been suggested that though the ventral stream sees the effects of attentional orienting, the dorsal stream is more heavily involved in directing attention (Itti & Koch, 2001). As the dorsal stream is also concerned with motion processing, this relationship could explain the larger attentional effects on motion stimuli than colour stimuli in our experiments.

Higher order attention regions have also been studied with regards to stimulus properties. When attending to either motion or colour in random dot patterns, larger, more extensive activation has been found following motion than colour cues (Liu, Slotnick, Serences, & Yantis, 2003; Shulman, d'Avossa, Tansy, & Corbetta, 2002). For example, Liu et al. (2003) found extensive activation in fronto-parietal regions that was greater for attention to motion than colour, but only two regions in which activation was greater for attention to colour than motion. The authors suggest that when attending to colour, the salience of motion means it will also be attended. Further, the shape of the BOLD response has been found to be more sustained following motion cues than colour cues in fronto-parietal regions (d'Avossa, Shulman, & Corbetta, 2003). Hence, there is seemingly a bias in higher order attentional regions for motion over colour. This suggests that motion may be prioritised in attentional processing such that motion is modulated to a greater degree, and, moreover, that in any stimulus containing motion, motion will be attended.

In summary, the results demonstrate that spatial attention can be biased by prior information regarding the stimulus likely to appear in the cued location, reflecting an interaction between spatial and feature based attention. Furthermore, the effects of attention depend on the dimension: Whereas the validity effect was modulated for motion, colour processing did not show the same effect. This is consistent with a view of motion as prioritised in visual streams and higher-order attention networks.

Chapter 4. Exogenous Cueing I: Manipulating Cue Size and Task Properties

Shifts of spatial attention evoked by sudden changes in the environment improve the analysis of sensory information at the attended location, resulting in both greater accuracy and shorter response latencies (e.g. Berger et al., 2005; Carrasco et al., 2004; Cheal & Lyon, 1991; Jonides, 1981). Exogenous shifts of attention are a reflex-like response (Giordano et al., 2009; Jonides, 1981; Yeshurun & Carrasco, 1998; Yeshurun et al., 2008), which can be quickly executed after the onset of the orienting stimulus (Cheal & Lyon, 1991; Muller & Rabbitt, 1989). Exogenous cues can be uninformative about upcoming target locations, yet participants are unable to ignore them (Awh, Matsukura, & Serences, 2003; Jonides, 1981), even when orienting impairs performance (Giordano et al., 2009; Yeshurun & Carrasco, 1998; Yeshurun et al., 2008).

A common assumption is that following exogenous cues, all stimuli and features at the cued location are attended. Support for the idea that the effects of exogenous attention generalise across features comes from two main lines of evidence: studies of location as the means of selection (e.g. Henderson, 1991; Henderson & MacQuistan, 1993), and investigations into the processing of irrelevant stimuli at the attended location (e.g. Eriksen & Hoffman, 1973; Eriksen & St. James, 1986). Further studies have shown that exogenous attention generalises only over task-relevant dimensions (e.g. Remington & Folk, 2001).

It has been suggested that exogenous attention affects performance by enhancing spatial resolution of stimuli at the attended location, resulting in greater visual acuity (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Henderson, 1996; Ling & Carrasco, 2006; Lu & Doshier, 2000; Pestilli & Carrasco, 2005; Yeshurun & Carrasco,

1998, 1999; Yeshurun et al., 2008). The *resolution hypothesis*, suggests that attention enhances fine spatial details of the visual stimulus (Yeshurun & Carrasco, 1998, 1999; Yeshurun et al., 2008). Yeshurun and Carrasco (1998) examined the effects of exogenous attention on a texture segmentation task and found that exogenous cues improved performance when stimuli appeared at intermediate retinal eccentricities, where spatial resolution is low, whereas exogenous cues impaired performance at foveal locations, where spatial resolution is high. These authors concluded that increasing the spatial resolution at foveal locations where it is already high could make the resolution too high to successfully perform the task, supporting the hypothesis that exogenous attention increases the spatial resolution at the attended location.

Earlier models of attention suggested that the size of the attended region can vary. The *zoom lens model* advocates that the spatial extent of the attentional effects are controlled by expanding or contracting the attended region (Eriksen & St. James, 1986; Eriksen & Yeh, 1985; Henderson, 1991; N. G. Müller et al., 2003); the smaller the attentional window, the more concentrated the (limited) processing resources and therefore the analysis of the stimulus can proceed more effectively (Eriksen & St. James, 1986). In support of this view, Eriksen and St James (1986) found that decreasing the number of contiguous locations that were simultaneously cued, decreased response latencies. Similarly, Castiello and Umiltà (1990) found that decreasing cue size decreased RT to targets appearing at the cued location.

On the other hand, Yeshurun and Carrasco (2008) did not find that the size of the cue modulated the effects of exogenous attention. Specifically, Yeshurun and Carrasco reported decreased performance on a texture segmentation task at the fovea when a small - but not larger - cue preceded the target. However, since there

was no gradual change in spatial resolution with changes in cue size, the authors concluded that exogenous attention does not depend on the size of the cue.

The overall view, endorsed by the literature reviewed above, is that exogenous attention is an involuntary, reflexive orienting response, which results in enhanced processing at the attended location, regardless of the task or properties of the cue. However, there is also evidence that the nature of the task establishes which visual properties of an exogenous cue determine its ability to capture attention (Folk et al., 1992; Folk et al., 1994). Since these effects are found under conditions in which the cue and target share a feature, it has been difficult to disentangle the role of top-down search from that of bottom-up processes.

The aim of the present study is to examine how the attentional field size is set during exogenously driven orienting, by asking the following questions: 1) Does the size of the exogenous cue set the size of the attentional field? 2) Do the effects of exogenous attention generalise across stimuli in the same location? 3) If the effects do not generalise, does the size of the attentional field lead to different effects on stimuli with different properties? To address these questions, a dual-task paradigm was designed, in which the sizes of exogenous cues were varied.

Experiment 7.

In this experiment the target display contained four random dot kinematograms (RDKs), each made up of 100 white dots. One RDK contained coherently moving dots. On each trial, participants discriminated the direction of coherent motion and detected the presence and location of a single red dot probe appearing briefly among one of the RDKs in half of the trials. A brief change in size and luminance of a circular frame preceded the target display as an exogenous cue,

and was uninformative as to the upcoming location of either task. For one group of participants, the cue surrounded one of the RDK locations. For the second group of participants, the frame was smaller, encompassing only the central region of the RDK, and the red dot probe was confined to the central region in each RDK.

Since the cue should summon attention to the cued location, one would expect better performance at cued than at uncued locations in both tasks if exogenous attention generalises over relevant features. If cue size affects attention deployment, these effects should be modulated by the size of the cue. Additionally, if the relation between the size of the cue and the size of the target can alter attentional effects, validity effects would be different in the two tasks.

Method.

Participants.

Twenty-one naïve participants (fourteen females) were recruited from the School of Psychology at Bangor University. Participants received course credit for their participation. Eleven participants (eight female) were tested in the large cue condition, and ten participants (six female) were tested in the small cue condition. All participants had normal or corrected to normal vision.

Stimuli and apparatus.

Stimuli were created using Matlab 7.6 with Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997) and generated by an Apple Mac Pro 1.1 computer. Stimuli were displayed on a LaCie Electron 22blue IV CRT screen, with a refresh rate of 60Hz. Head position was restrained by a chin rest at a distance of 70cm from the

monitor. The stimuli were shown against a black background, and participants were in a dark environment.

RDKs of 10° diameter were presented, one in each quadrant of the screen, at an eccentricity of 14° from the central fixation point. Each RDK contained 100 white dots, 0.2° in diameter. The dots' initial position was determined by sampling a pseudorandom uniform distribution over the circular window of each RDK. The dots were displaced at a speed of $15^\circ/\text{second}$ in a random direction and had a lifetime of three frames. This process created *dynamic noise*. In each trial, a 200ms period of *coherent motion* was inserted in one of the RDKs. During this time, a proportion of the dots were displaced either up, down, left or right. The proportion of coherent dots was set using a threshold, staircase procedure for each participant at the beginning of the session.

A red dot probe was presented in half the trials. The probe was 2.5 times larger than the white dots, and it was plotted as a randomly-moving dot within one RDK. The location of the probe was limited to the area within the cue, and participants were made aware of this before the task.

Thin, grey, annular placeholders, 11° in diameter, surrounded each RDK. The large spatial cue was a 80ms long increase in luminance and thickness of one of the placeholders. The small cue was an 80ms long increase in luminance of 4° diameter annular area of the background (thickness) centered on one of the RDKs (see right side of Figure 4.1). On neutrally cued trials, either small or large cues appeared in all four locations simultaneously.

Design.

The location of the coherent motion and the red dot probe were determined by sampling two independent distributions. Each location was equally likely to contain the coherent motion and the red dot probe. The exogenous cues provided no information about the location of the coherent motion, the red dot probe, or the direction of coherent motion. Sixty-four of the 416 trials were neutrally cued. Neutrally and spatially cued trials were intermixed.

Procedure.

The session lasted for 90 minutes. At the start of the session, participants completed 350 uncued motion discrimination trials on a staircase procedure. The coherence threshold of the motion dots was set at the level at which participants achieved 60% accuracy during the training, in order to allow for increased performance following the cue.

The trial structure is shown in Figure 4.1. The fixation point and four RDKs with dynamic noise were presented for 950ms until the response screens. Participants had to maintain fixation on the marker at the centre of the screen. Five hundred milliseconds after the onset of the trial, the exogenous cue was presented for 80ms. Coherent motion started 150ms after cue onset and lasted 200ms. Following the coherent motion, the dynamic noise was presented for another 100ms. The red dot probe was displayed in 50% of trials, 200ms after cue onset. The red dot probe was visible for 100ms. Then the response screens were presented and lasted until the participants' responses. Participants were asked to indicate the direction of motion by selecting the corresponding arrow in the response screen. The following screen outlined the four locations and a central circle, and the

participants selected the location where the probe appeared, or the central circle for an absent probe. Participants each completed 416 trials.

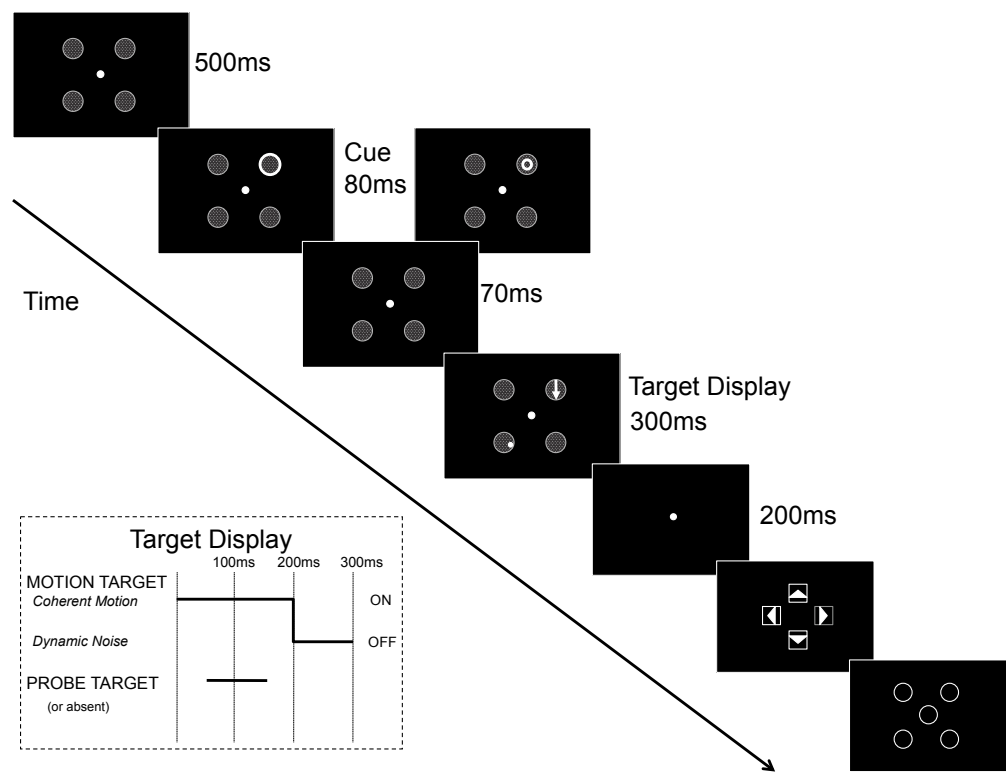


Figure 4.1. Trial structure for Experiment 7 (large cue shown on the left and small cue shown on the right). Stimuli not to scale. Arrow on display indicates direction of coherent motion and was not present in the experiment. The white dot represents the red dot probe. Inset box shows timings within the target display. Trial shown is cued for coherent motion and uncued for probe location.

Results.

The proportion of correct motion discriminations, and the proportion of correct red dot probe localisations were calculated for each participant, and are shown in Table 4.1. These values were normalised using the arcsine of the square

root, a standard transformation for proportional data, prior to the group level analyses.

Table 4.1.

Mean Accuracy (%) for Motion Discrimination and Probe Localisation Tasks on Cued and Uncued Trials for the Large and Small Cues in Experiment 7.

Task	Cued		Uncued	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Large cue				
Motion	74.36 (16.45)	[63.32, 85.41]	60.82 (11.67)	[52.98, 68.66]
Probe	67.18 (14.39)	[57.52, 76.85]	70.64 (8.89)	[64.66, 76.61]
Small cue				
Motion	66.00 (14.60)	[55.56, 76.44]	55.70 (12.87)	[46.50, 64.90]
Probe	68.20 (13.56)	[58.50, 77.90]	60.10 (19.24)	[46.33, 73.87]

Note. CI = confidence interval.

The motion validity effect, namely the difference between discrimination accuracy on cued and uncued trials, was not different in probe present and probe absent trials, whether preceded by the large cue, $t(10) = 1.04$, $p = .32$, or the small cue, $t(9) = 0.45$, $p = .66$. Therefore all trials were included in the analysis of the effects of cue size on motion accuracy.

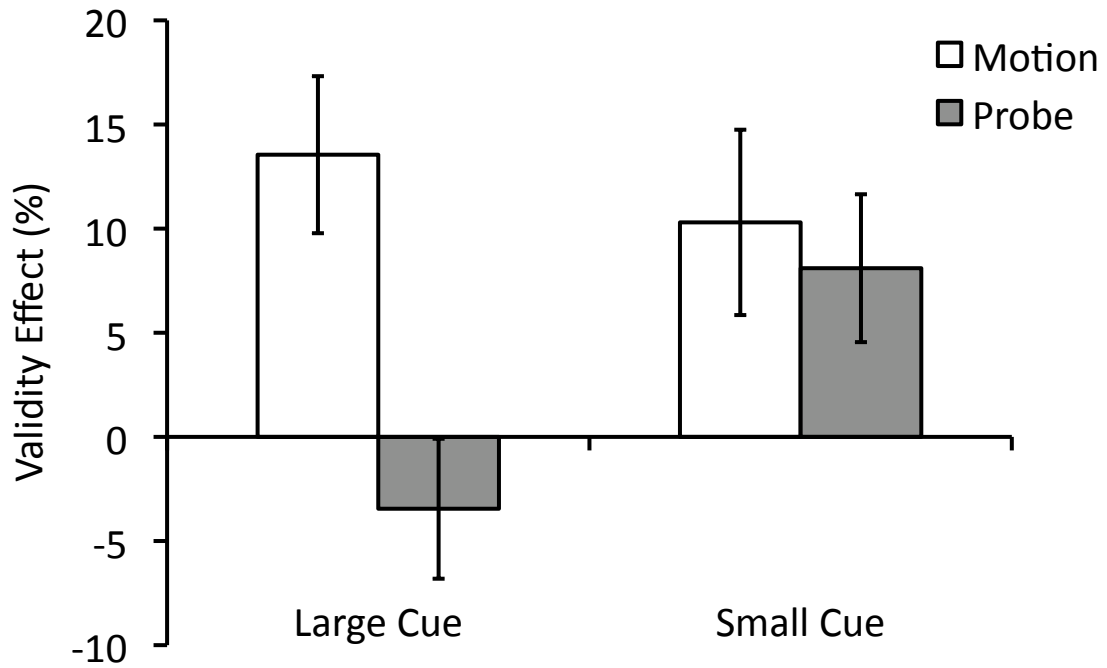


Figure 4.2. Results from Experiment 7. Validity effect was calculated by subtracting percent correct on uncued trials from percent correct on cued trials. White bars represent the validity effect for the motion task, and grey bars represent the validity effect for the probe task. Error bars represent +/- one standard error of the mean.

Normalised accuracies were entered into a 2 x 2 x 2 mixed ANOVA, with task (motion, probe) and validity (cued, uncued) as within-subjects factors and cue size (large, small) as a between-subjects factor. The validity effect was significant, $F(1, 19) = 15.32, p = .001, \eta_p^2 = .45$, with higher accuracy on cued than uncued trials, indicating that the cue attracted attention. However, as shown in Figure 4.2, this was not true across all tasks and conditions, resulting in both a significant 2-way interaction between task and validity, $F(1, 19) = 8.86, p = .008, \eta_p^2 = .32$, and, crucially, a 3-way interaction between task, validity and cue size, $F(1, 19) = 5.22, p = .034, \eta_p^2 = .22$. Remaining comparisons were all non-significant ($F < 1$).

In order to examine the 3-way interaction, these effects were analysed separately for the two tasks. Two repeated measures ANOVAs were conducted with cue condition (large, small) and validity (cued, uncued) as factors. For the motion task, there was a significant validity effect, $F(1, 19) = 19.41, p < .001, \eta_p^2 = .51$, but a lack of interaction with cue condition ($F < 1$) indicated that both cue sizes led to validity effects of similar magnitudes. Planned t tests support this conclusion, with a significant motion validity effect following both the large cue, $t(10) = 3.78, p = .004$, and the small cue, $t(9) = 2.48, p = .035$. For the probe task, there was a significant Validity x Cue interaction, $F(1, 19) = 5.84, p = .026, \eta_p^2 = .24$, suggesting that the validity effect was different for the two cue sizes. Planned t tests indicated that there was a validity effect following a small cue, $t(9) = 2.57, p = .030$, but not a large cue, $t(10) = -0.93, p = .37$. The analyses suggest that the 3-way interaction was driven by the validity effect being present for the probe localisation task following small but not large cues.

Discussion.

If the exogenous cue elicited an automatic, reflex-like orienting of attention, then one would expect its effects to generalise over stimuli and cue sizes. Experiment 7 shows that for the motion discrimination task, both cue sizes led to a validity effect. However, for the probe localisation task, only the small cue affected performance. This suggests that the attentional effects following an exogenous cue depend both on the size of the cue and the properties of the target stimuli. While the motion discrimination task required spatial summation of local motion in the coherent RDK, the red dot probe localisation task required detection of a local colour and size change. This difference in task requirements implies a difference in the size

of the perceptual fields used in the two tasks, and may, therefore, account for the difference in the effects of cue size.

The dual-task paradigm used could have led to differences in the number of switches required in order to complete both tasks. For example, when a trial is invalid there is a switch from the cued location to the location containing the target. In a dual-task, the targets could appear at the same (one switch) or different (two switches) invalid locations. There is no evidence that the probe validity effect differences result from different task-switching costs, as probe localisation performance was the same when tasks appeared at the same or different uncued locations. Equally, the motion validity effect was not different on probe present and probe absent trials, so that task switches do not appear to be affecting cueing effects. A second possible consequence of the dual-task paradigm is that one task could be prioritised over the other. As the coherent motion appeared on every trial, one could adopt a strategy to prioritise the motion task, and treat the probe localisation as a secondary task. However, there is no evidence that motion was prioritised over the probe task, as probes were detected equally at the cued location regardless of motion validity. Neither the switching costs nor motion prioritising contrasts interacted with cue size, indicating that these could not explain the probe localisation accuracy differences between the two cue sizes.

In the current experiment, the size of the cue was changed, as well as the region in which the probe could appear, thus it is not possible to distinguish between the effects of cue size and those of spatial uncertainty. Moreover, there is evidence that the effects of an exogenous cue are increased when there is a systematic relation between the cue and the target positions over trials (Kristjánsson, Mackeben, & Nakayama, 2001), raising the possibility that the effects observed were

due to differences between possible target locations relative to the cue. Experiment 8 was designed to examine the contribution of spatial uncertainty to the validity effect found in the small cue size condition.

Experiment 8.

Experiment 8 is a control experiment, designed to test whether the differences in validity effects in the probe localisation task were due to differences in cue size or target spatial uncertainty. The same large cue was used as in the large cue condition but the probe could only appear in a region, in the centre of the RDK, equal in size to the one used in the small cue condition. If the difference in validity effects is due to target spatial uncertainty then a validity effect for the red dot probe localisation task is expected. Instead, if the difference were due to the size of the cue, then we would expect the large cue not to evoke the validity effect.

Method.

Participants.

Twelve naïve participants (eight females) from Bangor University took part in Experiment 8. They received course credits for their time and had normal or corrected to normal vision. No participants had taken part in Experiment 7.

Stimuli and apparatus.

Stimuli and apparatus were the same as Experiment 7, except the following. The cue was equal in size to the large cue from Experiment 7, but the probe could only appear within an area of 4° diameter at the centre of the aperture, as in the small cue condition of Experiment 7.

Procedure.

The session lasted 90 minutes. Participants were trained on the motion discrimination task, and the motion coherence was set so that discrimination accuracy was 60%. The structure and timings of each trial were the same as Experiment 7, and participants completed 416 trials.

Results.

Motion validity effect was not different between probe present and probe absent trials, $t(11) = -0.19$, $p = .85$, so all trials were included for motion accuracy. Accuracies for the motion and probe tasks are displayed in Table 4.2.

Table 4.2.

Mean Accuracy (%) for Motion Discrimination and Probe Localisation Tasks on Cued and Uncued Trials for Experiment 8.

Task	Cued		Uncued	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion	84.17 (8.57)	[78.72, 89.61]	66.83 (9.85)	[60.57, 73.09]
Probe	55.67 (13.31)	[47.21, 64.12]	54.50 (13.64)	[45.84, 63.16]

Note. CI = confidence interval.

Validity effects are displayed in Figure 4.3. Accuracies were normalised and analysed in a 2 x 2 repeated measures ANOVA with task (motion, probe) and validity (cued, uncued) as the independent factors. There was a significant Task x Validity interaction, $F(1, 11) = 34.05$, $p < .001$, $\eta_p^2 = .76$, indicating a validity effect for the motion task, $t(11) = 8.29$, $p < .001$, but not the probe task, $t(11) = 0.44$, $p = .67$.

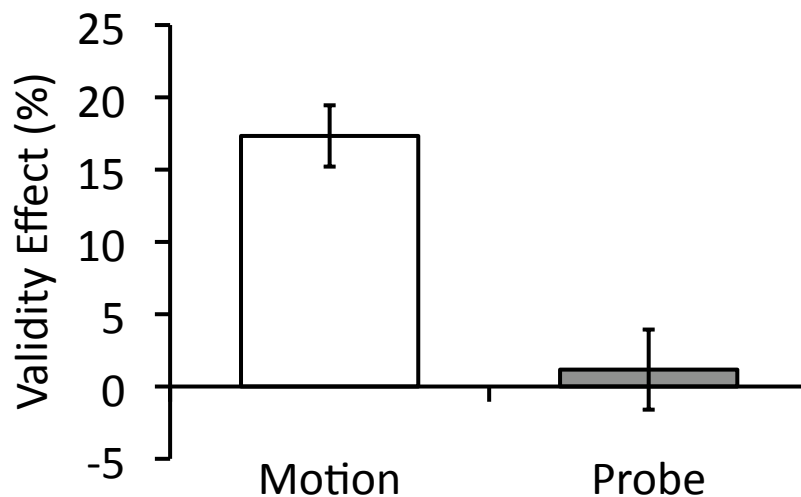


Figure 4.3. Results from the control experiment, Experiment 8. Validity effect was calculated by subtracting percent correct on uncued trials from percent correct on cued trials. The white bar represents the motion task validity effect and the grey bar represents the probe task validity effect. Error bars represent +/- one standard error of the mean.

Experiment 7 and 8 discussion.

The same exogenous cue can yield different attentional effects in two tasks performed simultaneously. A large cue improved accuracy for discrimination of coherent motion at the cued location, but did not affect localisation accuracy of the red dot probe. When the size of the cue was reduced, accuracy on both tasks was greater at cued than uncued locations. Experiment 8 showed that improved red dot probe localisation at the cued location compared to uncued locations following a small cue was not a result of reducing the area in which the probe could appear. These results strongly suggest that the size of the cue sets the size of the attentional field.

An interesting question is whether setting the attentional field reflects enhancement of sensory information within the cued area and/or suppression of surrounding information. A number of studies have found evidence for suppression of sensory data outside the attentional field. This idea was initially voiced by LaBerge, Brown, Carter, Bash, and Hartley (1991) and later supported by work using the flanker paradigm (Miller, 1991), attentional capture (Belopolsky, Zwaan, Theeuwes, & Kramer, 2007) and distractor proximity (Cutzu & Tsotsos, 2003). According to this view, the small cue affects performance on the probe task by excluding irrelevant sensory information that falls outside the area encompassed by the small cue.

On the other hand, Castiello and Umiltà (1990) examined the effect on detection latencies for targets whose location was varied in relation to the boundaries of a small and large cue. Responses to targets placed outside the small cue were faster than those falling within the large cue, indicating that there was not suppression outside the cue. While this finding may challenge the noise suppression explanation, the implication of this study may not generalise to paradigms in which distractors are present.

The next experiment was designed to examine whether the effects of a small cue on probe localisation are driven by enhancement, suppression, or a combination of the two. Red dot probe localisation was measured following a small cue, when the probe was equally likely to occur within the cue boundary or outside the cue boundary.

Experiment 9.

In Experiment 9, target processing inside and outside of the cue frame was examined. If the small cue leads to enhancement within the cued area, two results are expected: 1) greater localisation accuracy inside the cue than outside it, and 2) greater accuracy for probes appearing within the cued area than the equivalent location in uncued RDKs. However, if the small cue mainly suppresses processing of the surround, lower accuracy for probes appearing outside the cue than the equivalent region of uncued RDKs is expected.

Method.

Participants.

Seventeen naïve participants (ten females) from Bangor University took part in Experiment 9. They received course credits for their time and all had normal or corrected to normal vision. No participants had previously taken part in Experiment 7 or Experiment 8.

Design and stimuli and apparatus.

These were the same as the small cue in Experiment 7, aside from the area in which the probe could appear. The probe was equally likely to appear inside or outside the 4° diameter area at the centre of the RDK.

Procedure.

The session lasted 120 minutes. As in the previous experiments, participants had been trained on the motion task. They completed 200 trials on the coherence threshold training program before the experiment, and the coherence threshold was

set at the level at which participants achieved 60% accuracy. Participants also completed 200 trials on the red dot detection task, and the size of the red dot was set at the level at which participants achieved 60% accuracy. The structure and timings of each trial were the same as the above experiments. Participants completed 768 trials in the experiment, divided into two blocks.

Results.

The motion validity effect was not different between probe present and probe absent trials, $t(16) = 0.62$, $p = .54$ so all trials were included in the analysis of motion accuracy. As expected, motion accuracy was higher for cued ($M = 83.59\%$, $SD = 6.97$) than uncued trials ($M = 70.53\%$, $SD = 7.61$, $t(16) = 8.46$, $p < .001$).

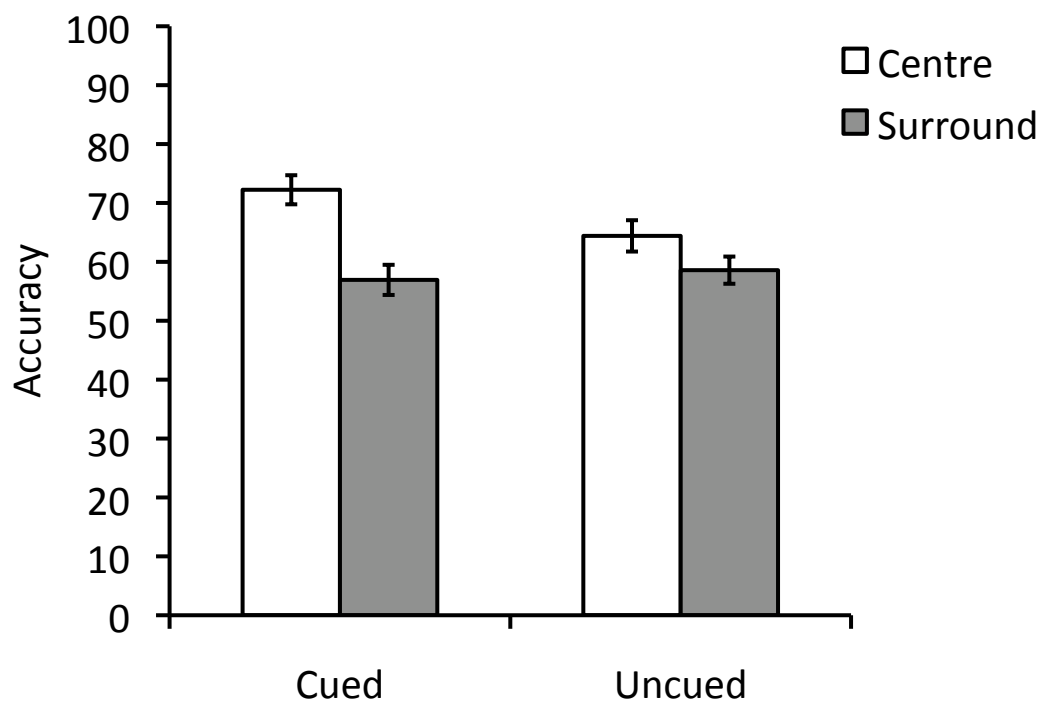


Figure 4.4. Accuracy scores for the probe localisation task in Experiment 9. White bars represent trials in which the probe appeared at the centre, gray bars represent trials in which the probe appeared in the surround. Error bars represent +/- 1 standard error of the mean.

The results for probe accuracy are shown in Figure 4.4. The probe accuracy was analysed in a 2 (validity: cued, uncued) x 2 (position: central region, surround region) ANOVA. Probes appearing in the central region were better localised than probes appearing in the surround region, $F(1, 16) = 29.09, p < .001, \eta_p^2 = .65$. Crucially, the ANOVA revealed a significant Validity x Position interaction, $F(1, 16) = 8.51, p = .010, \eta_p^2 = .35$. This interaction reflects a larger difference in probe localisation accuracy between central and surround regions at cued ($M = 20.77, SD = 18.39$) compared to uncued ($M = 7.76, SD = 8.29$) locations.

Planned comparisons showed that accuracy was higher in the central region at the cued location than in the central region at the uncued location, confirming the finding from Experiment 7, $t(16) = 4.21, p = .001$, but there was no difference between probe localisation accuracy in the surround region at cued and uncued locations, $t(16) = -.53, p = .60$. Importantly, there was a difference in probe localisation accuracy between central and surround regions at the cued location, $t(16) = 4.66, p < .001$. Finally, there was also an effect on localisation accuracy for probes appearing in the central versus surround regions of uncued locations, $t(16) = 3.86, p = .001$.

Discussion.

The results show that the small cue was effective in improving the localisation of the red dot probe. Importantly, this effect was only found when the probe appeared inside the cue; when the probe appeared in the surround region, there was no cueing benefit, suggesting that the cue indeed set the size of the attentional field.

The observation that probes appearing in the surround regions of RDKs were localised with similar accuracy at cued and uncued locations is inconsistent with the suggestion that the cue leads to suppression of the surround. Rather, the cue seems to have led to changes in visual sensitivity in the central region.

Interestingly, there was also a small benefit for probes appearing in the central region compared to the surround at uncued locations, even though this effect was much smaller than at cued locations. Previous results from Castiello and Umiltà (1990) suggest that this represents an effect of cueing that generalises across locations and depends on the size of the cue.

Chapter Discussion

In the present set of experiments, the size of exogenous cues was manipulated and the consequences on the magnitude of the validity effect were measured in two tasks performed simultaneously. Following both large and small cues, discrimination of motion was better at cued than uncued locations. However, localisation of a small red dot probe was better at cued than uncued locations following the small cue, but not the large cue. These results suggest that the attentional effects depend on both the size of the exogenous cue and the spatial properties of the task.

Specifically, the motion task depended on the integration of local motion signals over the window occupied by the coherent RDK; the localisation of the red dot probe required the detection of a localised size and colour change of one of the dots. The different spatial distributions of visual information in the two tasks would suggest that while the motion task relied on neural mechanisms with extensive

receptive fields, the red dot probe localisation task required mechanisms with localised receptive fields.

The differences in the properties of the two tasks can explain the effect of cue size. In the motion task, the size of the attentional field is mainly determined by large receptive fields of directionally tuned mechanisms and therefore changing the cue size has little consequence on the number of receptive fields involved. However, in the red dot localisation task, the size of the attentional field is mainly determined by the cue, because the number of small receptive fields engaged by the cue strongly depends on its size. Localisation accuracy is only improved at the cued location when a small number of receptive fields are engaged, thus limiting the amount of irrelevant sensory data that needs to be processed.

A number of different proposals have been put forward over the years regarding the nature of the processes involved in stimulus driven orienting of attention. The original proposal, based on observations in laboratory animals, was that exogenous orienting gives the animal the opportunity to inspect a novel stimulus, while other cognitive processes are temporarily suspended (Pavlov, 1922). One key element of this reflex-like response is that its effects should generalise across stimulus dimensions, contrary to the present finding that the large cue affected performance in the motion discrimination, but not the red dot probe localisation task. Others have found, in visual search tasks, that attention can be exogenously captured by stimuli which share visual features with the target, indicating that top-down biases can affect the saliency of bottom up, sensory signals (Folk et al., 1992; Folk et al., 1994). This is unlikely to explain the results, as the implication is that the large and small cues are equally similar to the coherent motion, whereas the small cue is more similar to the red dot probe than the large

cue. Moreover, the finding that the effects of the small cue on the red dot probe localisation are limited to probes appearing within the area encompassed by the cue indicates that the important similarity is the one between the locations of the cue and the probe, rather than between non-spatial dimensions.

A final suggestion is that exogenous cues alter locally the contrast sensitivity curve, shifting the sensitivity toward higher spatial frequencies (Yeshurun & Carrasco, 1998, 2008). This could account for the effects of cue size on the red dot probe task, however would not provide any obvious explanation of the cueing effects observed with both small and large cues in the motion discrimination task.

This account may go some way towards explaining Yeshurun and Carrasco's (2008) findings that a small cue led to attentional effects but larger cues did not. The authors concluded that exogenous attention is automatic and is therefore unable to alter its effect on resolution based on cue size. Following the findings, one could infer that only the smallest cue was the optimal cue for the task, while the larger cues were all equally inappropriate for the task.

Based on the dissociation between cueing effects on motion discrimination and probe localisation, it is reasonable to conclude that the effects observed reflect the involvement of receptive fields with different sizes in the two tasks. Therefore, these processes are more likely to have arisen in lower tiers of the visual hierarchy than to reflect feedback signals from higher order tiers of the visual hierarchy.

Chapter 5. Exogenous Cueing II: Matching Task Properties to Cue Size

In the previous chapter, the experimental evidence suggests that manipulating cue size alters the effects of exogenous attention. Using a large cue, there was a validity effect for a motion discrimination task that occupied the entirety of the cued location. However, following this large cue there was no evidence of an attentional effect for a small probe localisation task. When the cue size was reduced, there was a validity effect for the small probe task, which was attributed to enhancement inside the cue boundary. It was concluded that cue size alters the size of the attentional window, leading to distinct effects on tasks occupying different spatial extents.

An alternative explanation is that a large frame is not a suitable cue for the red dot colour task. It may be that this cue would never capture attention for colour, regardless of task size. It is therefore important to investigate whether there are conditions in which a large luminance cue can lead to attentional effects on a colour task.

Experiment 10 was designed to test the conclusion that cue size and task properties interact in exogenous attention. If attentional effects depend on the spatial match of the cue and task, any task occupying the entire RDK should benefit from a large cue. This experiment addressed the following: Can a large luminance cue lead to attentional effects on a colour task, and does a large cue benefit all spatially-matched tasks at the cued location? Therefore, in Experiment 10, instead of a red dot localisation, the second task was a colour discrimination task that filled the entire RDK, like the motion discrimination task. This task was also used in the

endogenous experiments in Chapter 3. It was predicted that both tasks would show a validity effect as the cue size matches the extent of the stimulus.

Method.

Participants.

Sixteen naïve participants (fifteen females) from Bangor University took part. They were selected using the online participation panel, received course credits for their time and had normal or corrected to normal vision. Each session lasted two hours, including 350 motion discrimination training trials, 200 colour discrimination training trials and 416 experimental trials.

Design and stimuli.

The moving RDK dots were orange, and were plotted in the same way as in the previous experiment. The second task was a colour discrimination task, in which some of the dots across a whole aperture changed to either red or green for 100ms. Firstly an equiluminance procedure was run to find the subjective ratio for green compared to red for each participant, as described in Chapter 3. Following this, in the training and the experiment, red was set at [255 0 0] and green set as the equiluminant [0 (255*ratio from the equiluminance program) 0]. These colours were then mixed slightly (80%) to increase difficulty of the discrimination task.

The red and green values were mixed together to create an orange shade that was equal in luminance to both the red and the green colour discrimination colours. This orange was the colour of all RDK dots other than the red and green colour discrimination dots. The number of colour discrimination dots was then determined using a staircase coherence program. The threshold at which participants were 70%

correct at the discrimination task was selected for use in the experiment. The number of coherently moving dots was determined using a 60% correct threshold as in the previous experiments.

Procedure.

Participants first completed an equiluminance procedure based on minimum motion, as described in Chapter 3. Then, participants completed 350 trials on the motion coherence training program, and 200 trials of colour discrimination, both on staircase procedures. In the experiment, the number of dots for motion discrimination and colour discrimination were set according to coherence thresholds from the training.

The structure of each trial is shown in Figure 5.1. The timings were the same as in the previous experiments, but the colour task here was discrimination of a colour change across the aperture. Participants were told to maintain fixation throughout the trial, and report the direction of coherent motion and the colour of the probe dots at the end of the trial.

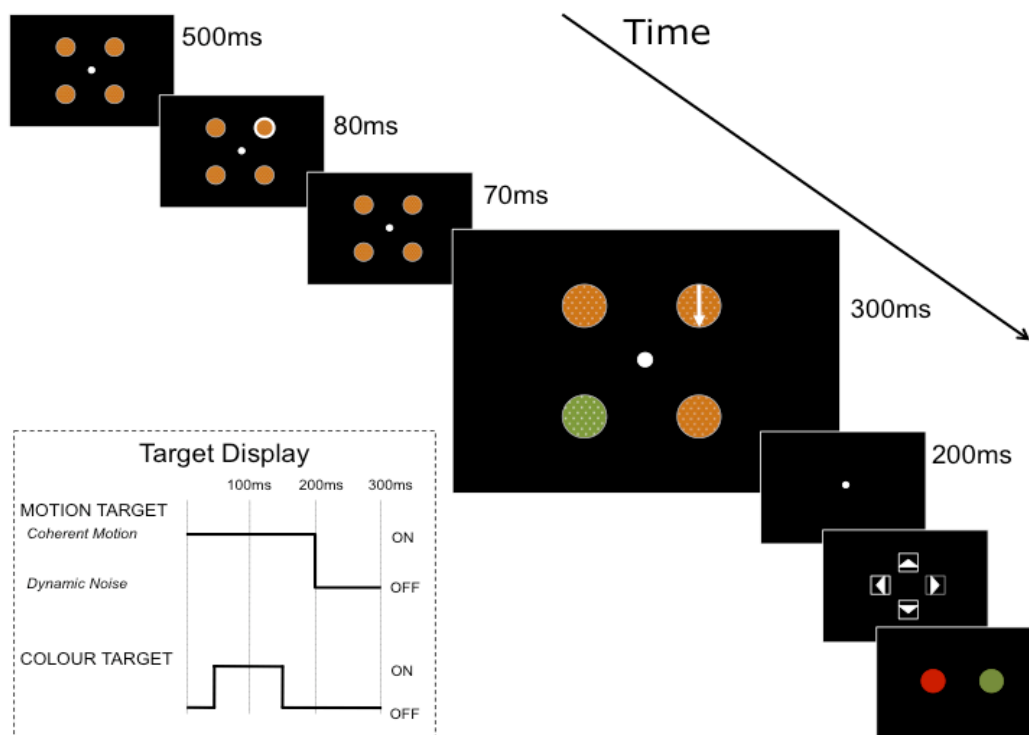


Figure 5.1. Trial structure for Experiment 10. Stimuli not to scale. Coloured circles represent the colour of the dots within the apertures. Arrow on display indicates direction of coherent motion, green RDK represents colour discrimination task. Valid trial for motion discrimination, invalid trial for colour discrimination. Inset box shows timings within the target display.

Results.

Two participants whose performance was not significantly different from chance on the colour task were excluded. Three participants who showed no validity effect for either task were also excluded, because presumably the cue had not been effective in attracting their attention.

Table 5.1

Mean Accuracy (%) for Motion Discrimination and Colour Discrimination Tasks on Cued and Uncued Trials in Experiment 10.

Task	Cued		Uncued	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Motion	80.64 (11.98)	[72.59, 88.68]	64.09 (10.81)	[56.83, 71.35]
Colour	66.91 (7.09)	[62.14, 71.67]	61.09 (5.84)	[57.17, 65.01]

Note. CI = confidence interval.

Accuracy was obtained in the same way as in the previous experiments, and data are shown in Table 5.1. Scores were arcsine corrected before group analysis. For the colour task, accuracy did not differ across the red and green trials, $t(10) = -1.58$, $p = .15$. Validity effects are shown in Figure 5.2.

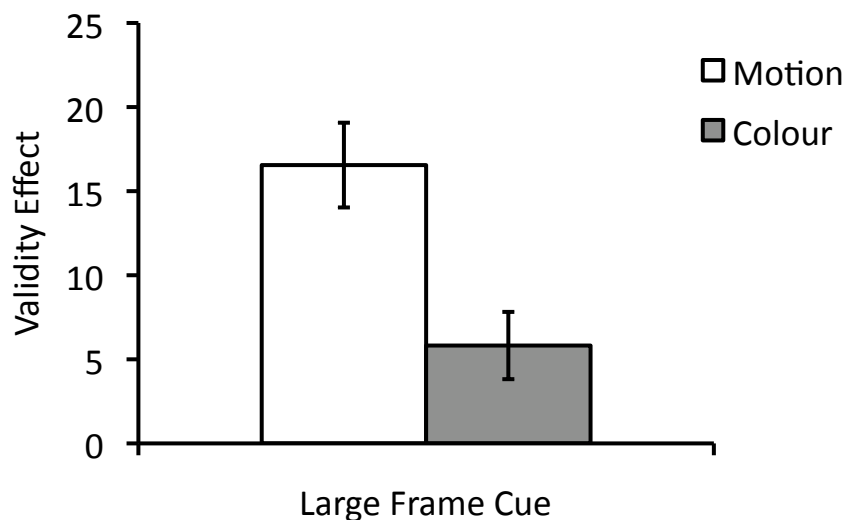


Figure 5.2. Validity effects were calculated by subtracting performance on uncued trials from performance on cued trials for the motion discrimination and colour discrimination tasks in Experiment 10. Error bars represent standard errors.

Data were analysed in a 2 (task: motion discrimination, colour discrimination) x 2 (validity: cued, uncued) ANOVA. This yielded a main effect of validity, $F(1, 10) = 31.25, p < .001, \eta_p^2 = .76$, as accuracy was higher at the cued location than at uncued locations. The significant validity effect was expected, due to the selection of participants who showed cueing effects. There was also a main effect of task, $F(1, 10) = 14.35, p = .004, \eta_p^2 = .59$, as performance on the motion discrimination task was higher than on the colour discrimination task. Interestingly, there was also an interaction of task and validity, $F(1, 10) = 24.82, p = .001, \eta_p^2 = .71$, indicating that the effects of the cue were different for the two tasks. Planned *t* tests confirmed validity effects for both the motion discrimination task, $t(10) = 6.13, p < .001$, and colour discrimination task, $t(10) = 2.92, p = .015$.

Discussion

The results of Experiment 10 show that when both stimuli are large, a large cue benefits both tasks; the large frame flash was able to attract exogenous attention to colour at the cued location. This supports the previous conclusion that the size of the cue alters the size of the attentional field, and therefore stimuli must be spatially matched to the cue in order to see an attentional effect. In Chapter 4, an effect on a small colour task – red dot localisation – was only evident following a small cue. When the colour task is large, as in the current experiment, the large cue is able to elicit attentional effects.

Exogenous attention is thought by many to be automatic and stimulus-driven (Theeuwes, 1992, 1994), so that an abrupt change leads to attentional capture that is the same regardless of its usefulness or relevance to an upcoming task. However, the results in Chapter 4 show that size, a low-level feature of a cue, impacts attentional

effects. This finding suggests the contribution of bottom-up effects originating in early visual cortex. Based on these results, it was predicted that altering the colour task so that the best strategy to be accurate was summation of signals across the RDK, and would lead to cueing effects following a large cue, as in the motion task. The current experiment verifies that a large cue can elicit attentional effects for a large colour task, supporting our previous conclusion that attentional effects depend on the match of cue size and cue properties. It is interesting to note, however, that there was a large difference in magnitude of the validity effect between the motion and colour discrimination tasks following the same cue.

We observed an asymmetry in the effects of the large cue on the large motion and colour tasks. Though both showed a significant validity effect, the effect was larger for the motion task than the colour task. One possible explanation is that cue properties affect attentional effects. The luminance of an exogenous cue has been shown to modulate attentional effects (Fuller, Park, & Carrasco, 2009) such that more luminant cues led to larger effects than less luminant cues, though simple detection of the luminance change was not mitigating the effects. Another support for this explanation is the fact that we have observed a cue size effect on exogenous attention. Thus, low-level properties play a role in modulating the effects of a cue, and this may go some way to explaining the asymmetry in the cueing effects on the motion and colour tasks.

The above exogenous experiment used a luminance cue, which could have led to the observed asymmetry. Two routes of visual processing have been proposed: ventral and dorsal (Ungerleider & Mishkin, 1982). The ventral pathway is concerned with object-based visual attributes such as colour, whereas the dorsal pathway has a role in motion and location (Ungerleider & Haxby, 1994; Ungerleider & Mishkin,

1982). Motion is predominantly processed via luminance channels in the dorsal stream (Livingstone & Hubel, 1988). Hence, the cue may have led to stronger effects on the motion task than the colour task, as it was processed in the same visual pathway.

In summary, a large exogenous cue does lead to attentional effects on a colour task. This supports the earlier conclusion that the relationship between cue size and properties of the task mediates the effects of attention. Additionally, there is an asymmetry in the effects of the cue on the motion and colour task, which may also be explained by the relationship of cue and task properties.

Chapter 6. Exogenous Cueing III: Manipulating Cue Dimension

In the previous experiments, the relationship of cue size and task properties has been shown to influence the effects of exogenous attention. In Chapter 5 it was predicted that if both tasks involved the summation of signals across the RDK, a large cue should affect both motion and colour tasks. There was a significant effect of the large frame cue for both tasks, supporting our previous conclusion that attentional effects depend on the match between task and cue properties. Further to this, there was also a significant difference in the effects of the cue on the two tasks. One possible explanation for the asymmetry in cueing effects on motion and colour tasks following a large frame cue is the two distinct relationships between cue and target properties.

Cue size makes a difference to attentional effects, and there is also evidence to suggest that other properties of exogenous cues, such as luminance contrast, can affect attention (Fuller et al., 2009; Steinman et al., 1997). Fuller et al. (2009) manipulated the contrast of a peripheral cue above the stimulus location, and measured the effects on perceived contrast and perceived motion speed of cued and uncued gabor stimuli. As cue contrast increased, the attentional effects on appearance increased, even when the cue contrast was well above threshold. Thus, the visual properties of a cue can modulate attentional effects.

The relationship between an exogenous cue and task has also been investigated under conditions in which participants have different task sets. Task sets were manipulated by changing the feature(s) contained in the target (Gibson & Kelsey, 1998; Lambert et al., 2003; Lien et al., 2010; Folk et al., 1992; Folk et al.,

1994). The findings suggest that attentional control settings are created by task demands, and that only stimuli that are compatible with an upcoming task will capture attention; contingent capture (Gibson & Kelsey, 1998; Lambert et al., 2003; Lien et al., 2010; Folk et al., 1992; Folk et al., 1994). For example, when a target is defined by its colour, a validity effect is only present following a colour cue but not a motion cue. Conversely, when a target is defined by motion, a motion cue leads to a validity effect but not a colour cue (Folk et al., 1994).

Pratt, Sekuler, and McAuliffe (2001) extended this research by presenting blocks in which the target was always the same, as in the above studies (Folk et al., 1992; Folk et al., 1994) and blocks in which the targets were mixed. When participants were unsure of the upcoming target, both onset and colour cues captured attention and both targets showed validity effects, corroborating the explanation of task set for the contingent capture in trials that were blocked by target. In the experiments described in Chapters 4 and 5 investigating the effects of cue size, both task sets would have been engaged so the asymmetric effects observed cannot be explained by task set. However, the results do provide further evidence that exogenous cues do not lead to reflexive attentional effects on upcoming stimuli, and that the properties of cues exert influence on attention. Indeed, authors have suggested that cues only capture attention if they share a feature with an upcoming target (Gibson & Kelsey, 1998).

Conversely, there is a body of work that suggests that salient visual events capture attention, such as new object onsets, motion and luminance changes, even when these are task-irrelevant (Al-Aidroos, Guo, & Pratt, 2010; Gellatly, Cole, & Blurton, 1999; Jonides & Yantis, 1988; Schreij, Owens, & Theeuwes, 2008; Yantis & Hillstrom, 1994), though not all visual stimuli capture attention. Comparing

properties of stimuli that capture attention, Theeuwes (1995) found that luminance-based changes do lead to attentional effects, yet equiluminant colour changes do not.

In contrast to the work of Theeuwes (1995), several studies have found evidence for attention capture following equiluminant colour cues (Cole, Kentridge, & Heywood, 2005; Lambert et al., 2003; Lu, 2006; Snowden, 2002; Steinman et al., 1997). For example, Snowden (2002) compared colour cues of different luminance contrast in a line orientation judgement task. All colour cues captured attention as demonstrated by a validity effect on RT, yet equiluminant colour cues were as successful as luminance-based cues, with no interaction of colour and luminance.

Lambert et al. (2003) found that a luminance cue always captured attention, whereas an equiluminant cue was only successful in capturing attention when participants were expecting an equiluminant target. These results are compatible with an adjusted version of contingent capture, and also reveal an asymmetry in luminance-based and equiluminant cueing, in that luminance-based cues cannot be ignored. Steinman et al. (1997) also compared luminance and colour cues, and concluded that both cues capture attention, but that luminance cues are more potent and the effects will override those of equiluminant colour cues. However, in their experiments the cue types were not well matched, with an equiluminant cue of a green ring and a luminance-based cue of a solid dot.

Though luminance cues provide a reliable capture effect across many experimental conditions, the effects following colour cues are seemingly less robust. Lambert et al. (2003) suggest an evolutionary explanation for the bias for luminance capture, as most real-world stimuli are accompanied by a luminance change, meaning a luminance-based attentional system will be more efficient. This asymmetry in cueing effects has been related to magno- and parvo-cellular pathways

in the brain (Theeuwes, 1995). Previous research suggests a bias for attentional orienting in the magnocellular pathway, which processes luminance and motion, over the parvocellular pathway, which processes colour and detail (Livingstone & Hubel, 1987, 1988; Steinman et al., 1997).

The effects of cue size from Chapter 4, cue luminance manipulations (Fuller et al., 2009; Steinman et al., 1997) and the effects of shared features with cues and targets (Gibson & Kelsey, 1998; Lambert et al., 2003; Lien et al., 2010; Folk et al., 1992; Folk et al., 1994) indicate the contribution of bottom-up mechanisms to exogenous attentional effects. The following experiment was designed to investigate the effects of cue-target similarity in the previously-used dual-task set up, in order to explore the asymmetry of attentional effects following a large luminance-change frame cue. The cues were designed according to visual organisation information: a luminance cue which should be more closely related to the motion stimulus (Livingstone & Hubel, 1987, 1988; Ramachandran & Gregory, 1978), and a colour change cue which should be more closely related to the colour stimulus. If attentional capture is contingent on attentional control settings, both cues should capture attention because both share features with target stimuli, and attentional effects should generalise across features following capture (Pratt et al., 2001). If bottom-up features bias attentional effects, the luminance cue should lead to a greater validity effect for the motion task than the colour cue and the colour cue should lead to a greater validity effect for the colour task than the luminance cue.

Method.

Participants.

Thirty-four undergraduate participants were recruited (22 female). Nineteen were selected via the online participant panel, and 15 replied to an advert on the student intranet at Bangor University. Participants were tested in a 2-hour session, which included training on both tasks and two experimental blocks amounting to 768 trials.

Stimuli and apparatus.

These were the same as in Experiment 10, with the exception of the cue. A schematic of the cues is presented in Figure 6.1. Four dots, each subtending 1 degree of visual angle, surrounded each of the RDKs, each dot centred on the RDK placeholder. In the luminance cue condition (A), these dots were grey, and surrounding the cued RDK these changed to white during the cue period. In the colour cue condition (B), the dots were orange and at the cued location the top and bottom dots turned to red, and the left and right dots turned to green. On neutrally cued trials, these changes happened in the dots at all four locations.

Design.

Trials were blocked by cue condition, so that each participant completed 384 trials of the luminance cue and 384 trials of the colour cue. In both cue conditions, participants reported the direction of coherent motion and the colour of the colour change dots on every trial.

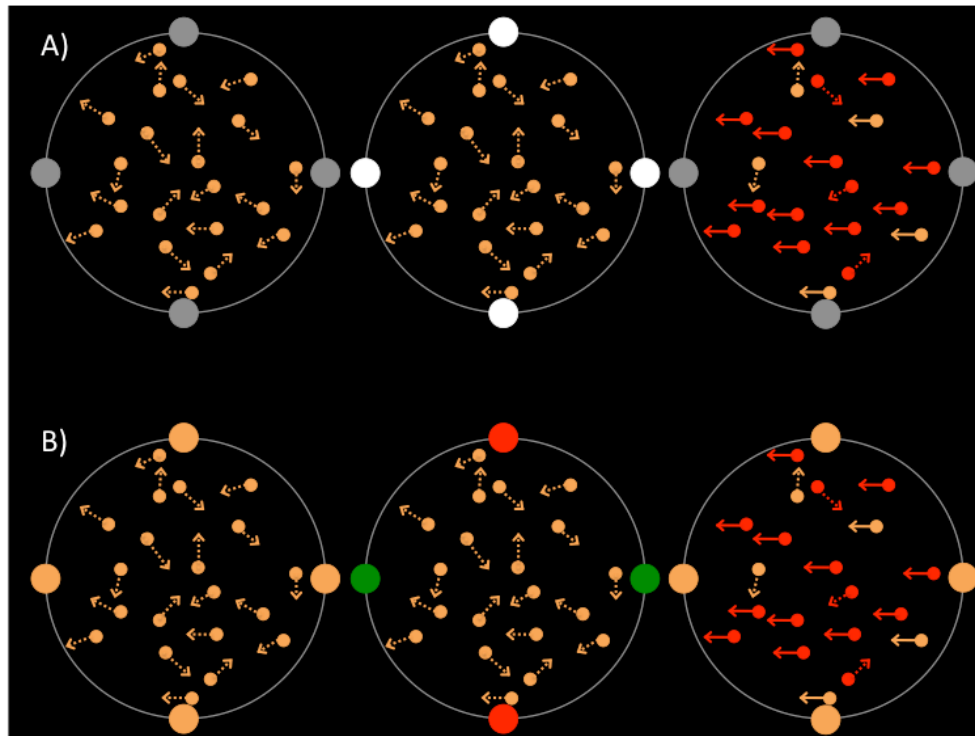


Figure 6.1. Schematic illustrations of luminance (top row, A) and colour (bottom row, B) cues. Four dots were present throughout the trial as on the left and right, and during the cue period, shown in the centre, these changed in luminance or colour.

Procedure.

An equiluminance procedure was run first to set the colour for all stimuli in the experiment. This procedure was based on minimum motion, and is further described in Chapter 3. Participants then completed 200 trials on the motion discrimination staircase procedure, and 200 trials on the colour discrimination procedure, as in the previous experiment (Chapter 5).

Trials were organised into two blocks, based on cue condition: luminance or colour. Participants were aware that the change in the cue dots was uninformative in both blocks, and that moving their eyes would make the tasks more difficult because of the speed of the trial. Trial timings were the same as in the previous experiment.

Results.

Six participants (4 female) were excluded because in at least one of the cue blocks they showed no cueing effect on both the motion and colour tasks, indicating that the cue had not been effective in attracting their attention. Accuracies were obtained in the same way as in the previous experiment, and are shown in Table 6.1.

Table 6.1

Mean Accuracy (%) for Motion Discrimination and Colour Discrimination Tasks on Cued and Uncued Trials.

Task	Cued		Uncued	
	<i>M (SD)</i>	95% CI	<i>M (SD)</i>	95% CI
Luminance cue				
Motion	78.93 (10.88)	[74.71, 83.15]	71.89 (9.87)	[68.07, 75.72]
Colour	70.89 (12.30)	[66.12, 75.66]	70.11 (8.51)	[66.81, 73.41]
Colour cue				
Motion	77.46 (9.26)	[73.88, 81.05]	72.68 (9.02)	[69.18, 76.18]
Colour	70.21 (9.87)	[66.38, 74.05]	67.18 (8.52)	[63.88, 70.47]

Note. CI = confidence interval.

The validity effects for the motion and colour tasks in both cueing conditions are shown in Figure 6.2. Data were arcsine corrected before group analysis, and analysed in a 2 (cue condition: luminance, colour) x 2 (task: motion, colour) x 2 (cue validity: cued, uncued) repeated measures ANOVA. Importantly, there was a 3-way interaction of cue condition, task and validity, $F(1, 27) = 4.73, p = .039, \eta_p^2 = .15$, indicating that the validity effects for the motion and colour tasks were different in the two cue conditions. There was also an interaction between task and validity, $F(1,$

27) = 11.345, $p = .002$, $\eta_p^2 = .30$, reflecting the larger attentional effects for the motion task than the colour task. The ANOVA also showed a validity effect, $F(1, 27) = 36.72$, $p < .001$, $\eta_p^2 = .58$, as expected based on the selection of participants who showed cueing effects, and a main effect of task, $F(1, 27) = 10.48$, $p = .003$, $\eta_p^2 = .28$. All remaining comparisons were non-significant.

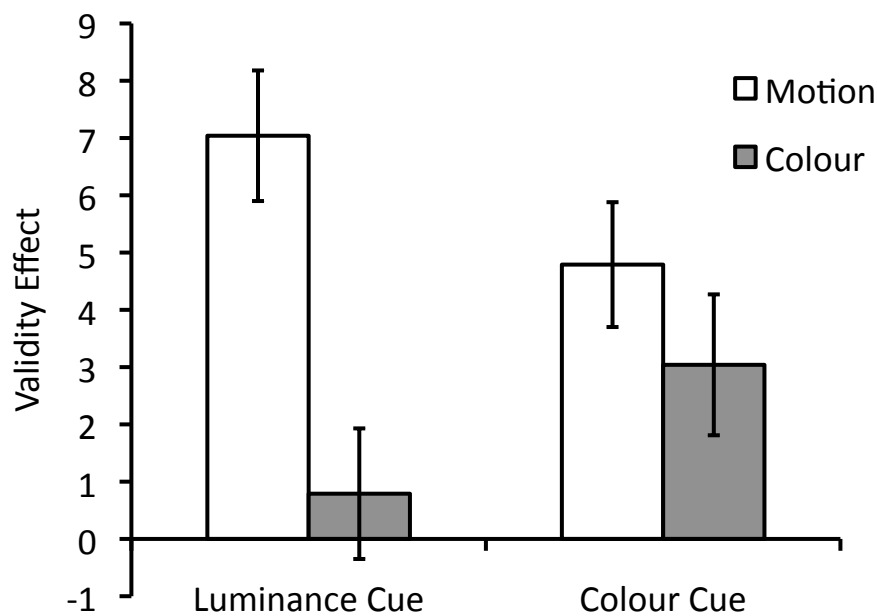


Figure 6.2. Mean validity effect for motion discrimination and colour discrimination tasks following a luminance or colour cue in Experiment 11. Error bars represent standard errors.

In order to examine the 3-way interaction, two 2 (task: motion, colour) x 2 (validity: cued, uncued) repeated measures ANOVAs were conducted separately for the two cueing conditions. Following a luminance cue, there was a Task x Validity interaction, $F(1, 27) = 14.60$, $p = .001$, $\eta_p^2 = .35$, indicating that the motion validity effect was larger than the colour validity effect, but following a colour cue, there was

no Task x Validity interaction, $F(1, 27) = 1.76, p = .20, \eta_p^2 = .06$, suggesting equal validity effects.

Planned t tests confirmed validity effects for the motion task following both a luminance cue, $t(27) = 5.76, p < .001$, and a colour cue, $t(27) = 4.30, p < .001$. There was a validity effect for the colour task following a colour cue, $t(27) = 2.69, p = .012$, but not a luminance cue, $t(27) = 1.14, p = .27$.

Discussion

The results show an interaction between cue features and target stimuli. Following a luminance cue, there was a validity effect for the motion task but not the colour task. Following a colour cue, both tasks showed a validity effect. Overall, motion effects were larger than colour effects. These findings indicate that cue properties affect exogenous attention, and that both luminance and equiluminant colour cues are capable of attracting exogenous attention. In addition, these provide further evidence of a motion and colour asymmetry in attention networks.

It is interesting to note that the size of these validity effects is drastically reduced in comparison to those following the large frame cue (Chapter 5). Both the luminance cue in this experiment and the luminance frame cue in Chapter 5 captured attention, but the frame cue led to a significant validity effect on the colour discrimination task and the four dot luminance change did not. As the effects were also smaller on the motion discrimination task, this could simply be a result of reduced salience, or because the overall luminance change was larger following the frame cue leading to larger effects (Fuller et al., 2009). It may be the case that there is a very small effect of the four dot luminance cue on the colour task that is not

significant here, but the important finding is that these effects are different depending on the properties of the cue.

Opinion has been divided over the ability of equiluminant colour change cues to capture exogenous attention (Cole et al., 2005; Gallatly et al, 1999; Lambert et al., 2003; Lu, 2006; Snowden, 2002; Steinman et al., 1997; Theeuwes, 1995). In this experiment we demonstrate attentional effects following equiluminant cue colour changes with a colour change duration of 80ms, in agreement with the research of Lu (2006). Furthermore, we see no evidence that the colour change cue was less effective than a luminance cue.

Though we see a relationship based on cue-target similarity, both cues led to larger validity effects for the motion task than the colour task. This finding is consistent with findings in endogenous cueing (Chapter 3) and imaging experiments (d'Avossa et al., 2003; Liu et al., 2003; Shulman et al., 2002). For example, participants viewing the same stimulus show larger, more extensive activation when attending motion rather than colour (Liu et al., 2003; Shulman et al., 2002). This suggests a bias towards motion in attentional systems, and it is therefore not surprising that we find larger attentional effects on the motion task than the colour task.

The key finding in this experiment is that low-level visual properties of exogenous cues influence attentional effects: The validity effect for colour was only present following a colour cue and not a luminance cue. These results extend previous findings that attentional effects are modulated by properties of exogenous cues, such as size (Chapter 4) and luminance contrast (Fuller et al., 2009; Steinman et al., 1997). Hence, the asymmetry in attentional effects for motion and colour

following the large luminance frame in Chapter 5 may be combined effects of low-level cue-target similarity and a bias for motion in attention networks.

The cues chosen for this experiment were based on the purported organisation of visual processing into magnocellular and parvocellular pathways (Livingstone & Hubel, 1988). Luminance information has been strongly linked to motion processing (Livingstone & Hubel, 1987, 1988; Ramachandran & Gregory, 1978) and both occur in the magnocellular stream, whereas the parvocellular stream responds to equiluminant colour information (Livingstone & Hubel, 1987, 1988). Accordingly, one can assume that the influence of cue properties on attentional effects is driven by bottom-up mechanisms of feature processing organised into streams. This result suggests that exogenous attentional capture is closely tied to within-pathway processes.

Previous studies have examined the relationship between properties of an exogenous cue and attentional control settings (Gibson & Kelsey, 1998; Lambert et al., 2003; Lien et al., 2010; Folk et al., 1992; Folk et al., 1994). These experiments suggest that exogenous attention will only be captured if a cue has similar properties to an upcoming target, because of top-down goals. Our results suggest that aside from task set and attentional control settings, simple cue-target similarities affect attentional effects without the influence of top-down signals. This is strong evidence for effects of exogenous cueing in low-level areas, likely without the control of feedback signals from higher-order attentional regions.

Chapter 7. General Discussion

Dimension-Specific Effects of Endogenous Spatial Cueing

Spatial attention is not purely location-based.

The studies in Chapters 2 and 3 were designed to investigate whether the effects of endogenous attention are similar for to all dimensions at the cued location. Two tasks were used, each requiring detection or discrimination on different dimensions. Central cues preceded the target display, and indicated the likely location of one dimension but were non-informative for the location of a second dimension. Validity effects were of greater magnitude for the likely dimension than for the dimension whose location was not predicted by the cue. The results in Chapters 2 and 3 imply that participants are able to bias attention towards the likely dimension at the cued location, suggesting that spatial attention does not necessarily generalise to all dimensions.

Previous research into compatibility effects is consistent with the finding that spatial attention may not generalise to all dimensions (Cohen & Magen, 1999; Cohen & Shoup, 1997, 2000). Cohen and Shoup (1997) used a flanker task, in which participants responded to either the colour or orientation of a central target, flanked by distractors whose features were either congruent or incongruent with the response required to the target feature. A congruency effect was only observed when the flankers were of the same dimension as the target, and did not affect RT to the target when they were of a different dimension. This suggests that participants only attended to the relevant dimension of the stimuli and therefore that attention did not generalise to the task-irrelevant dimension. Participants were unaware which dimension they were to respond to until they saw the target, so this is not a

reflection of preparatory processes. However, spatial attention was not manipulated in these experiments.

Others have also found that spatial cueing does not necessarily lead to improved processing of all dimensions at the cued location (Remington & Folk, 2001). In one key paper, Remington and Folk (2001) found that only task-relevant features of distractors were associated with attentional compatibility effects following exogenous cues. The results in the series of experiments presented in Chapters 2 and 3 extend these findings in several ways.

In Remington and Folk (2001), target letters contained features along two dimensions, and participants were informed of which dimension to report at the beginning of a trial. Compatibility effects of the task-relevant, but not task-irrelevant, dimension of a similar distractor (foil) were observed on response latency for the single target. However, in the present experiments described in Chapters 2 and 3, both dimensions were task-relevant, allowing the measurement of attentional effects on more than one dimension. These results suggest that the effects of spatial attention do not generalise across dimensions, even when both are task-relevant. Rather, attention can bias processing of the dimension expected to appear at the cued location.

One of the surprising findings reported by Remington and Folk (2001) was that the irrelevant dimension of a distractor did not interfere with the response, but the irrelevant dimension of the target did. This suggests that there is no global suppression of the interfering dimension, but that dimensions are processed differently at the cued target location compared to the cued distractor location. The authors suggest that this distinction is one of attending versus selecting the object at the cued location, such that all features of an object are processed only once it has

been selected as a target. This is consistent with the idea of object-based attention (e.g. Duncan, 1984; Egly et al., 1994), in which selection is object-based, and all features and dimensions of this object show attentional effects. For example, Egly et al. (1994) presented stimuli on two rectangles, either side of a fixation point. One end of one of the rectangles was spatially cued with a luminance change of the outline, and participants made a speeded response to a square target that could appear in four locations: within either end of either rectangle. Targets were detected most quickly when presented at the cued location. However, targets presented at uncued locations were detected more quickly when on the cued rectangle than the uncued rectangle, even though these were equidistant from the cue. A spatial attention explanation alone cannot explain these results, and the results suggest attention can be object-based.

The possibility that spatially-cued attention selects objects rather than locations may be relevant to the interpretation of the results in Chapter 2, in which the different dimensions of the target may have been perceived as belonging to separate objects, since the motion was defined by coherently moving white dots while the colour probe was a randomly moving dot. If the two targets were interpreted as being two separate objects, then directing attention to one dimension following the cue should have led to selection of either the white dots or the red dot probe, and not to selection of the other. However, this explanation fails to account for the results in Chapter 3 since the motion and colour dots were drawn from overlapping dot populations, making an argument for two separate objects in the cued location difficult. Therefore, the overall results cannot be explained by an object-based attention explanation.

Lachter et al. (2009) used the same experimental set up as Remington and Folk (2001), but manipulated both the dimension for which participants prepared, and that which they executed, as follows. The target was a red letter among white letter distractors. The letter identity of the target also instructed participants which task to perform: when the target letter was a slanted H, participants reported its orientation, and when it was a T or an L, participants reported the letter identity. Preparation was manipulated in different blocks, in which either both tasks were equally likely, or one task was more likely than the other. Interestingly, the authors found that preparation for a particular dimension played little part in the validity effect while the execution of a dimension was responsible for most of the effect. This result is highly surprising given that in order to know the dimension to execute, participants had to identify the target. When the cued location contained the foil, the dimension to execute was therefore recognised after attending to the foil, so it is not obvious why the dimension to execute led to compatibility effects. The authors suggest that all dimensions of an object are identified, even when they are believed to be task-irrelevant.

The findings of an execution effect are consistent with the work of Cohen and colleagues (Cohen & Magen, 1999; Cohen & Shoup, 1997, 2000) discussed above, in that they suggest separate response-selection mechanisms for different dimensions. Thus, attention selects all dimensions of an object, but response selection occurs within dimension-specific modules that drive compatibility effects. The results in Chapter 3 are not easily reconciled to this view. Both the motion and colour were contained in one RDK object so should benefit equally from attentional, and participants had to respond to both dimensions so there should be no response

execution effects. Nevertheless, there was a significant effect of the dimension for which the cue was informative.

The results cited above were based on experiments using exogenous cues (Lachter et al., 2009; Remington & Folk, 2001), or assumed that attention was allocated to the central target (Cohen & Magen, 1999; Cohen & Shoup, 1997, 2000), whereas the experiments in Chapters 2 and 3 used endogenous cues. This difference in the method of orienting of spatial attention may lead to different outcomes. The results in this thesis imply that top-down strategies linked to cue informativeness can bias attended dimensions at the cued location, and demonstrate that participants are able to use both the spatial and feature-related information of a cue in order to allocate attention effectively. Though the conclusion of Lachter et al. (2009) is that exogenous attention generalises across all dimensions of an object, using an endogenous cue this effect is not observed.

The interaction of spatial and feature-based attention

The pattern of results in Chapters 2 and 3 is at odds with an extensive body of work suggesting that spatial attention and feature-based attention are independent mechanisms (Andersen, Müller, & Hillyard, 2009; Sàenz et al., 2002; Theeuwes & Van der Burg, 2007; Zhang & Luck, 2009). It has been suggested that, spatially cued attention selects information purely on the basis of location, while feature-based attention generalises over space, and selects using non-spatial features (e.g. Andersen, Müller, & Hillyard, 2009; Fecteau et al., 2009; Liu & Mance, 2011; Sàenz et al., 2002, 2003; White & Carrasco, 2011).

Spatial attention has been described using analogies such as the spotlight (Posner et al., 1980), zoom lens (Eriksen & St. James, 1986; Eriksen & Yeh, 1985; N G.

Müller et al., 2003) or gradient (Henderson, 1991). These models are all built around the idea that attention is allocated across the visual field to relevant or salient locations, and based mainly on the a vast number of studies using spatial cueing (e.g. Jonides, 1980, 1981; Posner, 1980). For example, Heinze et al. (1994) measured neural responses while participants directed attention to either the left or right visual field. Increased PET activation was shown in the contralateral hemisphere, and taken as evidence that spatial attention is oriented in order to select all stimuli at the attended location for further processing. This view of spatial attention has an underlying assumption that attention generalises across all features and dimensions in the cued location.

Feature-based attention, conversely, has been shown to have no spatial selectivity since it generalises across all locations (e.g. Sàenz et al., 2002, 2003; White & Carrasco, 2011). For example, White and Carrasco (2011) found that attending to a particular feature in one visual field led to increased sensitivity for that feature across visual space. This effect has been demonstrated in multiple behavioural (Sàenz et al., 2003; White & Carrasco, 2011), single cell (Treue & Martinez-Trujillo, 1999; McAdams & Maunsell, 2000) and imaging experiments (Sàenz et al., 2002) and explained under the feature similarity gain model (see Treue & Martinez-Trujillo, 1999).

Spatial attention and feature-based attention have therefore been understood as independent and complementary mechanisms; one devoted to selecting all dimensions at the attended location(s), the other to selecting relevant features irrespective of their location. Neural data have been largely supportive of this view; spatial and feature-based attention signals having been found to be additive (e.g., Egner et al., 2008; Fecteau et al., 2009; Patzwahl & Treue, 2009; Sàenz et al., 2006;

Treue & Martínez-Trujillo, 1999). For example, in an imaging study, Egner et al. (2008) used cues that contained independent reliability information for both location and feature of an upcoming target. The results showed that there was no interaction between BOLD signals modulated by the reliability of the spatial cue and the reliability of the feature cue. However, the spatial and feature reliability levels were independent and varied orthogonally, and therefore optimal performance in this study design would be achieved by utilising the spatial and feature information independently. Thus, it is not clear whether the BOLD effects reflect the task demands, in that participants faithfully represented the independent cue reliabilities, or whether spatial and feature-based attention are truly independent and their effects can never interact.

The endogenous cueing experiments, described in Chapters 2 and 3, provided the opportunity to examine a situation in which optimal allocation of attention required the joint selection of spatial and dimension-specific information. If spatial and feature-based attention were independent, additive processes, then spatial attention would affect performance similarly in motion discrimination and colour localisation/discrimination at valid and invalid locations. In other words, both dimensions should show comparable validity effects. Secondly, feature-based attention would affect both dimensions, as both are relevant, so this should increase performance across the visual field for both tasks. The feature-based attention should have no spatially-specific effects. However, the observed results show that the validity effects did not generalise fully across dimensions, but were modulated by the dimension-specific information contained in the cue. In order to faithfully utilise the information contained in the cue for one dimension at a particular location, participants must use spatial and feature-based attention in concert. These

findings suggest that when the task demands are such that spatial cues are dimension-specific then the validity effects are biased.

A neural basis for the interaction of spatial and feature-based attention.

The architecture of the visual system, organised into feature-specific processing regions that are spatially selective, provides an obvious neural basis for joint selection by spatial and feature-based attention. For example, it appears plausible that spatial cues indicating the likely location of motion signals would be predominantly associated with changes in the MT complex, while spatial cues indicating the likely location of the colour target would result in changes in area V4 (Zeki et al., 1991).

These areas are spatially selective, with evidence that V4 is organised retinotopically (e.g. Sereno et al., 1995) and MT with a spatiotopic reference frame (d'Avossa, Tosetti, Crespi, Biagi, Burr, & Morrone, 2007). Patzwahl and Treue (2009) claim that cells within MT have preferences both for spatial location and direction. It has also been suggested that attention is related to these organisation patterns (Brefczynski & DeYoe, 1999; Bressler & Silver, 2010; Tootell et al., 1998), such that when attention is directed to a location, retinotopically organised areas in visual cortex show a modulation of response. The effects of attention on neural activity were first examined using single cell methods (McAdams & Maunsell, 1999; Moran & Desimone, 1985; Patzwahl & Treue, 2009; Treue & Martinez-Trujillo, 1999) in which visually evoked responses of cells in dimension-specific areas were measured when animals attended stimuli either inside or outside the cells' receptive fields. Treue and Martinez-Trujillo (1999) found that neural responses to a motion stimulus within the receptive fields of cells in MT showed a 10% increase when the monkey

attended the stimulus. They also reported that the effects of spatial and feature-based attention on the amplitude of neural responses were additive. Similar effects have been observed in area V4 using oriented Gabor stimuli (McAdams & Maunsell, 1999).

This attentional modulation of neural responses in retinotopic dimension-specific visual areas has also been shown in human imaging experiments (Beauchamp, Cox, & DeYoe, 1997; Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Liu, Pestilli, & Carrasco, 2005; Somers, Dale, Seiffert, & Tootell, 1999). In a key paper, Corbetta et al. (1991) showed that attending to different dimensions of the same object modulated activity in those areas specialised for processing the attended dimension.

Spatially precise effects in specialised visual areas have also been demonstrated during the delay between the presentation of a spatial cue and the visual target, that is, in the absence of visual stimulation. This was first observed using single cell research (Luck, Chelazzi, Hillyard, & Desimone, 1997), and then evidenced in humans (Kastner et al., 1999; McMains, Fehd, Emmanouil, & Kastner, 2007; N. G. Müller et al., 2003; Ress, Backus, & Heeger, 2000; Silver et al., 2007; Sylvester, Shulman, Jack, & Corbetta, 2007). For example, Kastner et al. (1999) examined the effects of preparation before a colour target appeared and found an increase in baseline signal in retinotopically appropriate regions of V1, V2 and V4.

There is recent imaging evidence that the effects of spatial attention may be limited to task-relevant features (Jehee et al., 2011). By analysing the patterns of visually evoked BOLD response, these authors showed that the accuracy in decoding the feature from the voxelwise pattern of BOLD response was higher when the feature belonged to the task-relevant dimension. This study also found an

interaction between spatial and feature-based attention since the effects of spatial attention did not generalise to task-irrelevant stimuli at the cued location. The behavioural results in this thesis extend the theoretical scope of this finding, because even though two target dimensions were task-relevant, the effects of spatially cued attention were larger for the dimension likely to appear at the cued location.

This top-down bias for particular features at the cued location is consistent with a limited amount of behavioural research (Cohen & Magen, 1999; Cohen & Shoup, 1997, 2000; Lachter et al., 2009; Remington & Folk, 2001) and is logical given the effects of attention on the architecture of visual cortex (Beauchamp et al., 1997; Brefczynski & DeYoe, 1999; Bressler & Silver, 2010; Corbetta et al., 1991; McAdams & Maunsell, 1999; Tootell et al., 1998; Treue & Martinez-Trujillo, 1999). These thesis experiments clearly demonstrate the interaction of spatial and feature-based attention, challenging the models of spatial attention as a ‘spotlight’ and feature-based attention as global (e.g. Sàenz et al., 2002, 2003; White & Carrasco, 2011), but rather favour unitary conceptions of attention whereby attention to specific locations and dimensions is jointly specified.

Exogenous Attention and Cue Properties

Low-level cue properties in exogenous attention.

The experiments in Chapters 4, 5, and 6 were designed to investigate the effects of exogenous cues on tasks with different properties. Both the dimension, and the spatial extent of the targets were manipulated. The spatial extent of the coherent motion direction discrimination target was the entire RDK, most of the area within the large cue. In Chapter 4, participants also reported the location of a randomly-moving red dot probe, whereas in Chapters 5 and 6, the colour task required discrimination of red or green dots filling the RDK, most of the area within the bounds of the cue. In this set of experiments, the peripheral cues presented were uninformative about the location of both target dimensions, yet did capture attention as demonstrated by greater accuracy for targets at cued than uncued locations. Nevertheless, the cueing effects for motion and colour targets also reflected the physical properties of the cue.

The experiment presented in Chapter 4 indicates that since the size of an exogenous cue sets the attentional field, attentional effects are dependent on the spatial extent of the target dimension. A large cue led to a validity effect on a motion direction discrimination task in which the motion filled most of the cued area, but did not affect localisation of a small red dot probe. When the size of the cue was reduced, the red probe localisation task also showed a validity effect. A further experiment demonstrated that the effects of cue size are due to stimulus enhancement within the cued region of visual space, rather than suppression outside it. These effects are apparently driven by modulation of early visual processing and are therefore unlikely to reflect feedback signals from higher order attentional regions.

This inference is further supported by the experiment in Chapter 6, which examined the contribution of other cue properties to the cueing effects. A motion direction discrimination task and a simultaneous colour discrimination task were preceded by either a luminance change cue or a colour change cue. The colour change cue led to a validity effect for the colour task, whereas the luminance change cue did not. Both cues led to a validity effect on the motion task, though this is seemingly larger following a luminance change cue than a colour change cue. Though both cues captured attention, the attentional effects were tied to the features of the cue. The interaction of cue type with the validity effect on the two tasks is indicative of the contribution of low-level visual features to cueing.

Modulation of cueing effects by manipulation of physical cue properties is consistent with previous literature. Firstly, the contrast of exogenous cues has been found to scale their attentional effect (Fuller et al., 2009), suggesting that attentional effects are gradual. Secondly, cues containing luminance change have been shown to be more effective than equiluminant cues (e.g. Steinman et al., 1997). This has led to many researchers accounting for attentional effects in terms of separate magnocellular and parvocellular pathways. The magnocellular pathway is colour-blind, yet has high contrast sensitivity and specialises in luminance and motion perception, whereas the parvocellular pathway specialises in colour and form (Livingstone & Hubel, 1988). The results from the exogenous research in this thesis suggest that attention has an effect in both the magnocellular and parvocellular pathways because motion and colour both show validity effects. However, there are some distinct effects following alterations of cue properties.

The effect of the size of the exogenous cue on the magnitude of attentional effects suggests that these are driven by low-level perceptual properties of the

cueing stimulus on mechanisms within the magnocellular and parvocellular visual streams. While the motion direction discrimination is best accomplished by spatially integrating local motion signals within the coherent RDK, the detection of the red dot is more likely to be impaired if surrounding, task-irrelevant stimuli are spatially integrated. A large motion task filling the entire RDK showed cueing effects following both small and large cues, but localisation of a single red dot probe showed cueing effects only following small cues. Since the two tasks are likely to rely on mechanisms with receptive fields of different sizes, the size of the cue may have led to different effects depending on which mechanisms were involved. Magnocellular mechanisms contain large and overlapping receptive fields, whereas parvocellular mechanisms contain small and numerous receptive fields (Livingstone & Hubel, 1988; Shapley, 1990). Indeed, the receptive field size of cells in the magnocellular pathway are up to three times larger than those in the parvocellular pathway in macaques at roughly homologous visual eccentricities (Derrington & Levie, 1984). Therefore, changing cue size should not have a large impact on the number of activated receptive fields in the magnocellular pathway, but could have a considerable impact on the number of receptive fields activated by the cue in the parvocellular pathway. This simple idea would account for the results from Chapter 4, as changing the cue size significantly impacted the red dot localisation task, but not the motion task.

Luminance cues have been shown to consistently capture attention (e.g. Steinman et al., 1997; Theeuwes, 1995), whereas findings with equiluminant cues are mixed (Cole et al., 2005; Theeuwes, 1995). The discrepancy between the effectiveness of equiluminant and luminance cues may suggest a priority for the magnocellular pathway in the guidance of attention, and indeed a few researchers

have inferred that attentional effects are dominated, if not purely driven by the magnocellular pathway (Breitmeyer & Ganz, 1976; Cheng, Eysel, & Vidyasagar, 2004; Egeth & Yantis, 1997; Steinman et al., 1997; Vidyasagar, 1999).

The question of whether attention can be summoned by stimuli that selectively engage the parvocellular system is still under debate. Previous experiments into parvocellular guidance of attention either employed colour onset cues, that is novel objects that are not accompanied by a concurrent luminance change (Gallatly et al., 1999; Snowden, 2002; Theeuwes, 1995), or colour change cues; equiluminant discontinuity in colour of an already present object (Lu, 2006; Theeuwes, 1995). Cole et al. (2005) compared these cue types and found a validity effect following colour onsets, but no significant validity effect following colour changes. The authors explained these results by attributing attentional capture to all new onsets, as they are salient stimuli, and suggesting that colour change alone cannot attract attention. In contrast, more recent research shows that colour changes of 75ms or more in duration do lead to attentional capture (Lu, 2006). The experiment in Chapter 6 used an equiluminant colour change of 80ms and showed evidence of attentional capture, suggesting that attention is not limited to luminance cues or equiluminant colour onset cues and can be attracted by stimuli selective for parvocellular processes.

The results from Chapter 6 may also clarify the nature of the attentional effects on early visual processing, since luminance and colour cues affected motion and colour tasks differently. While both cue types captured attention, the pattern of results suggests that the size of the effects depended on the similarity between the cue and the target. The cues were selected on the basis that a luminance change is closely related to motion processing and a colour change is related to colour

processing. As the luminance cue led to an attentional effect for motion processing but not colour processing, and the colour processing only showed an attentional effect following a colour cue, this implies that some influence on attentional effects is found within the separate pathways. Ries and Hopfinger (2011) examined the effects of cues designed to activate magnocellular or parvocellular pathways on the detection of magnocellular or parvocellular targets. RTs to parvocellular targets were faster following parvocellular cues than magnocellular cues, but RTs to magnocellular targets did not differ between cue types. The pattern of results in Chapter 6 replicates these findings, since equiluminant targets showed attentional effects following equiluminant cues, but not luminance cues, and the motion target showed attentional effects following both cue types.

Ries and Hopfinger (2011) examined ERPs under the behavioural conditions described above, and found no interactions between cue type and target type. This is surprising in light of the behavioural effects, but the authors concluded that activating either the magnocellular or parvocellular pathways leads to a broadly equivalent reflexive orienting of attention. This conclusion is inconsistent with the view that attention is dominated by the magnocellular stream (Breitmeyer & Ganz, 1976; Cheng et al., 2004; Egeth & Yantis, 1997; Steinman et al., 1997; Vidyasagar, 1999). It can be inferred that early effects within the visual pathways influence responses, as in the behavioural results in Chapter 6, though the higher-level attentional orienting processes are automatic regardless of dimension.

The priority map and exogenous cueing.

The influence of cue properties on attentional orienting adds to debate about the nature of exogenous attention. While exogenous attention has been described as

reflexive and stimulus-driven (Theeuwes, 1992, 1994), reflecting a bottom-up sensory process that attracts attention to salient stimuli, influences of top-down priorities suggest that internal goals and prior information can bias attentional capture (Folk et al., 1992; Folk et al., 1994; Theeuwes, 1991).

The results in Chapters 4 to 6 of this thesis speak to the ongoing debate about how the attentional *priority map* is computed (e.g. Koch & Ullman, 1985). Previous research has proposed the existence of a map that spatially represents salient visual locations in order to prioritise the allocation of attention (e.g. Itti & Koch, 2001; Koch & Ullman, 1985). Visual information is used to encode locations that contain salient stimuli, and these locations are plotted onto an internal spatial reference map pre-attentively and independently of information regarding the dimension of the salient stimulus (Itti & Koch, 2001; Li, 2002; Ullman & Koch, 1985). Top-down strategies are also encoded onto the internal map, so that priority is determined by a combination of visual salience and observer goals (Bundesen, 1990; Fecteau & Munoz, 2006; Serences & Yantis, 2006; Yantis & Hillstrom, 1994). The priority map is then used to deploy attention to locations of high relevance.

Exogenous cues lead to attentional effects regardless of their usefulness (e.g. Jonides, 1981), yet if attentional orienting were based only on top-down goals of the observer, one would not predict a validity effect following an uninformative peripheral cue. Therefore, exogenous cues are presumed to automatically capture attention in a bottom-up, stimulus-driven fashion (Theeuwes, 1992, 1994). Yantis and Jonides (1990) suggest that a salient cue, such as a new onset stimulus, would be encoded onto an internal map. This in turn may trigger an attentional orienting response by increasing the salience associated with the cued location, independent of dimension. If so, there would be no reason to expect that attention would benefit

processing of specific dimensions but not others at the cued location. That is, the nature of the cue may influence its saliency but should not determine which dimension should be attended, contrary to the results in Chapters 4, 5, and 6. Thus, a dimension-independent priority map cannot explain the difference in cueing effects on the two dimensions based on cue properties. Therefore, it is more plausible that priority maps are tightly related to bottom-up visual processing, and computed in regions in which dimensions such as motion and colour are still processed separately.

Contingent capture: Top-down influences on exogenous attention.

Some top-down feature information can modulate attentional capture even though the location of salient stimuli is not known (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994; Theeuwes, 1991). This reflects the priority map, in that attentional guidance can also be influenced by top-down knowledge of specific task goals (Bichot & Schall, 2002; Treisman & Sato, 1990; Wolfe et al., 1989). Research related to the contingent capture hypothesis suggests that under conditions in which participants must respond to a target based on a particular feature, only cues that share the feature will capture attention (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). The results in this thesis also suggest a bottom-up contribution of cue-target similarity to attentional effects.

Folk, Remington, and Johnston (1992) found that when participants knew a target would be a red letter, a colour cue grabbed attention but an onset cue did not, yet when participants knew a target would be an onset letter, an onset cue grabbed attention but a colour cue did not. More closely related to the experiments in this thesis, using an exogenous cue, Folk, Remington, & Wright, (1994) found that a

motion cue only showed attentional effects when preceding a motion target, and a colour cue only showed attentional effects when preceding a colour target. The authors conclude that participants engage top-down attentional control settings, and any stimulus that is consistent with these will capture attention, but a salient stimulus that does not share a feature with the task set will not capture attention.

In the first of these studies, the cue that captured attention shared a feature with an upcoming target (Folk, Remington, & Johnston, 1992). Following this, some cues were shown to capture attention for multiple upcoming targets, such as the relationship between motion and onset cues and targets (Folk, Remington, & Wright, 1994). The authors proposed that capture was based on a division of stimuli into broad categories of dynamic and static discontinuities (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). Folk, Remington, and Wright (1994) speculated that these broad categories map well onto the magnocellular and parvocellular pathways and that therefore these effects may be representative of visual processing streams.

The main finding from work into attentional control settings has been that attentional effects are dependent on whether the cue captured attention, and that capture is determined by task set. This conclusion has been supported by evidence that when participants do not know the features of the target in advance, all salient stimuli will capture attention (Pratt et al., 2001). The exogenous experiment in Chapter 6 provides evidence that cue-target similarities affect validity effects independently of task set. Participants completed two simultaneous tasks, so both task sets were presumably being maintained. The cue did capture attention, as validity effects were evident. However, the attentional effects for the tasks were modulated by the relationship between the cue and the target. This modulation

cannot be explained by attentional control settings determining cue capture, but is evidence of bottom-up influence.

Given this conclusion, if the results of the contingent capture hypothesis could be explained purely by bottom-up cue-target similarities within the magnocellular or parvocellular pathways, predictions for the experiments in Chapters 5 and 6 can be generated. A colour change cue would lead only to a colour discrimination validity effect, and a luminance change cue would lead only to a motion discrimination validity effect. This is the case with the luminance change cue in Chapter 6. However, the colour change cue led to both colour and motion validity effects, as did the large luminance frame cue in Chapter 5. Though these effects were modulated by cue type, indicating within-pathway influences, they demonstrate that attentional capture does generalise across stimuli processed in different visual pathways.

The difference between the two luminance cues is seen in the colour task: The large luminance frame in Chapter 5 led to validity effects for both tasks whereas the luminance change dot cue in Chapter 6 did not yield a validity effect for the colour task. The luminance cues were different in their extent and the number of objects presented. The results may be related to larger attentional effects for cues of higher contrast (Fuller et al., 2009). Alternatively, as the experiments in Chapter 4 show the impact of cue size on the attentional field, it is possible that the large frame cue led to selection of one contiguous area whereas the four dots led to selection of four attentional fields. This has not been tested in this thesis, and will require further study. In any case, this does not undermine the significance of the results; showing that following either of the luminance cues, attentional effects were greater for motion than colour.

In summary, not all exogenous cues capture attention, depending on task set (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). This reflects top-down influences on the priority map. Contingent capture cannot be explained by simple cue-target similarities, as under some dual-task conditions, two simultaneous tasks both show attentional effects when only one shares visual features with the cue. There are, however, bottom-up feature influences, as attentional effects are modulated by cue-target similarity. This suggests the involvement of bottom-up visual information, processed within-streams, and is difficult to reconcile to a dimension-independent priority map. In conclusion, the location-based priority map shows modulation due to dimension.

Consistently Stronger Effects for Motion Than Colour

Across both endogenous and exogenous experiments, there were stronger attentional effects for motion than colour targets. Following exogenous cues in Chapters 5 and 6, motion validity effects were stronger than colour validity effects, even when, in Chapter 6, the properties of the cue were manipulated to include colour changes and not luminance changes. Using endogenous cues in Chapter 3, the motion task showed larger validity effects than the colour task. Additionally, the magnitude of the motion validity effect was modulated by cue information whereas the magnitude of the colour validity effect was equal whether the cue was informative for location of the motion or the colour target. Taken collectively, these experiments suggest a stronger effect of attention in motion than colour processing.

This assertion is consistent with the link between attention and the magnocellular pathway, in which luminance and motion are processed (Breitmeyer & Ganz, 1976; Cheng et al., 2004; Egeth & Yantis, 1997; Steinman et al., 1997;

Vidyasagar, 1999). Thus, not only are magnocellular stimuli more apt to summon attention reflexively, as discussed previously, but they are also more likely to benefit from attentional effects. Therefore, an attentional cue may have a larger influence on stimuli processed within the magnocellular pathway.

However, research suggests that attention is biased to motion stimuli even without activating the magnocellular pathway (Abrams & Christ, 2003; Al-Aidroos et al., 2010; Guo, Abrams, Moscovitch, & Pratt, 2010). Using stimuli that were equiluminant with the background, Guo et al. (2010) showed a bias towards stimuli with onset motion in a target identification task. They suggest that as no luminance information was presented, these effects must be dependent on higher level processing and not low-level visual features. Therefore, the consistently stronger attentional effects for motion stimuli may depend on more than early visual processes.

Indeed, a series of imaging experiments have shown that motion information is more widely represented than colour information in higher order attentional regions (Liu et al., 2003; Shulman et al., 2002). Liu et al. (2003) had participants attend to either colour or motion in a large RDK. Regions that were more active when participants attended to motion were more numerous and more widespread than regions that were more active when participants attended to colour. d'Avossa et al. (2003) also analysed the shape of the BOLD response during the cue period and target period depending on whether participants attended colour or motion in a central RDK. During the cue period, the shape of the BOLD was modulated by the attention instructions, with some regions more sustained when motion was cued and some regions more sustained when colour was cued. Responses to the target were more sustained when participants attended to motion than when they

attended to colour in all but one brain region, suggesting that attending to motion leads, across most brain regions, to larger attentional effects.

Stoppel et al. (2007) designed an fMRI experiment in which the effects of location and feature attention were examined. Participants were cued to attend either a red or green population of dots in the left or right visual field. Key to this discussion is the finding that the unattended coloured moving dots showed BOLD modulation in motion-selective areas, but this was not observed in colour-selective areas. The authors attribute this to a motion-capture effect, such that motion is able to attract attention at unattended locations because of its relevance to survival. This is consistent with the finding that motion stimuli capture attention (Abrams & Christ, 2003, 2005, 2006; Franconeri & Simons, 2003, 2005; Howard & Holcombe, 2010) and produce cueing effects (Poggel, Strasburger, & MacKeben, 2007).

The motion and colour stimuli were closely matched. Both filled the extent of the RDK, and participants performed a discrimination task on each target. However, the tasks were not identical, as the motion discrimination was a four-alternative forced choice and the colour discrimination was a two-alternative forced choice. This distinction has important implications when attempting to match performance. In the experiments in this thesis, performance was matched by thresholding such that overall accuracy was equal on each task. However, the accuracy in relation to chance responding was not matched, possibly leading to greater facilitation for the motion task than the colour task given the larger difference between chance and ceiling (Cheal, Lyon, & Hubbard, 1991). Therefore, the differences in attentional modulation between the two tasks may have been influenced by the limitation of performance matching. Nevertheless, when taken alongside the research above, the finding that in

both exogenous and endogenous cueing motion shows larger attentional effects than colour is consistent with a view of motion as prioritised in attentional mechanisms.

The Integration of Endogenous and Exogenous Attention

Many researchers have claimed that endogenous and exogenous attention systems rely on separable mechanisms (Berger et al., 2005; Berlucchi et al., 2000; Briand & Klein, 1987; Friedrich et al., 1998; H. J. Müller & Humphreys, 1991; H. J. Müller & Rabbitt, 1989; Prinzmetal et al., 2009; Reuter-Lorenz & Fendrich, 1992; Warner et al., 1990). Evidence for the distinction of endogenous and exogenous attention systems comes from a series of observations of differences in timing (Cheal & Lyon, 1991; H. J. Müller & Rabbitt, 1989) and nature (Yeshurun & Carrasco, 1998, 2008) of endogenous and exogenous attention orienting.

Jonides (1981) identified four different characteristics of exogenous and endogenous attention. Firstly, endogenous attention is effortful and requires cognitive resources, so that cueing effects are diminished when load is high, whereas exogenous attention is automatic. Secondly, endogenous cues can be ignored but exogenous cues reflexively lead to deployment of attention. Thirdly, exogenous cues will always capture attention, but endogenous cueing effects require preparation, and are related to their apparent usefulness. Finally, the effects of exogenous attention are larger than those of endogenous attention.

These observations have since been supported by research contrasting endogenous and exogenous cues. For example, Berger et al. (2005) found that under conditions of low load, endogenous and exogenous attention had independent effects, but when task difficulty was increased there was an interaction between the

attentional effects. They conclude that the mechanisms are separate, yet compete for shared resources.

These behavioural observations have been corroborated with imaging experiments. Some neural circuitry has been shown to be distinct for top-down and stimulus-driven attention (Friedrich et al., 1998; Kim et al., 1999; Rosen et al., 1999; see Corbetta & Shulman, 2002 for a review). Furthermore, increased gamma band activity has been found following endogenous cues but not exogenous cues, suggesting that some of the underlying neural mechanisms for endogenous and exogenous attention are different (Landau, Esterman, Robertson, Bentin, & Prinzmetal, 2007). Nevertheless, imaging experiments highlight mainly common areas involved in both endogenous and exogenous attention, even when behavioural results show distinct patterns (Kim et al., 1999; Kincade et al., 2005; Nobre et al., 1997; Peelen et al., 2004; Rosen et al., 1999).

Despite differences in behavioural effects and some distinct brain regions, endogenous and exogenous attention do share features. The experiments in this thesis combined with previous research show that there are some similar effects under endogenous and exogenous cueing conditions. Firstly, on a fundamental level, both endogenous and exogenous spatial attention can lead to improved performance at a cued location when compared to uncued locations, indicating biased processing. Secondly, following both cues, these attentional effects do not generalise equally across all stimuli or even within objects at the cued location (Chapters 3 & 5).

Dimension information has been shown to influence endogenous attention allocation (Chapters 2 & 3), exogenous attentional effects (e.g. Remington & Folk, 2001) and exogenous capture (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). Thus, top-down processing can bias spatial effects on particular

dimensions, indicating an interaction between spatial and feature-based attention across both endogenous and exogenous attention. Also, in the experiments in this thesis, validity effects were larger for motion targets than colour targets in both types of attentional cueing. These influences of feature suggest that attentional effects can show similar patterns in endogenous and exogenous attention.

Exogenous attention is not as automatic as it might have been thought, as evidence suggests that it can be influenced by top-down spatial (Theeuwes, 1991; Yantis & Jonides, 1990) and feature (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994; Remington & Folk, 2001) information. Thus, the top-down influences on exogenous attention suggest that a dichotomy of endogenous attention as goal-oriented and exogenous attention as stimulus-driven is oversimplified. The experiments in this thesis highlight similarities between endogenous and exogenous spatial attention, which, along with previous literature, suggest integration of the attentional systems, possibly resulting from shared neural networks.

Exclusion Criteria

In several studies in this thesis, participants who did not show cueing effects were excluded from group analyses. This decision was made to ensure that all included participants were completing the tasks appropriately. However, this may have led to inflated effects and biases in the data presented. When all participants were included, the results were not substantially different, and the pattern of results remained intact.

Concluding Remarks

The experiments in this thesis make a substantial contribution to our understanding of spatial attention. Firstly, in the case of attention that is voluntarily allocated, participants can exploit both spatial and dimension information in a cue, in order to bias processing at an attended location in favour of a likely target dimension. Processing at the attended location can also be biased in involuntary attention, since spatial attention is biased by the physical properties of the capturing stimulus. Therefore, spatial attention is not a single entity; it can interact with feature-based attention. Secondly, in both endogenous and exogenous cueing, motion processing saw larger attentional effects than colour processing, a finding with substantial support in the literature. These similarities in the role of dimension in spatial attention also highlight some areas of overlap between endogenous and exogenous attention mechanisms.

References

- Abrams, R. A., & Christ, S. E. (2003). Motion onset captures attention. *Psychological Science, 14*, 427-432. doi:10.1111/1467-9280.01458
- Abrams, R. A., & Christ, S. E. (2005). The onset of receding motion captures attention: Comment on Franconeri and Simons (2003). *Perception & Psychophysics, 67*, 219-223. doi:10.3758/BF03206486
- Abrams, R. A., & Christ, S. E. (2006). Motion onset captures attention: A rejoinder to Franconeri and Simons (2005). *Perception & Psychophysics, 68*, 114-117. doi:10.3758/BF03193661
- Adams, R. C., & Chambers, C. D. (2012). Mapping the timecourse of goal-directed attention to location and colour in human vision. *Acta Psychologica, 139*, 515-523. doi:10.1016/j.actpsy.2012.01.014
- Al-Aidroos, N., Guo, R., & Pratt, J. (2010). You can't stop new motion: Attentional capture despite a control set for colour. *Visual Cognition, 18*, 859-880. doi:10.1080/13506280903343085
- Andersen, S. K., Müller, M. M., & Hillyard, S. A. (2009). Color-selective attention need not be mediated by spatial attention. *Journal of Vision, 9*, 1-7. doi:10.1167/9.6.2
- Awh, E., Matsukara, M., & Serences, J. T. (2003). Top-down control over biased competition during covert spatial orienting. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 52-63. doi:10.1037/0096-1523.29.1.52
- Awh, E., & Pashler, H. (2000). Evidence for split attention foci. *Journal of Experimental Psychology: Human Perception and Performance, 26*, 834-846. doi:10.1037/0096-1523.26.2.834
- Beauchamp, M. S., Cox, R. W., & DeYoe, E. A. (1997). Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *Journal of Neurophysiology, 78*, 516-520.
- Belopolsky, A., Zwaan, L., Theeuwes, J., & Kramer, A. F. (2007). The size of an attentional window modulates attentional capture by color singletons. *Psychonomic Bulletin and Review, 14*, 934-938. doi:10.3758/BF03194124
- Bergen, J. R., & Julesz, B. (1983). Parallel versus serial processing in rapid pattern discrimination. *Nature, 303*, 696-698. doi:10.1038/303696a0
- Berger, A., Henik, A., & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology: General, 134*, 207-221. doi:10.1037/0096-3445.134.2.207

- Berlucchi, G., Chelazzi, L., & Tassinari, G. (2000). Volitional covert orienting to a peripheral cue does not suppress cue-induced inhibition of return. *Journal of Cognitive Neuroscience*, 12, 648-663. doi:10.1162/089892900562408
- Bichot, N. P., & Schall, J. D. (2002). Priming in macaque frontal cortex during popout visual search: Feature-based facilitation and location-based inhibition of return. *The Journal of Neuroscience*, 22, 4675-4685.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 443-446. doi:10.1163/156856897X00357
- Brefczynski, J. A., & DeYoe, E. A. (1999). A physiological correlate of the 'spotlight' of visual attention. *Nature Neuroscience*, 2, 370-374. doi:10.1038/7280
- Breitmeyer, B. G., & Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychological Review*, 83, 1-36. doi:10.1037/0033-295X.83.1.1
- Brignani, D., Lepsien, J., & Nobre, A. C. (2010). Purely endogenous capture of attention by task-defining features proceeds independently from spatial attention. *NeuroImage*, 51, 859-866. doi:10.1016/j.neuroimage.2010.03.029
- Bressler, D. W., & Silver, M. A. (2010). Spatial attention improves reliability of fMRI retinotopic mapping signals in occipital and parietal cortex. *NeuroImage*, 53, 526-533. doi:10.1016/j.neuroimage.2010.06.063
- Briand, K. A., & Klein, R. M. (1987). Is Posner's "Beam" the same as Treisman's "Glue"? On the relation between visual orienting and feature integration theory. *Journal of Experimental Psychology: Human Perception and Performance*, 13, 228-241. doi:10.1037/0096-1523.13.2.228
- Büchel, C., Josephs, O., Rees, G., Turner, R., Frith, C. D., & Friston, K. J. (1998). The functional anatomy of attention to visual motion: A functional MRI study. *Brain*, 121, 1281-1294. doi:10.1093/brain/121.7.1281
- Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, 97, 523-547. doi:10.1037/0033-295X.97.4.523
- Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, 7, 308-313. doi:10.1038/nn1194
- Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research*, 40, 1203-1215. doi:10.1016/S0042-6989(00)00024-9
- Castiello, U., & Umiltà, C. (1990). Size of the attentional focus and efficiency of processing. *Acta Psychologica*, 73, 195-209. doi:10.1016/0001-6918(90)90022-8

- Cavanagh, P., MacLeod, D. I. A., & Anstis, S. M. (1987). Equiluminance: Spatial and temporal factors and contribution of blue-sensitive cones. *Journal of the Optical Society of America A*, 4, 1428-1438.
- Cepeda, N. J., Cave, K. R., Bichot, N. P., & Kim, M.-S. (1998). Spatial selection via feature-driven inhibition of distractor locations. *Perception & Psychophysics*, 60, 727-746. doi:10.3758/BF03206059
- Chawla, D., Rees, G., & Friston, K. J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience*, 2, 671-676.
- Cheal, M., & Gregory, M. (1997). Evidence of limited capacity and noise reduction with single-element displays in the location-cuing paradigm. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 51-71. doi:10.1037/0096-1523.23.1.51
- Cheal, M., & Lyon, D. R. (1991). Central and peripheral precuing of forced-choice discrimination. *The Quarterly Journal of Experimental Psychology*, 43A, 859-880. doi:10.1080/14640749108400960
- Cheal, M., Lyon, D. R., & Hubbard, D. C. (1991). Does attention have different effects on line orientation and line arrangement discrimination? *The Quarterly Journal of Experimental Psychology*, 43A, 825-857.
- Cheng, A., Eysel, U. T., & Vidyasagar, T. R. (2004). The role of the magnocellular pathway in serial deployment of visual attention. *European Journal of Neuroscience*, 20, 2188-2192. doi:10.1111/j.1460-9568.2004.03675.x
- Cohen, A., & Magen, H. (1999). Intra- and cross-dimensional visual search for single-feature targets. *Perception & Psychophysics*, 61, 291-307. doi:10.3758/BF03206889
- Cohen, A., & Shoup, R. (1997). Perceptual dimensional constraints in response selection processes. *Cognitive Psychology*, 32, 128-181. doi:10.1006/cogp.1997.0648
- Cohen, A., & Shoup, R. (2000). Response selection processes for conjunctive targets. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 391-411. doi:10.1037/0096-1523.26.1.391
- Cole, G., Kentridge, R., & Heywood, C. (2005). Object onset and parvocellular guidance of attentional allocation. *Psychological Science*, 16, 270-274. doi:10.1111/j.0956-7976.2005.01527.x
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1990). Attention modulation of neural processing of shape, color, and velocity in humans. *Science*, 248, 1556-1559. doi:10.1126/science.2360050

- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Peterson, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emission tomography. *The Journal of Neuroscience*, *11*, 2383-2402.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 215-229. doi:10.1038/nrn755
- Cutzu, F., & Tsotsos, J. K. (2003). The selective tuning model of attention: Psychophysical evidence for a suppressive annulus around an attended item. *Vision Research*, *43*, 205-219. doi:10.1016/S0042-6989(02)00491-1
- d'Avossa, G., Shulman, G. L., & Corbetta, M. (2003). Identification of cerebral networks by classification of the shape of BOLD responses. *Journal of Neurophysiology*, *90*, 360-371. doi:10.1152/jn.01040.2002
- d'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D. C., & Morrone, M. C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nature Neuroscience*, *10*, 249-255. doi:10.1038/nn1824
- Derrington, A. M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 219-240.
- Dobkins, K. R., & Bosworth, R. G. (2001). Effects of set-size and selective spatial attention on motion processing. *Vision Research*, *41*, 1501-1517. doi:10.1016/S0042-6989(01)00038-4
- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, *113*, 501-517. doi:10.1037/0096-3445.113.4.501
- Egeth, H. E. & Yantis, S. (1997). Visual attention: Control, representation, and time course. *Annual Review of Psychology*, *48*, 269-297. doi:10.1146/annurev.psych.48.1.269
- Egly, R., Driver, J., & Rafal, R. D. (1994). Shifting visual attention between objects and locations: Evidence from normal and parietal lesion subjects. *Journal of Experimental Psychology: General*, *123*, 161-177. doi:10.1037/0096-3445.123.2.161
- Egner, T., Monti, J. M. P., Trittschuh, E. H., Wieneke, C. A., Hirsch, J., & Mesulam, M.-M. (2008). Neural integration of top-down spatial and feature-based information in visual search. *The Journal of Neuroscience*, *28*, 6141-6151. doi:10.1523/JNEUROSCI.1262-08.2008
- Eriksen, C. W., & Collins, J. F. (1969). Temporal course of selective attention. *Journal of Experimental Psychology*, *80*, 254-261. doi:10.1037/h0027268

- Eriksen, C. W., & Hoffman, J. E. (1973). The extent of processing of noise elements during selective encoding from visual displays. *Perception and Psychophysics*, 14, 155-160. doi:10.3758/BF03198630
- Eriksen, C. W., & St. James, J. D. (1986). Visual attention within and around the field of focal attention: A zoom lens model. *Perception and Psychophysics*, 40, 225-240. doi:10.3758/BF03211502
- Eriksen, C. W., & Yeh, Y. (1985). Allocation of attention in the visual field. *Journal of Experimental Psychology: Human Perception and Performance*, 11, 583-597. doi:10.1037/0096-1523.11.5.583
- Estes, W. K., & Taylor, H. A. (1966). Visual detection in relation to display size and redundancy of critical elements. *Perception, & Psychophysics*, 1, 9-16. doi:10.3758/BF03207814
- Fecteau, J. H., Korjoukov, I., & Roelfsema, P. R. (2009). Location and color biases have different influences on selective attention. *Vision Research*, 49, 996-1005. doi:10.1016/j.visres.2009.03.013
- Fecteau, J. H., & Munoz, D. P. (2006). Saliency, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences*, 10, 382-390. doi:10.1016/j.tics.2006.06.011
- Folk, C. L., & Egeth, H. (1989). Does the identification of simple features require serial processing? *Journal of Experimental Psychology: Human Perception and Performance*, 15, 97. doi:10.1037/0096-1523.15.1.97
- Folk, C. L., & Remington, R. (1998). Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 847-858. doi:10.1037/0096-1523.24.3.847
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 1030-1044. doi:10.1037/0096-1523.18.4.1030
- Folk, C. L., Remington, R. W., & Wright, J. H. (1994). The structure of attentional control: Contingent attentional capture by apparent motion, abrupt onset, and color. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 317-329. doi:10.1037/0096-1523.20.2.317
- Found, A., & Müller, H. J. (1996). Searching for unknown feature targets on more the one dimension: Investigating a "dimension-weighting" account. *Perception & Psychophysics*, 58, 88-101. doi:10.3758/BF03205479

- Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention. *Perception & Psychophysics*, 65, 999-1010. doi:10.3758/BF03194829
- Franconeri, S. L., & Simons, D. J. (2005). The dynamic events that capture visual attention: A reply to Abrams and Christ (2005). *Perception & Psychophysics*, 67, 962-966. doi:10.3758/BF03193623
- Friedrich, F. J., Egly, R., Rafal, R. D., & Beck, D. (1998). Spatial attention deficits in humans: A comparison of superior parietal and temporal-parietal junction lesions. *Neuropsychology*, 12, 193-207. doi:10.1037/0894-4105.12.2.193
- Fuller, S., Park, Y., & Carrasco, M. (2009). Cue contrast modulates the effects of exogenous attention on appearance. *Vision Research*, 49, 1825-1837. doi:10.1016/j.visres.2009.04.019
- Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences*, 96, 3314-3319. doi:10.1073/pnas.96.6.3314
- Gellatly, A., Cole, G., & Blurton, A. (1999). Do equiluminant object onsets capture visual attention? *Journal of Experimental Psychology: Human Perception and Performance*, 25, 1609-1624. doi:10.1037/0096-1523.25.6.1609
- Gibson, B. S., & Bryant, T. A. (2005). Variation in cue duration reveals top-down modulation of involuntary orienting to uninformative symbolic cues. *Perception & Psychophysics*, 67, 749-758. doi:10.3758/BF03193530
- Gibson, B. S., & Kelsey, E. M. (1998). Stimulus-driven attentional capture is contingent on attentional set for displaywide visual features. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 699-706. doi:10.1037/0096-1523.24.3.699
- Giordano, A. M., McElree, B., & Carrasco, M. (2009). On the automaticity and flexibility of covert attention: A speed-accuracy trade-off analysis. *Journal of Vision*, 9, 1-10. doi:10.1167/9.3.30
- Guo, R. M., Abrams, R. A., Moscovitch, M., & Pratt, J. (2010). Isoluminant motion onset captures attention. *Attention, Perception, & Psychophysics*, 72, 1311-1316. doi:10.3758/APP.72.5.1311
- Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Münte, T. F., . . . Hillyard, S. A. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature*, 372, 543-546. doi:10.1038/372543a0

- Henderson, J. M. (1991). Stimulus discrimination following covert attentional orienting to an exogenous cue. *Journal of Experimental Psychology: Human Perception and Performance*, 17, 91-106. doi:10.1037/0096-1523.17.1.91
- Henderson, J. M. (1996). Precues affect target discrimination in the absence of visual noise. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 780-787. doi:10.1037/0096-1523.22.3.780
- Henderson, J. M., & MacQuistan, A. D. (1993). The spatial distribution of attention following an exogenous cue. *Perception and Psychophysics*, 53, 221-230. doi:10.3758/BF03211732
- Hoffman, J. E. (1979). A two-stage model of visual search. *Perception & Psychophysics*, 25, 319-327. doi:10.3758/BF03198811
- Hopfinger, J. B., & Ries, A. J. (2005). Automatic versus contingent mechanisms of sensory-driven neural biasing and reflexive attention. *Journal of Cognitive Neuroscience*, 17, 1341-1352. doi:10.1162/0898929055002445
- Howard, C. J., & Holcombe, A. O. (2010). Unexpected changes in direction of motion attract attention. *Attention, Perception, & Psychophysics*, 72, 2087-2095. doi:10.3758/APP.72.8.2087
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2, 194-203.
- James, W. (1890). *The principles of psychology*. New York: Holt.
- Jehee, J. F. M., Brady, D. K., & Tong, F. (2011). Attention improves encoding of task-relevant features in the human visual cortex. *The Journal of Neuroscience*, 31, 8210-8219. doi:10.1523/JNEUROSCI.6153-09.2011
- Jonides, J. (1980). Towards a model of the mind's eye's movement. *Canadian Journal of Psychology*, 34, 103-112. doi:10.1037/h0081031
- Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's movement. In J. B. Long & A. D. Baddeley (Eds.), *Attention and performance VIII*. Hillsdale, NJ: Erlbaum.
- Jonides, J. (1983). Further toward a model of the mind's eye's movement. *Bulletin of the Psychonomic Society*, 21, 247-250.
- Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics*, 43, 346-354. doi:10.3758/BF03208805
- Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature Neuroscience*, 8, 679-685. doi:10.1038/nn1444

- Kamitani, Y., & Tong, F. (2006). Decoding seen and attended motion directions from activity in the human visual cortex. *Current Biology*, 16, 1096-1102. doi:10.1016/j.cub.2006.04.003
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, 22, 751-761. doi:10.1016/S0896-6273(00)80734-5
- Kim, M.-S., & Cave, K. R. (1995). Spatial attention in visual search for features and feature conjunctions. *Psychological Science*, 6, 376-380. doi:10.1111/j.1467-9280.1995.tb00529.x
- Kim, Y.-H., Gitelman, D. R., Nobre, A. C., Parrish, T. B., LaBar, K. S., & Mesulam, M.-M. (1999). The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *NeuroImage*, 9, 269-277. doi:10.1006/nimg.1999.0408
- Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *The Journal of Neuroscience*, 25, 4593-4604. doi:10.1523/JNEUROSCI.0236-05.2005
- Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: Towards the underlying neural circuitry. *Human Neurobiology*, 4, 219-227. doi:10.1007/978-94-009-3833-5_5
- Kravitz, D. J., & Behrmann, M. (2011). Space-, object-, and feature-based attention interact to organise visual scenes. *Attention, Perception, & Psychophysics*, 73, 2434-2447. doi:10.3758/s13414-011-0201-z
- Kristjánsson, Á., Mackeben, M., & Nakayama, K. (2001). Rapid, object-based learning in the deployment of transient attention. *Perception*, 2001, 1375-1387. doi:10.1068/p3251
- LaBerge, D. (1983). Spatial extent of attention to letters and words. *Journal of Experimental Psychology: Human Perception and Performance*, 9, 371-379. doi:10.1037/0096-1523.9.3.371
- LaBerge, D., & Brown, V. (1989). Theory of attentional operations in shape identification. *Psychological Review*, 96, 101-124. doi:10.1037/0033-295X.96.1.101
- LaBerge, D., Brown, V., Carter, M., Bash, D., & Hartley, A. (1991). Reducing the effects of adjacent distractors by narrowing attention. *Journal of Experimental Psychology: Human Perception and Performance*, 17, 65-76. doi:10.1037/0096-1523.17.1.65

- Lachter, J., Remington, R. W., & Ruthruff, E. (2009). Space, object, and task selection. *Attention, Perception, & Psychophysics*, 71, 995-1014. doi:10.3758/APP.71.5.995
- Lambert, A., Wells, I., & Kean, M. (2003). Do isoluminant color changes capture attention? *Perception & Psychophysics*, 65, 495-507. doi:10.3758/BF03194578
- Landau, A. N., Esterman, M., Robertson, L. C., Bentin, S., & Prinzmetal, W. (2007). Different effects of voluntary and involuntary attention on EEG activity in the gamma band. *The Journal of Neuroscience*, 27, 11986-11990. doi:10.1523/JNEUROSCI.3092-07.2007
- Li, Z. (2002). A saliency map in primary visual cortex. *Trends in Cognitive Sciences*, 6, 9-16. doi:10.1016/S1364-6613(00)01817-9
- Lien, M.-C., Ruthruff, E., & Johnston, J. C. (2010). Attentional capture with rapidly changing attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 36, 1-16. doi:10.1037/a0015875
- Ling, S., & Carrasco, M. (2006). Sustained and transient covert attention enhance the signal via different contrast functions. *Vision Research*, 46, 1210-1220. doi:10.1016/j.visres.2005.05.008
- Liu, T., & Mance, I. (2011). Constant spread of feature-based attention across the visual field. *Vision Research*, 51, 26-33. doi:10.1016/j.visres.2010.09.023
- Liu, T., Pestilli, F., & Carrasco, M. (2005). Transient attention enhances perceptual performance and fMRI response in human visual cortex. *Neuron*, 45, 469-477. doi:10.1016/j.neuron.2004.12.039
- Liu, T., Slotnick, S. D., Serences, J. T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral Cortex*, 13, 1334-1343. doi:10.1093/cercor/bhg080
- Livingstone, M., & Hubel, D. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *The Journal of Neuroscience*, 7, 3416-3468.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, 240, 740-749. doi:10.1126/science.3283936
- Lu, S. (2006). Cue duration and parvocellular guidance of visual attention. *Psychological Science*, 17, 101-102. doi:10.1111/j.1467-9280.2005.01671.x
- Lu, Z.-L., & Doshier, B. A. (2000). Spatial attention: different mechanisms for central and peripheral temporal precues? *Journal of Experimental Psychology: Human Perception and Performance*, 26, 1534-1548. doi:10.1037/0096-1523.26.5.1534

- Lu, Z.-L., Lesmes, L. A., & Doshier, B. A. (2002). Spatial attention excludes external noise at the target location. *Journal of Vision*, 2, 312-323. doi:10.1167/2.4.4
- Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, 77, 24-42.
- Madden, D. J. (1992). Selective attention and visual search: Revision of an allocation model and application to age differences. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 821-836. doi:10.1037/0096-1523.18.3.821
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, 22, 657-672. doi:10.3758/BF03209251
- Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Perception & Psychophysics*, 58, 977-991. doi:10.3758/BF03206826
- McAdams, C. J., & Maunsell, J. H. R. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *The Journal of Neuroscience*, 19, 431-441.
- McAdams, C. J., & Maunsell, J. H. R. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. *Journal of Neurophysiology*, 83, 1751-1755.
- McMains, S. A., Fehd, H. M., Emmanouil, T.A., & Kastner, S. (2007). Mechanisms of feature- and space-based attention: Response modulation and baseline increases. *Journal of Neurophysiology*, 98, 2110-2121. doi:10.1152/jn.00538.2007
- Miller, J. (1991). The flanker compatibility effect as a function of visual angle, attentional focus, visual transients and perceptual load: A search for boundary conditions. *Perception and Psychophysics*, 49, 270-288. doi:10.3758/BF03214311
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, 229, 782-784. doi:10.1126/science.4023713
- Müller, H. J., Heller, D., & Ziegler, J. (1995). Visual search for singleton feature targets within and across feature dimensions. *Perception & Psychophysics*, 57, 1-17. doi:10.3758/BF03211845
- Müller, H. J., & Humphreys, G. W. (1991). Luminance-increment detection: Capacity-limited or not? *Journal of Experimental Psychology: Human Perception and Performance*, 17, 107-124. doi:10.1037/0096-1523.17.1.107

- Müller, H. J., & Rabbitt, P. M. A. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 315-330. doi:10.1037/0096-1523.15.2.315
- Müller, H. J., Reimann, B., & Krummenacher, J. (2003). Visual search for singleton feature targets across dimensions: Stimulus- and expectancy-driven effects in dimensional weighting. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 1021-1035. doi:10.1037/0096-1523.29.5.1021
- Müller, N. G., Bartelt, O. A., Donner, T. H., Villringer, A., & Brandt, S. A. (2003). A physiological correlate of the “zoom lens” of visual attention. *The Journal of Neuroscience*, 23, 3561-3565.
- Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, 29, 1631-1647. doi:10.1016/0042-6989(89)90144-2
- Neill, W. T. (1977). Inhibitory and facilitatory processes in selective attention. *Journal of Experimental Psychology: Human Perception and Performance*, 3, 444-450. doi:10.1037/0096-1523.3.3.444
- Nobre, A. C., Sebestyan, G. N., Gitelman, D. R., Mesalum, M. M., Frackowiak, R. S. J., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, 120, 515-533. doi:10.1093/brain/120.3.515
- O’Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A., & Savoy, R. L. (1997). Voluntary attention modulates fMRI activity in human MT-MST. *Neuron*, 18, 591-598. doi:10.1016/S0896-6273(00)80300-1
- Patzwahl, D. R., & Treue, S. (2009). Combining spatial and feature-based attention within the receptive field of MT neurons. *Vision Research*, 49, 1188-1193. doi:10.1016/j.visres.2009.04.003
- Pavlov, I. P. (1927). *Conditioned reflexes: An investigation of the physiological activity of the cerebral cortex* (G. V. Anrep, Ed. & Trans.). London, England: Oxford University Press.
- Peelen, M. V., Heslenfeld, D. J., & Theeuwes, J. (2004). Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *NeuroImage*, 22, 822-830. doi:10.1016/j.neuroimage.2004.01.044
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437-442. doi:10.1163/156856897X00366

- Pestilli, F., & Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research*, 45, 1867-1875. doi:10.1016/j.visres.2005.01.019
- Poggel, D. A., Strasburger, H., & MacKeben, M. (2007). Cueing attention by relative motion in the periphery of the visual field. *Perception*, 36, 955-970. doi:10.1068/p5752
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32, 3-25. doi:10.1080/00335558008248231
- Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and Performance X* (pp. 531-556). London, England: Erlbaum.
- Posner, M. I., Nissen, M. J., & Ogden, W. C. (1978). Attended and unattended processing modes: The role of set for spatial location. In H. L. Pick & I. J. Saltzman (Eds.), *Modes of perceiving and processing information*. Hillsdale, NJ: Erlbaum.
- Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109, 160-174. doi:10.1037/0096-3445.109.2.160
- Pratt, J., Sekuler, A. B., & McAuliffe, J. (2001). The role of attentional set on attentional cueing and inhibition of return. *Visual Cognition*, 8, 33-46. doi:10.1080/13506280042000018
- Prinzmetal, W., Zvinyatskovskiy, A., Gutierrez, P., & Dilem, L. (2009). Voluntary and involuntary attention have different consequences: The effect of perceptual difficulty. *The Quarterly Journal of Experimental Psychology*, 62, 352-369. doi:10.1080/17470210801954892
- Ramachandran, V., & Gregory, R. (1978). Does colour provide an input to human motion perception? *Nature*, 275, 55-56. doi:10.1038/275055a0
- Remington, R. W., & Folk, C. L. (2001). A dissociation between attention and selection. *Psychological Science*, 12, 511-515. doi:10.1111/1467-9280.00394
- Ress, D., Backus, B. T. & Heeger, D. J. (2000). Activity in primary visual cortex predicts performance in a visual detection task. *Nature Neuroscience*, 3, 940-945.
- Reuter-Lorenz, P. A., & Fendrich, R. (1992). Oculomotor readiness and covert orienting: Differences between central and peripheral precues. *Perception & Psychophysics*, 52, 336-344. doi:10.3758/BF03209150

- Ries, A. J., & Hopfinger, J. B. (2011). Magnocellular and parvocellular influences on reflexive attention. *Vision Research*, 51, 1820-1828. doi:10.1016/j.visres.2011.06.012
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25, 31-40. doi:10.1016/0028-3932(87)90041-8
- Rosen, A. C., Rao, S. M., Caffarra, P., Scaglioni, A., Bobholz, J. A., Woodley, S. J., . . . Binder, J. R. (1999). Neural basis of endogenous and exogenous spatial orienting: A functional MRI study. *Journal of Cognitive Neuroscience*, 11, 135-152. doi:10.1162/089892999563283
- Sàenz, M., Buraças, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. *Nature Neuroscience*, 5, 631-632. doi:10.1038/nn876
- Sàenz, M., Buraças, G. T., & Boynton, G. M. (2003). Global feature-based attention for motion and color. *Vision Research*, 43, 629-637. doi:10.1016/S0042-6989(02)00595-3
- Sàenz, M., Boynton, G. M., & Koch, C. (2006). Combined effects of spatial and feature-based attention in human visual cortex [Abstract]. *Journal of Vision*, 6.
- Schenkluhn, B., Ruff, C. C., Heinen, K., & Chambers, C. D. (2008). Parietal stimulation decouples spatial and feature-based attention. *The Journal of Neuroscience*, 28, 11106-11110. doi:10.1523/JNEUROSCI.3591-08.2008
- Schreij, D., Owens, C., & Theeuwes, J. (2008). Abrupt onset captures attention independent of top-down control settings. *Perception & Psychophysics*, 70, 208-218. doi:10.3758/PP.70.2.208
- Sekular, R., & Ball, K. (1977). Mental set alters visibility of moving targets. *Science*, 198, 60-62. doi:10.1126/science.897682
- Serences, J. T., & Boynton, G. M. (2007). Feature-based attention modulations in the absence of direct visual stimulation. *Neuron*, 55, 301-312. doi:10.1016/j.neuron.2007.06.015
- Serences, J. T., Schwarzbach, J., Courtney, S. M., Golay, X., & Yantis, S. (2004). Control of object-based attention in human cortex. *Cerebral Cortex*, 14, 1346-1357. doi:10.1093/cercor/bhh095
- Serences, J. T., & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends in Cognitive Sciences*, 10, 38-45. doi:10.1016/j.tics.2005.11.008

- Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., . . . Tootell, R. B. H. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, 268, 889-893. doi:10.1126/science.7754376
- Shapley, R. (1990). Visual sensitivity and parallel retinocortical channels. *Annual Review of Psychology*, 41, 635-658. doi:10.1146/annurev.ps.41.020190.003223
- Shaw, M. L., and Shaw, P. (1977). Optimal allocation of cognitive resources to spatial locations. *Journal of Experimental Psychology: Human Perception and Performance*, 3, 201-211. doi:10.1037/0096-1523.3.2.201
- Shulman, G. L., d'Avossa, G., Tansy, A. P., & Corbetta, M. (2002). Two attentional processes in the parietal lobe. *Cerebral Cortex*, 12, 1124-1131. doi:10.1093/cercor/12.11.1124
- Silver, M. A., Ress, D., & Heeger, D. J. (2007). Neural correlates of sustained spatial attention in human early visual cortex. *Journal of Neurophysiology*, 97, 229-237. doi:10.1152/jn.00677.2006
- Snowden, R. J. (2002). Visual attention to color: Parvocellular guidance of attentional resources? *Psychological Science*, 13, 180-184. doi:10.1111/1467-9280.00433
- Sokal, R. R., & Rohlf, J. F. (1981). *Biometry: the principles and practice of statistics in biological research* (2nd ed.). San Francisco: W.H. Freeman and Company.
- Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. H. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of the Sciences*, 96, 1663-1668. doi:10.1073/pnas.96.4.1663
- Steinman, B. A., Steinman, S. B., & Lehmkuhle, S. (1997). Transient visual attention is dominated by the magnocellular stream. *Vision Research*, 37, 17-23. doi:10.1016/S0042-6989(96)00151-4
- Stoppel, C. M., Boehler, C. N., Sabelhaus, C., Heinze, H.-J., Hopf, J. M., & Schoenfeld, M. A. (2007). Neural mechanisms of spatial- and feature-based attention: A quantitative analysis. *Brain Research*, 1181, 51-60. doi:10.1016/j.brainres.2007.07.019
- Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18, 643-662. doi:10.1037/h0054651
- Sylvester, C. M., Shulman, G. L., Jack, A. I., & Corbetta, M. (2007). Asymmetry of anticipatory activity in visual cortex predicts the locus of attention and perception. *The Journal of Neuroscience*, 27, 14424-14433. doi:10.1523/JNEUROSCI.3759-07.2007

- Theeuwes, J. (1991). Exogenous and endogenous control of attention: The effect of visual onsets and offsets. *Perception & Psychophysics*, 49, 83-90. doi:10.3758/BF03211619
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, 51, 599-606. doi:10.3758/BF03211656
- Theeuwes, J. (1994). Stimulus-driven capture and attentional set: Selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 799-806. doi:10.1037/0096-1523.20.4.799
- Theeuwes, J. (1995). Abrupt luminance change pops out; abrupt color change does not. *Perception & Psychophysics*, 57, 637-644. doi:10.3758/BF03213269
- Theeuwes, J., Kramer, A. F., & Atchley, P. (1999). Attentional effects on preattentive vision: Spatial precues affect the detection of simple features. *Journal of Experimental Psychology: Human Perception and Performance*, 25, 341-347. doi:10.1037/0096-1523.25.2.341
- Theeuwes, J., & Van der Burg, E. (2007). The role of spatial and nonspatial information in visual selection. *Journal of Experimental Psychology: Human Perception and Performance*, 33, 1335-1351. doi:10.1037/0096-1523.33.6.1335
- Tipper, S. P. (1985). The negative priming effect: Inhibitory priming by ignored objects. *The Quarterly Journal of Experimental Psychology Section A*, 37, 571-590. doi:10.1080/14640748508400920
- Tipper, S. P. (2001). Does negative priming reflect inhibitory mechanisms? A review and integration of conflicting views. *The Quarterly Journal of Experimental Psychology Section A*, 54, 321-343. doi:10.1080/02724980042000183
- Tootell, R. B. H., Hadjikhani, N., Hall, E. K., Marrett, S., Vanduffel, W., Vaughan, J. T., & Dale, A. M. (1998). The retinotopy of visual spatial attention. *Neuron*, 21, 1409-1422. doi:10.1016/S0896-6273(00)80659-5
- Treisman, A. M. (1988). Features and objects: The fourteenth bartlett memorial lecture. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, 40, 201-237. doi:10.1080/02724988843000104
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12, 97-136. doi:10.1016/0010-0285(80)90005-5
- Treisman, A. M., & Sato, S. (1990). Conjunction search revisited. *Journal of Experimental Psychology: Human Perception and Performance*, 16, 459-478. doi:10.1037/0096-1523.16.3.459
- Treue, S., & Martínez-Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, 399, 575-579.

- Ungerleider, L. G., & Haxby, J. V. (1994). 'What' and 'where' in the human brain. *Current Opinion in Neurobiology*, 4, 157-165.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of Visual Behavior* (pp. 549-586). Cambridge, MA: MIT Press.
- Vidyasagar, T. R. (1999). A neuronal model of attention spotlight: Parietal guiding the temporal. *Brain Research Reviews*, 30, 66-76. doi:10.1016/S0165-0173(99)00005-3
- Vossel, S., Theil, C. M., & Fink, G. R. (2006). Cue validity modulates the neural correlates of covert endogenous orienting of attention in parietal and frontal cortex. *NeuroImage*, 32, 1257-1264. doi:10.1016/j.neuroimage.2006.05.019
- Warner, C. B., Juola, J. F., & Koshino, H. (1990). Voluntary allocation versus automatic capture of visual attention. *Perception & Psychophysics*, 48, 243-251. doi:10.3758/BF03211524
- White, A. L., & Carrasco, M. (2011). Feature-based attention involuntarily and simultaneously improves visual performance across locations. *Journal of Vision*, 11, 1-10. doi:10.1167/11.6.15
- Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 419-433. doi:10.1037//0096-1523.15.3.419
- Yantis, S., & Hillstrom, A. P. (1994). Stimulus-driven attentional capture: Evidence from equiluminant visual objects. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 95-107. doi:10.1037/0096-1523.20.1.95
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, 16, 121-134. doi:10.1037/0096-1523.16.1.121
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, 396, 72-75.
- Yeshurun, Y., & Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Research*, 39, 293-306. doi:10.1016/S0042-6989(98)00114-X
- Yeshurun, Y., & Carrasco, M. (2008). The effects of transient attention on spatial resolution and the size of the attentional cue. *Perception and Psychophysics*, 70, 104-113. doi:10.3758/PP.70.1.104

- Yeshurun, Y., Montagna, B., & Carrasco, M. (2008). On the flexibility of sustained attention and its effects on a texture segmentation task. *Vision Research*, 48, 80-95. doi:10.1016/j.visres.2007.10.015
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in human visual cortex. *The Journal of Neuroscience*, 11, 641-649.
- Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual processing. *Nature Neuroscience*, 12, 24-25. doi:10.1038/nn.2223