Paul, Liza (2003) Investigating the determinants of temporal integration. PhD thesis

http://theses.gla.ac.uk/6570/

Investigating the Determinants of Temporal Integration

Liza Paul

Department of Psychology
University of Glasgow

Presented for the degree of
Doctor of Philosophy
at the University of Glasgow
August 2003

Acknowledgements

I would like to thank my supervisor Professor P.G. Schyns. In addition, I would like to thank my second supervisor Dr D. Simmons, Dr W. Adams, Dr F. Gosselin, and Dr P. Mamassian for their additional advice and support.

I would also like to thank my family, my mum and brother Findlay for their support and encouragement and my dad for teaching me the gift of learning. And of course Craig for his continued encouragement, support and tolerance.

"Perception is not a science of the world, it is not even an act, a deliberate taking up of a position; it is the back-ground from which all acts stand out, and is presupposed by them: The world is not an object such that I have in my possession the law of its making; it is the natural setting of, and field for, all my thoughts and all my explicit perceptions."

Merleau-Ponty, M.

Phemononology of Perception.

"The eye sees only what the mind is prepared to comprehend."

Henri Bergson

The research was supported by a postgraduate studentship awarded by the Economic and Social Research Council.

Contents

Chapter 1 **Introduction**

Chapter 5. Investigating the temporal dynamics of an attentionally induced bias.

Chapter 6. Discussion

2.Chapter Summaries

List of Figures

Abstract

Physiological, clinical and empirical studies suggest that visual input is functionally segregated (e.g. Livingstone and Hubel, 1988; Hubel and Livingstone, 1987; Zeki, 1973). Moreover, this functional processing results in concurrently presented feature attributes being processed and perceived at different times (Moutoussis and Zeki, 1998). However, findings from the attentional and categorisation literature call into question a fixed account of feature processing (Posner, 1980; Stelmach and Herdman, 1991; Carrasco and McElree, 2001; Oliva and Schyns; 2000; Goldstone, 1995). In particular, previous research has demonstrated a processing advantage for attended information. From this literature it seems likely that the enhanced saliency of an attribute will accelerate the processing time of this dimension and consequently should modulate any perceptual asynchrony between concurrently presented features. Moreover, if attention offers a selective processing advantage this should induce processing asynchrony between attended and unattended information across the visual field. The present research set out to examine how the visual system constructs a seemingly unified and veridical representation from this asynchronous information. Results add weight to the proposal that visual processing is not synchronous. Secondly, because this asynchrony is revealed in perception it seems that the visual system fails to account for these asynchronies. Finally, asynchrony does not appear to be fixed. Instead the experimental or attentional demands of the task seem to modulate the perceptual processing of attribute or localised information.

Chapter 1

Introduction

1. Evidence for Asynchrony of visual processing.

Visual processing is not synchronous. Firstly, neural activity transduced by the retina from photons entering the eye is immediately divided for the analysis of visual information (Livingstone and Hubel, 1988, Zeki 1973). From the offset visual structures are stratified for parallel and functional analysis of different types of visual information (for example, colour, motion and form). It seems quite unlikely that these different functional streams will process information in exactly the same time. Presumably temporal asynchrony will arise from physiological differences between different functional areas, such as transient versus sustained neuronal responses and slow versus fast conduction of neural information. Moreover, factors that accelerate information processing by increasing the saliency of an attribute (for example, attention, categorisation, task constraints) could also introduce temporal asynchrony. To illustrate, it is now well established that attention selectively speeds up information processing resulting in temporal asynchrony between attended and unattended information. Surely, if this processing advantage is offered to one attended stimulus attribute then this dimension will be processed faster than a second concurrently presented but unattended attribute.

Processing asynchrony between object attributes is not the only possible source of visual asynchrony. Attentional acceleration of visual information also presents a problem for attended versus unattended information across the visual field. Thus it seems likely that spatial information is also processed asynchronously.

Yet, despite these sources of temporal asynchrony our phenomenological experience of the world is temporally unified and veridical. We do not perceive a dislocated patchwork across the visual field. Moreover, our representation of the world allows successful interaction with our environment implying that the output of the visual system is temporally veridical. It is this achievement of the visual system, a seemingly unified and veridical representation derived from temporally asynchronous information that is considered here.

2. Asynchronous processing of feature attributes.

2.1. Physiological evidence for the functional processing of feature attributes: Livingstone & Hubel and Zeki's account.

The notion of the visual system as an ensemble of subsystems functionally processing information in parallel has emerged from neurological, physiological and empirical studies. In their seminal paper Livingstone and Hubel (1988) cited physiological evidence to claim that the visual system consists of several anatomically distinct subdivisions that functionally process visual input in parallel and independent processing streams.

It is well established that the division of retinal input occurs early in visual processing (Livingstone and Hubel, 1988). After entering the retina visual input is transmitted to the stratified lateral geniculate nucleus (LGN) where information is functionally divided between the first two small cell layers (parvocellular laminae) and four layers of large cells (magnocellular laminae) (DeValois and DeValois, 1990)[1]. Importantly, these magno and parvo cells differ in four functional respects, wavelength, speed, acuity and contrast sensitivity.

Approximately ninety percent of parvo cells are colour-opponent combining information from the short, medium and long wavelength cone photoreceptors into the following three distinct wavelength channels. The red-green channel (which takes the difference between medium wavelengths from long), the blue-yellow channel (which takes the difference between long and medium wavelengths from short) and the luminance channel (which adds long and medium wavelengths) (Gegenfurtner, 1997). In addition, cells of the parvocellular system have smaller receptive fields than cells of the magnocellular system therefore they possess higher spatial resolution for any given eccentricity. In contrast magno cells are effectively colour-blind[2] displaying no wavelength sensitivity, their transient response is faster than that of the parvocellular system and they are more sensitive to low-contrast stimuli. Thus from the outset it seems that the parvocellular system is optimally designed for encoding colour information whereas the magnocellular system seems better suited to processing information about motion.

---

[1] There is recent evidence for an additional retino-genicular-striate pathway that innervates the Koniocellular (K) layers of the LGN and further projects to the blobs in layers 2 and 3 of V1. Although the role of this pathway is currently the subject of controversy it is potentially important for colour vision (Hawken and Gegenfurtner, 2001).

[2] It should be noted that some magnocellular cells do respond to flickering colour stimuli however these cells display a "frequency-doubled" response that is chromatically uninformative because it responds to either direction of polarity (e.g. red-green and green-red) (Gegenfurtner and Hawken, 2001).

This subdivision of visual input continues in the laminated primary visual cortex (primate V1, Brodmann's area 17 or striate cortex), located in the calcarine sulcus, where cells of the magnocellular system arborize with cells in area 4 Cα and on to area 4B. This system further projects to the middle temporal lobe (MT or V5) (Zeki, 1980). As the cells of this processing stream respond to speed and direction of movement MT is commonly regarded as the motion centre of the brain and the magnocellular pathway leading to it as the motion pathway.

Disparity tuned cells, which make their first appearance in V1 (see Cumming and De Angelis, 2001 for a review), also project to area MT. Histological mapping of V2 reveals three anatomically distinct regions, thick dark, thin dark and pale stripes. Single cell recording studies (Livingstone and Hubel, 1988) reveal that these disparity tuned cells found in area 4B of V1 arborize with the thick stripes of area 18 (V2) on their way to MT. By definition, the response of these cells depends critically on the horizontal position of the stimulus in the two eyes. There are several classes of disparity tuned cells (Poggio, 1995). Tuned excitatory (T.E.) cells respond maximally to zero or near-zero disparity and are subdivided into tuned zero (respond at zero disparity), near cells (respond at uncrossed disparity) and far cells (which respond at crossed disparity). In addition, tuned inhibitory cells display the inverted response to T.E. cells. Livingstone and Hubel (1988) claim that in addition to motion perception the magnocellular branch of the visual system may also carry out depth perception.

In parallel, cells of the parvocellular system further project to area 4Cβ of V1. At this point histological mapping of the cortex using cytochrome oxidase (CO) staining reveals a further anatomical division between the blobs and the interblobs of the upper area of the primary visual cortex. From single cell recording studies Livingstone and Hubel (1988) report a functional distinction consistent with this anatomical division. Optimum cell responses implicate the blobs in colour perception and the interblobs in the perception of form. In particular, three types of unoriented cells predominant the CO blobs namely, colour opponent, broad band and double opponent cells. Colour opponent (or Type 2) cells elicit an on response to wavelengths in one part of the electromagnetic spectrum and an off response to wavelengths in another part. Broadband cells show no such colour opponency and display either centre on or off with an antagonistic surround. Double opponent cells display both a receptive field versus surround antagonism and colour opponency. Together these cells provide the information necessary for colour processing implicating this division of the parvocellular system in colour perception.

This wavelength sensitive subdivision further projects to the thin stripes of V2 where all three types of unoriented cells can be found. In addition, Hubel and Livingstone (1987) report finding complex unoriented cells that are also found in broadband and colour opponent varieties. These cells respond to an optimally placed spot placed anywhere within their receptive field (as distinguished from the uncomplex broadband and colour opponent cells of V1 which only respond to a spot placed in a particular position). This system further projects to V4 and V4 alpha which is regarded by many as the colour centre of the cortex (Zeki, 1973). Moreover, recent imaging evidence suggests that this area selectively responds to colour as a property of objects (Zeki and Marini, 1998; Tanaka, 2001).

Hubel and Livingstone (1987) and Livingstone and Hubel (1988) postulate a third functionally distinct pathway this time specialising in form perception. This second, CO interblob, subdivision of the parvocellular system further projects to the pale stripes of V2 and is populated by specialised oriented cells. Firstly oriented complex cells respond to an optimal stimulus placed anywhere within their receptive field (as distinguished from simple cells that are phase dependent excited solely by an optimal stimulus in a particular region of their receptive field). In addition, this pathway is characterised by end-stopped cells that share functional characteristics with oriented complex cells but also respond to the length of a stimulus. This characteristic that makes these cells ideal edge detectors. Recall that smaller cells of the parvocellular system also have higher acuity than the cells of the magnocellular system. Thus, this highly acute subsystem seems well suited for the perception of form. The fact that these cells are not explicitly colour-coded and only seem to respond to colour information constituting an oriented boundary supports this theory.

To conclude, Livingstone and Hubel (1988) suggest that these three main functional divisions constitute three subsytems of visual processing. These three distinct subsystems seem to be specialised for processing information about motion/stereopsis, colour and form in parallel processing streams.

This supposition that the brain functionally divides information receives ardent support from Zeki's theory of micro consciousness (2001). Zeki contends that the brain is a collection of autonomous micro-systems each acquiring information about different types of knowledge. Accordingly, the properties of cells in each region reflect the type of knowledge processed. Clear examples of the information specific properties of different neural areas were discussed above. The early division between the temporally non-veridical [3] wavelength sensitive cells of the parvocellular laminae and the transient, colour blind cells of the magnocellular system to more complex cells such as the colour-opponent, end-stopping and stereoscopic cells of V2 illustrates this information specific division. Clearly, this division of information is necessary. In order to process different types of information the brain must consist of subsystems each capable of encoding the distinct types of knowledge required for vision. Cells with quite different properties (e.g. wavelength sensitivity, temporal veracity, response from both eyes) are required to encode each distinct type of information that is required for visual processing (e.g. colour, motion and depth perception). Moreover, this parallel processing of different types of information offers efficient and fast information processing. In Zeki's theory there is no need for the visual system to "bind" these quite different processing streams. Rather, each subsystem gives rise to its own micro-consciousness' that when appreciated

---

[3] Remember that the parvocellular pathway carries slow, high contrast information. Moreover, this is a slow conducting pathway. Consequently, we might expect information carried by this pathway to be perceived later than information carried by the magnocellular pathway. Therefore, this information should be less temporally reliable (Moutoussis and Zeki, 1997a; 1997b).

together give us the rich and varied experience that constitutes our visual world. This leads us to the interesting proposal that the unitary nature of consciousness is itself an illusion.

2.2. Physiological evidence for the functional processing of feature attributes: a note of caution.

As we might expect recent evidence suggests that the story is not this simple and the parallel processing account of visual processing does not receive unequivocal support.

To illustrate, Gegenfurtner *et al* (1996) hypothesise that the anatomically distinct pathways of the visual cortex do not reflect a corresponding functional segregation. In an anatomical study reminiscent to Livingstone and Hubel's these authors took single cell recordings from V2 of macaque monkeys followed by histological mapping this brain region. Despite contending the functional segregation theory these authors found that specialised cells did occur more frequently in the CO compartment associated with the corresponding stimulus attribute. In particular, they found that end-stopped cells were more frequently found in the inter-stripe region (41%) than in the thin (19%) or thick stripes (13%). Colour- selective cells were more frequent in the thin stripes and more cells in the thin stripes were not responsive to colour (27%) than in any other region. These findings are remarkably similar to those reported by Hubel and Livingstone (1987). However, these authors claim that they found few cells that were solely responsive to one attribute and accordingly cell classification cannot be made on this basis. Yet, the cells they do report as being, for example, both colour and motion selective are just marginally responsive to one of these attributes. Therefore, this weak secondary response does not seem ample to justify ruling out a specialised account of cell processing. Gegenfurtner *et al* (1995) freely admit that the interpretation of their data varies more from Hubel and Livingstone's account than the data itself. The functional processing account would consider this secondary neural response as noise. If cells and neural areas become functionally specialised as an organism develops (as is most certainly the case in the primate visual system) then it seems highly improbable that each functional area and indeed each individual cell will display a pure response to a single attribute. Rather, one would expect an optimal response for a higher proportion of cells in a given area. Indeed, one would expect the results reported in the studies discussed above.

However, cells that display an equal response to two attributes have recently been reported. Johnson *et al* (2001) studied colour selective cells in the macaque primary visual cortex. They measured spatial frequency response functions by stimulating 167 cells with a drifting sinusoidal grating. Luminance and colour sensitivity was examined by measuring response curves to either black-white or equiluminant red-green gratings. They reported that 19 of the cells responded solely to the equiluminant gratings. Fourteen of these chromatic cells were low-pass and thus similar to parvocellular neurons of the LGN. Whereas, 60% of the neurons responded preferentially to luminance. However, perhaps surprisingly, 48 cells, found in layers 2 and 3, responded to both luminance and chromatic information. 83% of these colour-luminance cells were spatially selective. Moreover, these cells were double opponent. The authors conclude that these spatially selective chromatic neurons may respond to cues for form such as boundaries. Therefore, they posit them as colour and form selective cells. However, such cells are functionally suited to computing colour constancy (Gegenfurtner, 2001). This ability of the visual system to attach constant colours to objects despite differences in luminance conditions has long presented a quandary to vision scientists. Cells responsive to both colour and luminance information may enable the visual system to disentangle colour information from inconstant luminance information. So perhaps these cells are another variety of specialised colour cells.

Lennie (2001) proposes perhaps the most ardent view against the functional processing account. He proposes that each neuron is tuned to more than one attribute. In this view a neuron can be thought of as occupying a position in a multi-dimensional space. Lennie cites contingent after-effects such as the McCullough effect (a colour after-effect contingent on orientation patterns) as evidence for this "close-coupled" account of neural processing. Moreover, this author concludes that neurons display a response to more than one attribute in many single unit studies.

To conclude, it is important to note that the evidence for distinct functional pathways is not unequivocal. In view of recent literature the account proposed by Livingstone and Hubel (1988) and Zeki (1973) seems oversimplified at best. However, the criticisms posited against this theory do not falsify it and a complete alternative account has not yet been proven. Indeed it is still widely accepted that some degree of functional processing exists in the visual cortex.

2.3. Neuroimaging evidence for the functional processing of feature attributes.

One criticism of the studies cited above is the subject under study. For obvious reasons physiological studies have mapped the visual cortex in non-human primates (most commonly the macaque monkey). Although such investigations have undoubtedly furthered our understanding of neural functioning caution must be taken when making assertions about the human brain based on these findings. For this reason the emergence of neuroimaging techniques, which can be directly applied to the human brain, offers a welcome alternative means of investigating neural processing. Here, two such imaging techniques are discussed, Positron Emission Tomography (PET) which measures changes in regional cerebral blood flow and Functional Magnetic Resonance Imaging (fMRI) which is an indirect measure of neural activity that measures changes in the local blood oxygenation level. A change in the oxygenated to deoxygenated blood ratio produces a local magnetic field which is picked up by the MRI scanner. This second means of neuroimaging offers a superior spatial resolution to PET (Wandell, 2003). We are just beginning to learn whether the functional properties of the human visual cortex are the same as those described in monkeys. So far both (PET) and (fMRI) studies provide encouraging data.

Using PET Zeki (1990) identified a region in the human brain that is sensitive to moving stimuli. By subtracting and comparing scans derived from exposure to stationary versus moving black and white squares Zeki found an area of maximal activity in Broadmann's areas 19 and 37. Zeki proposed that area should be referred to as human area V5 based on its homology with macaque area V5. Zeki also reported activity in areas corresponding to monkey V1 and V2 when the moving stimulus was presented concluding that these areas appear to feed the motion centre in much the same way as they do in the macaque cortex. Tootell *et al* (1995) also identified this motion selective region of the human brain by stimulating the visual system with a flickering checkerboard. In addition, they also reported a strong signal between the primary visual cortex and this area known as MT+ (because it is unclear whether the recorded signal is also derived from areas just outside MT).

Again by exploiting PET, Zeki (1990) and Bartels and Zeki (2000) have reported activation in the lingual and fusiform gyri when participants view multi-coloured Land Mondrian displays versus equiluminant grey and white patches. Zeki proposes that this area is the human homologue of macaque area V4, the colour centre of the brain. Again, area V1 and V2 were also activated by the coloured stimuli suggesting that these areas feed the colour centre of the human brain. Wandell (2003) also report activation of the fusiform gyrus with coloured stimuli in an fMRI study. They presented participants with checkerboards composed of two opponent colours. They also report activity in areas V1 and V2.

However, once more a note of caution. Some authors point out that neuroimaging data based on the subtractive method does not conclusively support the functional segregation theory. In particular, Wandell *et al* (2001) point out that the existence of one large difference does not mean that smaller differences should be ignored. Indeed, authors favouring a distributed account would use this evidence to conclude that the presence of activity in more than one area provides evidence for this alternative theory.

On the whole these neuroimaging studies suggest that the human brain is functionally divided in a homologous manner to the macaque brain. The human brain seems to accommodate a homologue of both the motion and colour centres discovered in the macaque cortex. However, the evidence does not unequivocally support the functional segregation account and more studies employing these relatively new techniques are required.

2.4. Clinical Evidence for the Functional processing of Feature Attributes

Further evidence for functional processing in the human brain comes from the selective loss or sparing of attribute processing after neural damage. This clinical evidence reveals that each type of visual knowledge can be lost or spared in isolation strongly suggesting that each type of knowledge is processed independently.

Cerebral achromatopsia, first reported by Steffan in 1881, is a syndrome in which patients loose the ability to perceive colour (Zeki, 1990). Such patients report a world that varies in shades of grey. Although reported since as early as 1881 the proposal that this syndrome reveals a colour centre in the cortex provoked much controversy until recently. This was partly due to the common co-occurrence of a scotoma or hemianopia with the inability to perceive colour. Before the neuroanatomy of the visual system was mapped it made sense to attribute any visual disorder that co-occurred with a scotoma to damage in the primary visual area. However, it is now known that the lower border of the primary visual cortex, which represents the upper field of view, extends onto the lingual gyrus next to which lies the fusiform gyrus. Thus the coincidence of these symptoms does not rule out a colour centre in the cortex. Rather, it makes sense in terms of current knowledge about neural physiology. Moreover, clean cases of this disorder have been reported. Oliver Sacks (1995) reports the visual world of a painter who acquired a pure achromatopsia after a car accident,

> "as soon as he entered, he found his entire studio, which was hung with brilliantly colored paintings, now utterly grey and void of color. His canvases, the abstract color paintings he was known for, were now greying or black and white. His painting once rich with associations, feelings, meanings now looked unfamiliar and meaningless to him."

Zeki (1990) also reports that the fusiform and lingual gyri have been reported in every reported case of cerebral achromatopsia adding weight to his proposal that this area is the human homologue of macaque V4.

It seems that the colour system can also operate autonomously. Selective sparing of colour vision has also been reported. Zeki *et al* (1999) report PB a patient who suffered from blindness after prolonged respiratory arrest induced by an electric shock. Yet, despite apparently suffering from blindness PB still reported being consciously aware of colour. This phenomenon is commonly reported after carbon monoxide poisoning and has long been thought to result from the selective sparing of the metabolically more active and vascular wavelength sensitive blobs of V1 and stripes of V2. However, when PB's colour constancy ability was tested using Land's Mondrian experiments it became clear that he was not able to discount the illuminant and that his colour perception was actually purely wavelength based. Further fMRI analysis revealed that chromatic stimuli significantly activated V1and not area V4. Thus, although PB was still able to see colour this perception was based on spared V1 processing enabling perception of wavelengths. However, it seems that damage to his fusiform gyrus has diminished his ability to attribute constant colours to objects despite differences in luminance conditions.

Selective loss and sparing of motion perception has also been reported. Zihl *et al* (1983) reported a case of motion blindness know as akinetopsia in his patient LM. LM suffered from bilateral lesions including the human homologue of area V5. In contrast, Riddoch's syndrome, the selective residual ability to perceive motion, was first reported in first world war patients by Riddoch in 1917. Despite appearing to have lost their vision these patients could consciously detect the presence of motion (as distinguished from blindsight, a phenomenon reported by Weiskrantz (1990) whereby patients are unconsciously aware of residual vision). Their perception was that of a shadowy "something moving" devoid of form or colour. In particular, Zeki (1997) reports a patient, GY, who could detect whether high contrast, fast moving stimuli was moving to the left or to the right. A PET study revealed that areas V3, V5 and the parietal cortex were activated by this motion. Thus, Zeki postulates that this residual motion results from a second motion system that bypasses V1 and projects directly to MT from the LGN and from the pulnivar (which receives input from the superior colliculus).

The selective loss of form perception has also been reported. Patients suffering from apperceptive visual agnosia loose the ability to name objects despite being able to report their colour, motion, luminance and being able identify them from tactile, olfactory or auditory cues (Farah, 2000, p98). However, these patients can identify visually presented stimuli if they are drawn slowly (Bender and Feldman, 1972) leading Zeki (1990) to the conclusion that their perception of form is supplemented by part of the magnocellular pathway that projects to V3 and constructs form from motion.

In conclusion, these clinical cases provide convincing evidence for functional specialisation of the human cortex. The selective sparing or loss of the perception of individual attributes makes a strong case for the autonomy of these attributes and their parallel processing. Moreover, post-mortem and neuroimaging data from these cases indicate that the functionally specialised areas of the human brain corresponds to those discovered in physiological studies of the macaque cortex.

2.5. Empirical Evidence for the Functional Processing of Feature Attributes

If the visual system is divided into parallel processing streams of colour, form and motion then the perception of each of these attributes should mirror the characteristics of each processing stream. We know that cells of magnocellular system are effectively colour-blind, fast and have large receptive fields (thus offering poorer visual acuity). Conversely, cells of the parvocellular system are wavelength sensitive, smaller and their response is slower. Thus the perception of colour and motion should have different temporal and spatial resolution and wavelength sensitivity. Perception of motion should be colour blind, fast and have a low acuity. Remember that stereoscopic cells were also found in the magnocellular system therefore these characteristics may also apply to this attribute too. Conversely, perception of colour and form should be slower. In addition, recall that the interblob sub-pathway of the parvocellular system does not appear to explicitly code colour therefore this attribute should not be necessary for form perception. Moreover, this subsystem has a higher visual acuity than the blob system. Thus form perception should have a higher spatial resolution than not just motion and stereo perception but also colour perception.

Several psychophysical studies confirm these predictions. Campbell and Maffei (1980) reported that motion perception is impaired at high spatial frequencies. Observers were required to match the frequency of rotation of a square wave grating of varying spatial frequencies with a high contrast reference grating. The spatial frequency of the reference gratings was set at 1cycles/degree. They found for frequencies greater than 2-4 c/deg the apparent motion of the test grating appeared slower than that of the reference grating. Indeed, at 16-32 c/deg the test grating was perceived as almost stationary. This effect was even more pronounced for peripheral stimuli. These findings suggest that high spatial frequency information is processed by neurons with slower temporal properties a finding that concurs with the above predictions. Impaired motion processing at high spatial frequencies presumably reflects the temporal limitations of the parvocellular system that processes this information. Conversely, veridical processing of low spatial frequencies probably reflects the temporally accurate magnocellular pathway.

Moreover, Cavanagh *et al* (1984) reported that perceived speed is dramatically reduced for equi-luminant stimuli. Observers were required to match the motion of a sinusoidal luminance grating presented in the top half of the visual display with a test sine-wave of variable chrominance and luminance modulation presented in the bottom half of the visual display. The gratings, which were equated in spatial frequency, moved in opposite directions. All observers showed pronounced slowing of perceived velocity at a preset equi-luminance point for low spatial frequency stimuli. Indeed, the gratings often appeared to stop. Thus, when only colour information is available perception of speed is dramatically impaired. This is presumably because of the temporal limitations of the colour processing parvocellular system. Lu and Fender (1972) report a similar result for perception of depth (although some evidence contradicts this finding, Kingdom and Simmons (2000)). Thus as predicted it seems that perception of both movement and steroscopic depth fail at equiluminance.

However, Gegenfurtner and Hawken (1996) expose a significant problem occurs with studies that compare chromatic stimulus that have been equated in luminance contrast with luminant stimuli. In particular, they point out that the subtractive nature of colour processing means that colour contrast cannot be directly compared with luminance contrast. Indeed, the maximum cone contrast that can be produced for isoluminant gratings is about 30% significantly lower than the 100% contrast that can be produced for luminance gratings. Therefore, they suggest that it may be this reduction in contrast that diminishes the processing of motion and depth in Cavanagh *et al* (1984) and Lu and Fender's (1972) studies. This is obviously an important criticism that undermines the impact of this psychophysical evidence.

Finally, Zeki (1997) reports that the phenomenon of colour bleeding provides evidence of separate colour and form processing systems. Colour bleeding is a phenomenon in which a stimulus' colour leaks beyond its defining edges. Zeki suggests that this phenomenon is a product of the higher resolution form system producing a pattern that is too fine for the relatively low acuity of the colour system. Therefore, the colour "leaks out" of the more accurately represented form.

Together the physiological, neuroimaging, clinical and empirical studies discussed above provide compelling evidence for the parallel processing of object information in functionally specialised pathways.

3. Asynchronous perception of feature attributes

If the different attributes of an object are processed in parallel then it seems unlikely that each pathway would process information in exactly the same time. In particular, the magnocellular pathway responds faster to stimuli and conducts this activity at a faster rate than the parvocellular system. Therefore, temporal synchrony of neural processing seems to be a quite unlikely property of a functionally distributed system. This has led to some interesting studies of perceptual asynchrony pioneered by Moutoussis and Zeki (1997). These studies have produced perhaps the most compelling evidence for the parallel processing account of colour, form and motion revealing that these attributes are actually perceived at different times. Moreover, this finding suggests that any temporal asynchrony introduced by parallel processing of different types of visual information is not compensated for at a later stage in visual processing.

In their seminal paper, Moutoussis and Zeki (1997a, 1997b) employed a psychophysical method revealing perceptual asynchrony between colour, form and motion. The stimuli were composed of two features (e.g. motion and colour) alternating between two values each (e.g. up versus down and green versus red). Observers were required to report which feature changed in value first for different asynchronies between the stimulus alterations. From these subjective reports, the authors derived the physical asynchrony required between the stimulus dimensions for synchronous perception. Remember that the magnocellular pathway thought to carry information about motion responds more transiently than the parvocellular pathway that carries information about colour and form. Therefore, Moutoussis and Zeki expected to find a perceptual advantage for motion over colour and form. Surprisingly the authors found that colour is perceived 118msec before motion and 63ms before orientation, whereas orientation has a 52ms perceptual advantage over motion. The authors proposed that this perceptual advantage, the antithesis to the expected asynchrony, might reflect a compensatory mechanism introduced by the visual system to counterbalance the faster neural processing of motion. However, there are several methodological problems with this study. In particular, the participants task was difficult and subjective providing a subjective measure of temporal asynchrony. Moreover, the relative salience was not controlled across attributes and the CIE chromaticity coordinates of the colours employed were not reported making it unclear if luminance levels were controlled.

Arnold *et al* (2001) exploited the colour-contingent motion after effect to demonstrate a perceptual advantage for colour over motion. When observers view a given direction of motion subsequently viewed objects appear to move in the opposite direction. This effect can be made contingent with another attribute for example colour. To illustrate, after viewing a green object moving in a clockwise direction subsequently viewed green objects appear to rotate in a counter-clockwise direction. These authors found that a physically asynchronous direction of motion and colour gave rise to such a colour-contingent motion after effect. Using this effect they revealed an 80 ms advantage of colour over motion. Thus despite being physically asynchronous, the attributes were perceptually synchronous substantiating Moutoussis and Zeki's (1997) finding. This finding also calls into question one of Lennie's (in Gegenfurtner and Hawken, 2001) main criticisms of distinct functional processing. He cites contingent effects as evidence against the parallel processing account. However, this evidence suggests that such contingent effects occurs post attribute processing and therefore do not support his 'close-coupled' account of neural processing.

More, if quantitatively different, evidence for perceptual asynchrony of object attributes comes from Viviani and Aymoz (2001). In a study reminiscent of Moutoussis and Zeki (1997) these authors pitted colour, form and motion against each other in pair-wise comparisons. Again each attribute alternated between two values with differing asynchrony and observers were required to report which attribute changed first. They estimated perceptual processing time by solving a convolution equation and found that perceptual processing times for colour and form are equivalent whereas motion perception requires an additional 50ms.

The findings from studies probing perceptual asynchrony are far from unequivocal. Holcome and Cavanagh (2001) report that observers could correctly identify spatially superimposed pairings of orientation with colour or luminance patterns even for remarkably high rates of presentation. Consequently they claim that such features are combined very early in the visual system eliminating the "Binding Problem".

Nishida and Johnston (2002) also found that perceptual asynchrony depends critically on the alteration rate of stimulus changes. When the alteration rate was slowed down to a change every 2000ms perceptual asynchrony between colour and form almost disappeared. Whereas for alteration rates significantly faster than 250ms judgements about the temporal relationship between colour and motion were impossible. In addition, they found that the subjective asynchrony reported is not found in reaction time measures or if response is measured with a motor response using a mouse rather than a key press. These findings have led Nishida and Johnston (2001) to propose an alternative to the "processing delay" account of perceptual asynchrony. These authors postulate that the processing delay account, which assumes an implicit coding of stimulus timing, raises some philosophical problems. They contend instead that temporal coding is time locked to events by "metaneurons" which are sensitive to the time course of neural processing in the brain. Perception of temporal order is achieved by comparing temporal markers of which there are two types. Transitions which are first order changes requiring measurement at two points in time, for example a change in colour and turning points which are second order changes that require measurements at three points in time, for example motion. At high alteration rates (250ms) asynchronies arise because transitions (of e.g. colour) are more salient than turning points (of e.g. motion). However, this theory does not account for the reported perceptual asynchrony between two temporal markers of the same type (transitions, e.g. colour and form).

Alternatively, the discrepancy between these studies could be accounted for by a non-fixed account of attribute processing. If one assumes that more salient attributes are processed faster then factors such as task, attention and categorisation will influence which attribute enjoys the perceptual advantage. Such an account could explain why different perceptual asynchronies are reported when different tasks are employed both between studies (e.g. Moutoussis and Zeki, 1997 and Viviani and Aymoz, 2001) and within the same study (e.g. Nishida and Johnston, 2002) and why under certain circumstances no such asynchrony is reported at all (Holcombe and Cavanagh, 2001). It is to these possible determinants of perceptual asynchrony that we now turn.

4.Possible Determinants of Asynchronous Processing

4.1. Selectively attended information.

In the studies discussed above different experimental conditions yield different temporal asynchronies between attributes. This anomaly has led us to the proposal that rather than a fixed account of attribute processing the perceptual processing time may be flexible. Although physiological differences between processing streams may introduce constant temporal asynchronies between information "higher level" factors may modulate asynchrony by selectively speeding up information processing. This modulation of perceptual processing may account for the different perceptual asynchronies reported across and between studies. Here, factors that may influence the perceptual processing time of an attribute are considered.

Attention seems an obvious source of processing acceleration. The notion that attending to a stimulus brings forward its perception in time dates back as far as Tichener (in Pashler, 1999) who included the law of prior entry in his laws of attention.

The attention literature suggests that attention speeds up information processing. For example, in a seminal study Posner *et al* (1980) demonstrated that the knowledge of an objects location significantly enhances its detection. In this study reaction time was significantly decreased when an objects location was given prior to presentation. Studies of temporal order also suggest that attention speeds up information processing (Pashler, 1999). To illustrate in one such study (Stelmach and Herdman, 1991) direction of attention was manipulated while observers judged the temporal order of two stimuli. Observers were directed to fixate centrally and attend either to the left, right or to the centre. On each trial two brief flashes of light were then presented one to the left and one to the right. Observers were required to indicate which light flashed first. The SOA between the first and second flash was adjusted until each location was selected 50% of the time, in other words until the temporal order of the stimuli was indiscriminable. The authors found that in the attend-centre condition temporal order was indiscriminable (i.e. mean performance was at the 50% level at SOA = 0ms) at 0ms. Thus, attention was directed equally to both stimulus locations. Whereas, in the attend right condition temporal order was indiscriminable when the left stimulus preceded the right stimulus by about 40ms. The same but converse effect was found for the attend left condition. These findings are consistent with the idea that an attended stimulus is processed faster.

However, some authors contend that studies of temporal order and of reaction time are susceptible to response bias (Pashler, 1999) or may reflect a change in decision criterion rather than attentional acceleration of information (Carrasco and McElree, 2001). Recent work by Carrasco and McElree (2001) attempts to overcome these failings using the speed-accuracy trade-off procedure (SAT).

Carrasco and McElree (2001) asked observers to respond to either the tilt (feature condition) or the tilt and spatial frequency (conjunction condition) of an oriented gabor patch presented amongst zero, three or seven gabor distracters. On 50% of the trials a cue was presented which indicated the target location. On the remaining trials a neutral cue was presented. The authors measured disriminability and speed of information co-jointly by presenting a tone at one of 7 intervals ranging from 40-2000ms. Observers were required to respond within 300ms of the tone. In the SAT paradigm the effect of attention on accuracy and processing time can be examined by pitting these variables against each other. Theoretically, if cueing only increases response accuracy then optimal performance (i.e. when accuracy reaches an asymptote) should be higher in the cueing condition. Whereas, if cueing solely increases speed of processing then optimal performance should be reached earlier in the cueing condition although given enough time it will be the same in both cued and uncued conditions. In other words, the rate of approach to asymptote is higher. Carrasco and McElree found that a peripheral cue increased both accuracy and, more importantly for our purposes, speed processing dynamics in both feature and conjunction conditions. In particular, in the feature condition, cueing the target reduced processing time by 45ms. In the conjunction condition, where processing time slowed with increasing set size, peripheral cueing reduced processing time for each set size (by 38, 84, and 106ms for set sizes of 1, 4 and 8 gabor patches respectively). Therefore, this study strongly supports the idea that attention speeds up information processing.

Attention then seems like a probable determinant of perceptual asynchrony. Moreover, if attention speeds up information processing then tasks that require an observer to selectively attend to information should also modulate perceptual asynchrony.

The categorisation literature has established that observers selectively attend to an attribute that is relevant for the task at hand. To illustrate, previous literature suggests that both spatial scale and colour can be selectively attended to.

In particular, the use of different spatial scales appears to be diagnostically driven (Oliva and Schyns, 1997; Schyns and Oliva, 1999). Because spatial frequency channels can be selectively impaired in their contrast sensitivity it is commonly thought that such channels can operate independently (see Morrison and Schyns, 2001, for a review). Schyns and Oliva (1999) exploited hybrid stimuli in a neat demonstration of the flexible usage of these channels. Each hybrid stimulus was comprised of a low and high component, for example, a low pass spatial frequency (LSF) filtered image of a neutral female was superimposed with a high pass spatial frequency (HSF) filtered angry male face. They found that observers were biased to HSF when performing an expression judgement whereas observers performing a categorisation judgement (happy versus unhappy) were biased to LSF. Importantly, when subsequently asked to categorise the gender (an unbiased task) of hybrid stimuli the observers' response significantly depended on the original task. Thus despite being presented with identical stimuli observers reported the stimuli as being male or female depending on whether they had initially performed an expression or categorisation judgement. In other words, it seems that observers select the spatial scale that supplies the perceptual cues required to determine the categorisation judgement.

Recent evidence adds support to this flexible account of spatial frequency processing. Sowden *et al* (in Press) used hybrid plaids to demonstrate that observers selectively attend to a cued spatial frequency component. In a study reminiscent of Schyns and Oliva (1999) observers were presented with hybrid plaids comprised of a left and right oriented component either 4 octaves or 0.5 octaves apart. The authors found that observers selectively attended to the spatial frequency that was cued by a tone. However, this finding only held true when the components were sufficiently separated to be processed by two different spatial frequency channels (i.e. in the 4 octave condition). This finding strongly suggests that observers can selectively attend to a spatial frequency channel.

The categorisation literature also suggests that colour can be selectively attended to. Oliva and Schyns (2000) found that colour mediates scene recognition when it is diagnostic for the task at hand. In particular, these authors found enhanced recognition of diagnostic scenes when they were properly coloured. However, they found no such advantage for categorisations that did not depend on colour.

The phenomena known as acquired distinctiveness and equivalence also reveals that the properties of an attribute can be modified with categorisation experience. Research has shown that training can improve an observers' ability to discriminate between two stimuli (Goldstone, 1994). This perceptual learning is manifested in one of two ways, either the observers' perceptual space is shrunk and within category information is compressed (acquired equivalence). In this case any information between two distinctive values is easily confused.

Alternatively the perceptual space is stretched (acquired distinctiveness) and the observer is better able to discriminate between different values of a dimension that were previously indiscernible. These categorical effects have been demonstrated for colour perception (Goldstone, 1995; Özgen and Davies, 2002). To illustrate, Özgen and Davies, (2002) trained observers to discriminate between two colours that were previously within a category (e.g. blue 1 and blue 2). Post training same-different judgments revealed improved discrimination between pairs of colours that cross this new boundary (e.g. acquired distinctiveness).

In sum, these studies suggest that different classifications of a stimulus will influence the attribute extracted by the visual system. If the categorisation task can influence which attribute is attended it seems likely from the attention literature that this diagnostic dimension will be processed faster.

To conclude, it seems likely that both attention and categorisation tasks requiring the observer to selectively attend to one attribute will accelerate the perceptual processing time of an attribute. Accordingly, these factors will modulate the perceptual asynchrony between different attributes. In other words, these factors seem probable determinants of perceptual asynchrony.

4.2. Treisman's Feature Integration Theory

From the literature discussed above it seems plausible that attention may serve to modulate the perceptual asynchrony between two attributes by selectively increasing the perceptual processing time of one attribute. However, the story is not this simple. Previous literature suggests that selectively attending to a location enhances the integration of information at this locus.

Although previously unconsidered in the perceptual asynchrony literature the role of attention on the integration of stimulus attributes has been extensively examined. Indeed it is the subject of Treisman's Feature Integration Theory (FIT) (Treisman, 1980). According to FIT the role of attention is to correctly integrate the features of an object. Treisman and Gelade (1980) postulate that features are registered early and their processing is automatic. However, the integration of these features into a coherent object is a later process requiring focused attention. When an object is selected its properties and location are actively represented. This momentary assembly of the object's defining characteristics allows these attributes to be integrated correctly. Conversely, without focused attention, feature attributes "free float" and may lead to incorrect feature conjunctions known as "illusory conjunctions".

The most compelling evidence for FIT comes from visual search experiments. In a visual search experiment the target can be defined either by separate features (e.g. pink or O) or by feature conjunctions (a pink O). In such studies, the time required to search for a single feature does not typically increase with the number of distracters present in the stimulus array. This is a finding that one would expect if features were processed automatically and in parallel. Whereas, the time required to search for a conjunction of features (e.g. a pink O) scales linearly with the number of distracters presented in the array. One would expect such an increase in search time as possible locations are added if feature conjunction requires focal attention to be delivered serially to each location.

Further evidence for FIT and indeed for the parallel processing of feature attributes comes from illusory conjunctions (Treisman, 1982). To illustrate Treisman (1982) found that observers performed well in a primary task requiring them to report two black digits. However, they frequently make conjunction errors in a secondary task requiring them to describe anything they had observed about concurrently presented coloured letters. Conjunction errors combining two simultaneously presented features significantly exceeded those combining one correct feature and one that was not present in the display. Similar results were found for a stimulus-matching task. Treisman (1982) concludes that these recombination errors further demonstrate that without time to attend the brain cannot correctly integrate features.

Clinical evidence also supports FIT. Damage to the parietal lobes results in a disorder of attention known as Balint's syndrome (see Rizzo and Vecera, 2002 for a review). Patients with this disorder make conjunction errors during free viewing. Moreover, recent FMRI studies show that, in normal observers, regions of the parietal cortex are more engaged in feature conjunction tasks than when multiple objects are presented (Shafritz, 2002) implicating this region of the cortex, commonly thought to be involved in attention, in feature conjunction.

To conclude, from these studies it seems that attention enhances the integration of attribute information. Moreover, recent empirical and neurological work suggests that attention may enhance feature integration by increasing spatial resolution thereby conserving information about the location of attended information.

4.3. Spatial Resolution Theory of Attention

Recent, neurological evidence supports the hypothesis that attention facilitates the integration of attribute information (Reynolds and Desimone, 1999). It seems that attention modulates the competition between simultaneously presented information. When two stimuli are present within the receptive field of a single cell (here, in V4) the neural response to an attended stimulus is as large as when this stimulus is presented alone. In other words, attention appears to filter out the competition and effectively increases the spatial resolution of the cell. Indeed, attention seems to play a different role depending on the levels of processing. Early in the visual system it seems to increase the strength of the attended stimulus. However, later attentional effects seem to filter out any response to the unattended stimuli.

The theory that attention facilitates feature integration by increasing the spatial resolution of attended features makes sense in terms of the attentional literature. To illustrate, Yeshurun and Carrasco (1998) report an interesting study that strongly supports the spatial resolution theory of attention. These authors employed a task in which performance was diminished by heightened spatial resolution. For this stimulus it is likely that performance is poorer when the stimulus is foveated because the average size of the spatial filters at the fovea are too high for the size of the stimulus. However, around the mid-peripheries the average size of the filters is probably optimal. Observers were required to detect a texture target composed of 9 oriented lines appearing at a large range of eccentricities in a background of orthogonally orientated lines. Peak performance for this task occurs at mid-peripheries, in other words at a medium spatial resolution. The authors found that attention enhanced performance for peripheral stimuli. Interestingly, they also found that attention actually impaired performance for foveated stimuli. Thus, attention improved performance when the spatial resolution of the stimuli was too low (for peripheral stimuli) but diminished performance when the spatial resolution was too high (for foveated stimuli).

To conclude, behavioural and physiological evidence suggests that attention to a location should enhance the integration of an object's features by increasing spatial resolution at an attended location. However, attention also seems to selectively speed up information processing. Therefore, selectively attending to one attribute might actually enhance the perceptual asynchrony between an object's attributes. These possible orthogonal influences of attention on the integration of object information across time are investigated here.

5. Asynchronous processing across the visual field

Temporal asynchrony induced by functional processing does not present the only problem to vision. If attention speeds up information processing then visual processing of information from across the visual field must also be asynchronous. This proposal is neatly demonstrated in the motion line illusion (Hikosaka *et al*,1993). When attention is directed to a cue presented above a line observers perceive motion propagated from the cued location. Motion centres seem to construct a motion sensation from the asynchronously processed information around the attentional focus. This illusion suggests that attention does produce temporal asynchrony across the visual field. Moreover, this asynchrony seems to be mirrored in perception. This proposal is further considered in the current investigation.

6. The present research.

Together the physiological, neuroimaging, clinical and empirical studies discussed above provide compelling evidence for the parallel processing of object information in functionally specialised pathways. Moreover, this functional processing of object attributes results in concurrently presented attribute information, for example colour and form, being processed and perceived at different times (Moutoussis and Zeki, 1998). However, discrepancies between the different empirical studies of perceptual asynchrony call into question a fixed account of attribute processing. For example, whereas Moutoussis and Zeki (1998) reported a 63ms temporal advantage for colour over form Viviani and Aymoz (2001) found no such perceptual asynchrony. Indeed it seems likely from studies of attention and categorisation that enhanced saliency of an attribute may accelerate the processing time of this dimension and accordingly should modulate the perceptual asynchrony between concurrently presented features. In other words, the perceptual asynchrony between attributes is probably flexible reflecting the relative saliency of each dimension. It is this possibility that is examined in Chapter 2. In Experiment 1 we developed a novel method to examine the temporal dynamics of feature integration. We employed this paradigm in Experiment 2 to examine whether the requirements of the task at hand can modulate the perceptual asynchrony between two attributes, here colour and orientation. In Experiment 3 we replicated this experiment in a between participants design and in Experiment 4 for colour and spatial frequencies.

From the literature discussed above one would expect that selectively attending to one attribute could modulate perceptual asynchrony by selectively accelerating the processing time of this dimension. However, unfortunately, the role of attention is not this simple. Attention also seems to play a role in the integration of features most likely by enhancing the spatial resolution of an attended location. Evidence suggests that selectively attending to a location enhances the integration of information at this location. We examined the influence of attention on the integration of colour and form in Chapter 3. In Experiment 5 we modified the method developed in Chapter 2 to examine how attention modulates the integration of coloured shapes arranged in a line. In Experiment 6 we extended this design across the visual field.

That attention accelerates information processing also has interesting implications for the temporally veridical integration of information across the visual field. If attention to a portion of the visual field can speed up the processing of information within its focus this will result in temporal asynchrony between attended and unattended information. In Chapter 4 we examined whether this asynchrony across the visual field is mirrored in perception. In Experiment 7 we investigated how attention modulates the threshold of asynchrony that is tolerated between the elements of a line stimulus. We extended this paradigm to a square stimulus in Experiment 8.

We extended these studies in Chapter 5 to examine whether the integration of information across the visual field is time dependent around the focus of attention. In Experiment 9 we examined the influence of attention on the integration of identical desynchronised elements to form the orthogonal perceptions of a two vs a five. We extended this further in Experiment 10 to examine how attention modulates the exact temporal relationships required between the elements of these figures.

Chapter 2

Investigating the influence of task requirements on feature integration.

In the introductory chapter we argued that functional processing of object attributes results in different processing times for distinct attributes (such as color, form and motion). Moreover, the visual system does not seem to compensate for this temporal asynchrony and consequently it is revealed in perception (Moutoussis and Zeki, 1997a; 1997b; Arnold *et al*, 2001; Viviani and Aymoz , 2001). In short, functional processing induces perceptual asynchrony between different attributes.

Current literature (Moutoussis and Zeki, 1997) assumes a fixed processing account of perceptual asynchrony. However, findings from the attention and categorisation literature suggest that these factors could modulate the perceptual processing of an attribute.

In particular, studies of reaction time (Posner, 1980), temporal order (Stelmach and Herdman, 1991) and using the speed-accuracy trade-off procedure (Carrasco and McElree, 2001) have revealed a temporal processing advantage for attended information. Moreover, the categorisation literature has established that participants selectively attend to an attribute that is relevant for the task at hand. For example, the use of different spatial scales appears to be diagnostically driven (Oliva and Schyns, 1997) and colour mediates scene recognition when it is diagnostic for the task at hand (Oliva and Schyns, 2000). Together these studies suggest that the task at hand will influence the attribute extracted by the visual system. If the categorisation task can influence which attribute is attended it seems likely from the attention literature that this diagnostic dimension will be processed faster.

Intuitively then it seems likely that the task at hand could modulate perceptual asynchrony by differentially modulating the perceptual processing of each attribute. In other words, these factors may determine temporal integration by modulating the perceptual asynchrony between attributes. In the current chapter we examined how the task at hand modulates the integration of two stimulus attributes into a unitary perception. In Experiment 1 we developed a novel method to examine feature integration. We employed this method in Experiments 2, 3 and 4 to examine whether perceptual asynchrony can be modulated by the task at hand.

To examine feature integration a novel method was designed. By desynchronising the attributes (for example, colour and orientation) of two alternating orthogonal stimuli (e.g. *red-left* and *green-right*) we developed a method to examine the time that participants require to perceive a stimulus (e.g. *red-right*) emerging as a result of this asynchrony. The perception of this emergent stimulus crucially depends on the integration of both attributes. Therefore we can examine the time scale of binding itself rather than the time-scale of perceived simultaneity (Moutoussis and Zeki, 1997) or a response to a target presented from the offset as a conjunction of features (Treisman and Gelade, 1980; Yershurun and Carrasco, 1998). Moreover, by manipulating the direction of asynchrony (colour first or orientation first) we can examine the time-scale of binding for each attribute independently. Consequently we can compute any perceptual advantage offered to either attribute by comparing these conditions.

Experiment 1.

Investigating the temporal integration of colour and orientation.

In a study of perceived simultaneity Moutoussis and Zeki (1997) reported that participants perceive colour changes 60 ms before orientation changes. In particular, these authors presented participants with two stimulus attributes (for example, colour and orientation) alternating between two values (for example, red and green and left and right). Each attribute was presented in different halves of the same screen. The phase of each attribute alteration was manipulated and participants had to decide which two attribute values were presented simultaneously. Specifically, participants were requested to report the colour of an alternating checkerboard presented in one half of the screen whilst a bar on the other side of the checkerboard was tilted to the left and which colour it was whilst the bar was tilted to the right. From this response the authors computed the asynchrony required between the changes in each attribute to perceive these changes as occurring simultaneously.

In Experiment 1 we examined this finding with the novel method described above. Using this paradigm we found that colour and form are perceived at the same time. Therefore, we found no perceptual asynchrony between these attributes. These results are discussed in relation to the methodological problems of previous studies of perceptual asynchrony.

Method

Participants. 11 University of Glasgow students (6 male and 5 female under 35 years of age) with normal or corrected to normal vision were paid to participate in the experiment. All participants were screened for colour blindness using the Ishihara tests for coloured blindness (1978) to exclude any with colour blindness.

The data of one deuteranomolous participant was analysed separately.

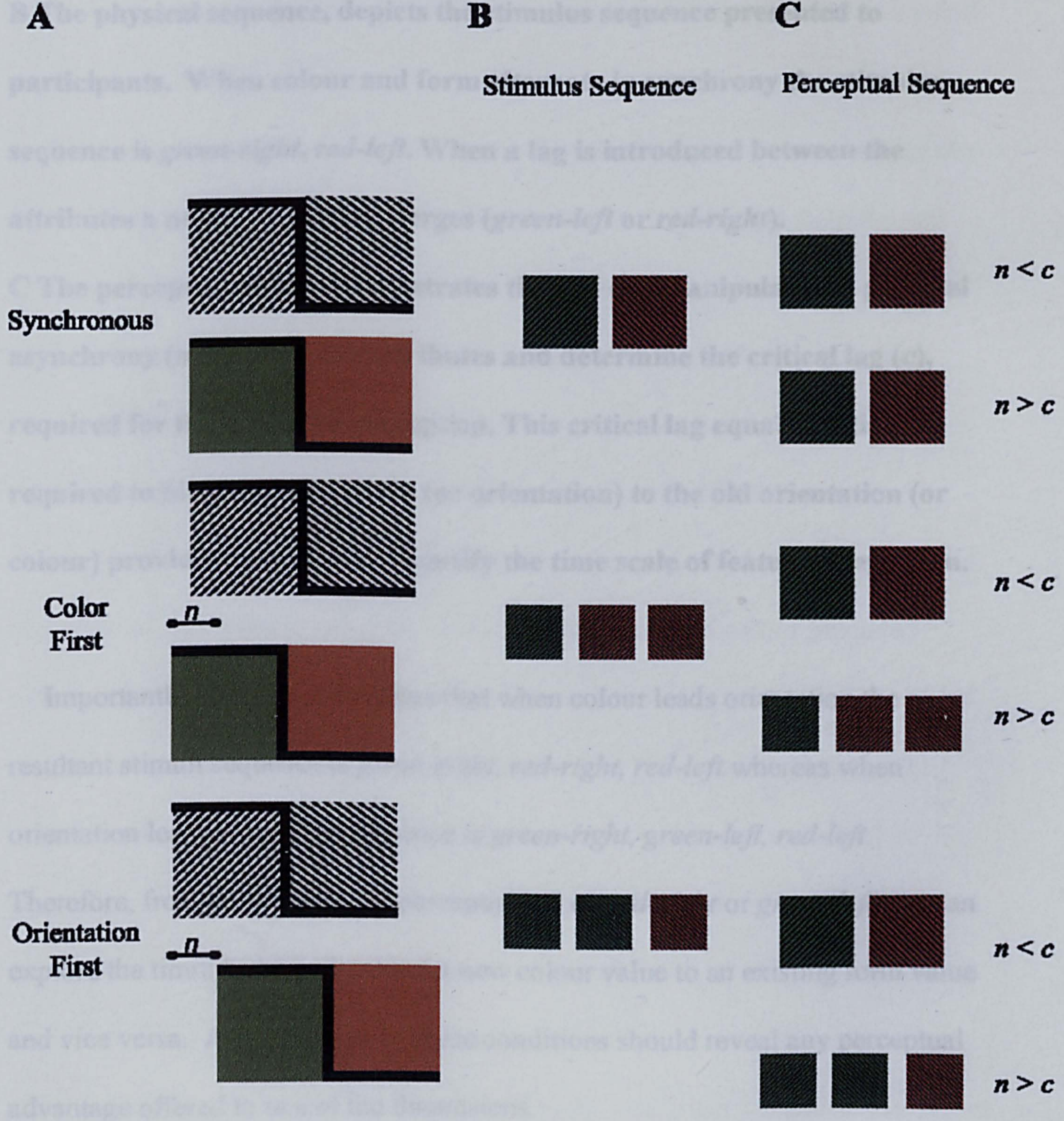
Materials. The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab (Brainard, 1997; Simoncelli, 1997; Pelli, 1997). The frame rate of the monitor was 75 Hz.

We examined the integration of orientation and colour, using the emergence of a new perception from binding. To illustrate, consider Figure 1. in which two orientations (right, 45° and left, -45° relative to the horizontal) alternate with two colours (green and red, see Figure 1). The stimulus sequence alternates between *green-right/red-left* when these attributes are presented in synchrony (Fig 1, synchronous). Desynchronising these attributes produces an emergent perception. In Figure 1. (Colour First, or Form First conditions), the *red-right* perception (in Colour First) or *green-left* perception (in Orientation First) emerges when orientation and colour are asynchronous. Perception of this emergent stimulus[4] (e.g. *red-right*) crucially depends on integrating a new value of the leading attribute (e.g red) with an existing value of the orthogonal dimension (e.g. right). Therefore, the time required to perceive this emergent stimulus is the time required to bind colour and orientation. Specifically, we can manipulate the physical asynchrony (in Figure 1, lag (*n*)) between orientation

---

[4] The notion emergent perception should not be confused with the illusory conjunctions perceived in Triesman's (1982) experiments. Here, the emergent stimulus is physically presented.

and colour and use the emergent perception (*red-right* vs. *green-left*) to determine the critical lag (c) at which the attributes are successfully integrated.



<u>Figure 1</u>. The Emergence of a Perception from Binding.

A depicts the two attributes to be bound (colour, alternating between green and red and orientation, alternating between right and left). CIE

chromaticity coordinates: green [L= 7.77, x = 0.31, y = 0.52] and red [L = 7.9, x = 0.54, y = 0.32]. (Luminance values measures in candelas per square metre).

B The physical sequence, depicts the stimulus sequence presented to participants. When colour and form alternate in synchrony the stimulus sequence is *green-right, red-left.* When a lag is introduced between the attributes a new perception emerges (*green-left* or *red-right*).

C The perceptual sequence, illustrates that we can manipulate the physical asynchrony (*n*) between the attributes and determine the critical lag (*c*), required for the emergent perception. This critical lag equals the time required to bind the new colour (or orientation) to the old orientation (or colour) providing a means to quantify the time scale of feature integration.

Importantly, Figure 1. illustrates that when colour leads orientation the resultant stimuli sequence is *green-right, red-right, red-left* whereas when orientation leads colour the sequence is *green-right, green-left, red-left.* Therefore, from these emergent perceptions (i.e., *red-right* or *green-left*) we can explore the timing required to bind a new colour value to an existing form value and vice versa. A comparison of these conditions should reveal any perceptual advantage offered to one of the dimensions.

We manipulated the leading dimension (colour vs. orientation) to reveal any perceptual asynchrony between these attributes. Here, we attribute any modulation in the threshold required to perceive the emergent perception as arising from a modulation in the perceptual processing of the leading attribute.

The test stimuli spanned 5.8 x.5.8 degrees of visual angle. The orientations and colours used were selected from opposing poles of their attributes to try and control their relative salience.

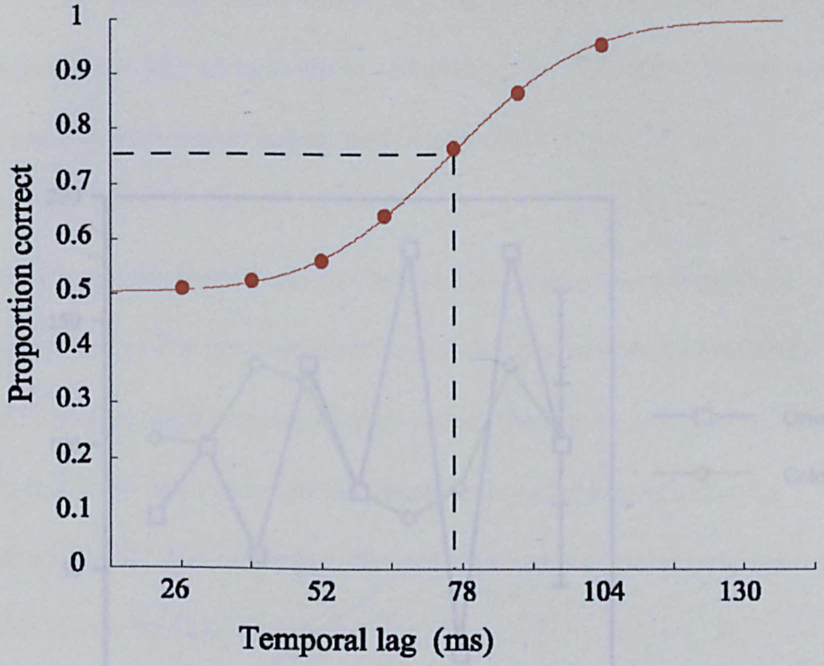
To investigate temporal integration, the stimuli alternated between e.g. *green-right* and *red-left* over a 667 ms interval. In other word, on a given trial there was one alternation between the two main stimuli. We manipulated the temporal asynchrony between colour and orientation by randomly sampling amongst 7 possible temporal asynchronies ranging from 0 ms to 156 ms by equal increments. We introduced an 8th asynchrony of 390 ms to ensure discrimination of the emergent perception on at least one trial. To illustrate, the sequence of *green-right, red-right, red-left* appeared when colour preceded orientation (Colour First, see Figure 1). The sequence of *green-right, green-left, red-left* appeared when orientation preceded colour (Orientation First). The sequence of *green-left, red-left, red-right,* (colour preceding orientation) or *green-left, green-right, red-right* (orientation preceding colour) were included to counterbalance the main stimuli. Likewise the order of both of these conditions was reversed to control for stimulus driven effects.

Participants were tested in two blocks, the trials in which the target stimuli were *green-left* and *red-right* (half) were combined. Likewise the trials in which the target stimuli were *red-left* and *green-right* (half) were combined. This gave a 2-AFC task in which participants had to indicate either whether a *red-right* or a *green-left* appeared or they had to indicate whether a *green-right* or a *red-left* appeared. For example, participants made one key press on a keyboard if they perceived a *red-right* and different key-press if they perceived a *green-left.* For both colour and form first trials there were 40 repetitions for each of the eight temporal lags giving 1280 trials in total.

Colour First and Orientation First trials were randomly interleaved. Participants were instructed to guess if they were unsure. A headrest maintained viewing distance at one metre.

Results

Figure 2 illustrates that for each participant we fitted a cumulative Gaussian curve to the temporal asynchrony data to determine the 75% discrimination threshold of the emergent perceptions (the critical lag).



<u>Figure 2.</u> The 75% threshold lag required for target detection was derived by fitting a cummulative Gaussian curve to the temporal lag data for each participant.

A cummulative Gaussian curve was employed because it is a standard and simple psychometric function with two free parameters (standard deviation and slope) which provided a good fit to the participants' data.

The data from one participant who did not reach threshold performance was discarded. An additional participants' data had to be discarded because his performance was above threshold from the offset. The distribution for orientation and colour first trials across the remaining 8 participants is depicted in Figure 3.

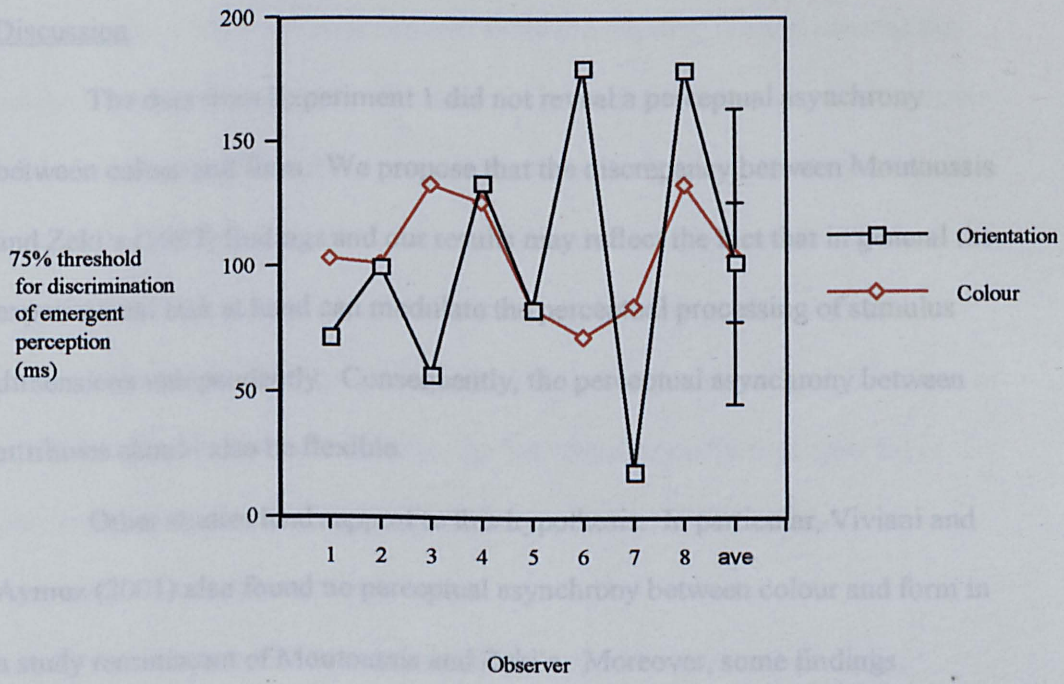


Figure 3. **75% threshold discrimination of the emergent perception for colour and orientation first trials for 8 participants. On average participants required the same time to bind a new colour value to an existing form value and vice versa. Therefore, these results do not support a perceptual asynchrony between the perceptual processing of colour and form. The error bars here and throughout this thesis depict the standard deviation from the mean.**

On average, it took participants 102 ms (s = 24 ms) to bind a new orientation value to an existing colour value. Whereas, it took 104 ms (s = 59 ms) to bind a new colour with an existing orientation value. Therefore there was no perceptual asynchrony between colour and orientation.

Discussion

The data from Experiment 1 did not reveal a perceptual asynchrony between colour and form. We propose that the discrepancy between Moutoussis and Zeki's (1997) findings and our results may reflect the fact that in general the experimental task at hand can modulate the perceptual processing of stimulus dimensions independently. Consequently, the perceptual asynchrony between attributes should also be flexible.

Other studies lend support to this hypothesis. In particular, Viviani and Aymoz (2001) also found no perceptual asynchrony between colour and form in a study reminiscent of Moutoussis and Zeki's. Moreover, some findings contradict this perceptual asynchrony theory (Holcombe and Cavanagh, 2001) or contend that it is only revealed in certain tasks (for example, at high alteration frequencies, Nishida & Johnston, 2002). A flexible account of perceptual processing and consequently of perceptual asynchrony would account for the discrepancy between these results.

It seems likely that perceptual asynchrony between attributes will depend on the relative salience of these dimensions. Specifically, previous literature suggests that the perceptual processing time of an attribute should depend on how informative this dimension is for the task at hand (Oliva and Schyns, 2000;

Goldstone, 1994; Goldstone, 1995; Özgen and Davies, 2002). If observers can easily discriminate between the opposing values of one attribute (e.g. colour; red and green) but have more difficulty discriminating between the values of the other dimension (e.g. orientation; left and right) then this could lead to a difference in processing times between these dimensions. This is because the easily discriminable attribute will enjoy the perceptual advantage. In the current study we selected values from opposing poles of each dimension in an attempt to control the relative salience of colour and orientation. This control of salience may have diminished any perceptual processing advantage offered to one attribute because observers could discriminate equally between the two values of colour and of orientation. Likewise, the perceptual asynchronies reported in previous studies may have arisen because salience was not controlled between dimensions in this way.

An additional methodological difference between the methodology employed in the current experiment and previous studies may account for the current findings. In the current paradigm the participants' task is a 2AFC discrimination task. Recall that Moutoussis and Zeki's (1997a; 1997b) participants were requested to report the colour on one half a screen that corresponded with an orientation on the other half of the screen. This task is difficult and subjective. Whereas in our design the perceptual asynchrony was derived objectively therefore it provided us with a direct measure of this phenomenon.

Experiment 2

Investigating the effect of task requirements on the temporal integration of colour and orientation.

The results from Experiment 1 were inconsistent with previous findings of perceptual asynchrony between colour and form (Moutoussis and Zeki, 1997). To account for the discrepancy between these results and previous findings we proposed that perceptual processing of distinct visual information (for example, colour and orientation) is flexible. Consequently, the perceptual asynchrony between these attributes should also be flexible.

Moreover, although the direction of asynchrony is largely in agreement across previous studies of perceptual asynchrony they differ in magnitude. To recap, Moutoussis and Zeki (1997a; 1997b) revealed a 60 ms temporal asynchrony between color and orientation attributes, and a 118 ms asynchrony between color and motion. In addition, they reported a 50 ms advantage of orientation over motion. Whereas, using the color-contingent motion after effect Arnold *et al* (2001) found an 80 ms advantage of color over motion. In addition, Viviani and Aymoz (2001) reported a 50 ms advantage of color over motion, and of form over motion. However, they did not find such asynchrony between color and form. Moreover, some findings contradict the perceptual asynchrony theory entirely (Holcombe and Cavanagh, 2001) or contend that it is only revealed in certain tasks (for example, for high alteration frequencies, Nishida & Johnston, 2002). To account for these differences we suggest a flexible rather than fixed account of attribute processing and consequently of perceptual asynchrony.

Several lines of evidence converge to suggest that the processing time of attributes is flexible. In particular, studies of reaction time (Posner, 1980), temporal order (Stelmach and Herdman, 1991) and using the speed-accuracy trade-off procedure (Carrasco and McElree, 2001) have revealed a temporal processing advantage for attended information. The categorisation literature has established that participants selectively attend to an attribute that is relevant for the task at hand. For example, the use of different spatial scales appears to be diagnostically driven (Oliva and Schyns, 1997) and colour mediates scene recognition when it is diagnostic for the task at hand (Oliva and Schyns, 2000).

The phenomena known as acquired distinctiveness and equivalence also reveals that the properties of an attribute can be modified with categorisation experience. Research has shown that training can improve an observers' ability to discriminate between two stimuli (Goldstone, 1994). This perceptual learning is manifested in one of two ways, either the observer's perceptual space is shrunk and within category information is compressed (acquired equivalence). In this case any information between two distinctive values is easily confused. Alternatively the perceptual space is stretched (acquired distinctiveness) and the observer is better able to discriminate between different values of a dimension that were previously indiscernible. These categorical effects have been demonstrated for colour perception (Goldstone, 1995; Özgen and Davies, 2002). Furthermore, research has demonstrated a perceptual advantage when the values of an attribute can be easily discriminated (Goldstone, 1994; Goldstone, 1995; Özgen and Davies, 2002). To illustrate, Özgen and Davies, (2002) trained observers to discriminate between two colours that were previously within a category (e.g. blue 1 and blue 2). Post training same-different judgements revealed improved discrimination between pairs of colours that cross this new boundary a phenomenon known as acquired distinctiveness. Therefore, one way to manipulate the perceptual processing time of an attribute might be to manipulate how discriminable the values along this dimension are. By differentially manipulating the number of values of two attributes we should be able to differentially modulate the perceptual processing time of each attribute. In turn, we might also modulate the perceptual asynchrony between these attributes.

In sum, categorisation studies suggest that the task at hand will influence the attribute extracted by the visual system. If the task can influence which attribute is attended it seems likely from the attention literature that this attribute will be processed faster. Here, we examined how the task at hand modulates the integration of two stimulus attributes (namely, colour and spatial frequency) into a unitary perception.

Therefore, in Experiment 2 we examined whether the perceptual processing of colour and orientation can be modulated by task requirements. Consequently, we can also examine whether the perceptual asynchrony between these attributes is modulated. The paradigm developed in Experiment 1 was employed to examine whether task requirements can modulate the perceptual processing time of two attributes.

In a between-participants design participants were randomly assigned to one of two conditions, Multi-colour (Figure 7) or Multi-orientation (Figure 8) in which multiple values of this attribute were employed to decrease discriminability of this dimension. We predicted that by decreasing how discriminable one attribute was (e.g. multi-colour) participants would depend more on the orthogonal dimension (e.g.orientation) to perform the task. Consequently, perceptual processing of the "less discriminable" dimension should be slowed relative to the orthogonal dimension.

Method

Participants. 20 University of Glasgow students (9 male and 11 female under 35 years of age) with normal or corrected to normal vision were paid to participate in the experiment. All participants were screened for colour blindness using the Ishihara tests for coloured blindness (1978) to exclude any with colour blindness.

Stimuli. Stimuli spanned 4 x 4 degrees of visual angle. Stimuli were generated from 2D white noise using a rectangular filter (i.e. without attenuation). Oriented white noise rather than gratings were employed because it is more difficult to match noise across frames therefore apparent motion across trials is less likely.

We investigated 7 possible temporal asynchronies ranging from 13 ms to 93 ms by equal increments. An 8th asynchrony of 200 ms was also investigated. The paradigm developed in Experiment 1 was employed.

To investigate the effect of task requirements on perceptual asynchrony we employed this paradigm in two conditions, one in which we decreased the discriminability of orientation (multi-orientation condition) and one in which we decreased the discriminability of colour (multi-colour condition). We employed QUEST (Watson and Pelli, 1979) to calibrate psychologically equi-distant colour and orientation values.

QUEST (Watson and Pelli, 1979) is a Bayesian psychometric adaptive method that was used in the current experiment to determine 8 psychologically equi-distant colours and 8 psychologically equi-distant orientations. For this procedure, on a given trial, participants made same-different judgements about two simultaneously presented colours or two simultaneously presented orientations. They made one key press if they perceived the simultaneously presented stimuli as the same and a different key press if they perceived these stimuli as different. Using a linear function colours were manipulated from red to green along the x-y axis of the CIE colour space. The CIE chromaticity co-ordinates of the original red and green between which the equi-distant values were calibrated are (red, $L = 8$, $x = 0.54$, $y = 0.32$ and green, $L = 8$, $x = 0.34$, $y = 0.54$). Orientation was similarly manipulated in radians from the vertical origin to 0.78 radians (45°). Four equi-distant values that deviated to the left of the vertical and four values that deviated to the right of the horizontal were selected independently. Using QUEST eight values of colour and orientation were calibrated for three observers in both the colour and orientation conditions. We selected the data from the participant that was intermediary between the two other observers to determine the colour and orientation values for the experiment. Figure 4. and Figure 5. display the CIE chromaticity coordinates of the colours and the angles of the eight orientations employed respectively. The eight orientations and colours were equally divided into left or right attribute values and red or green attribute values respectively.

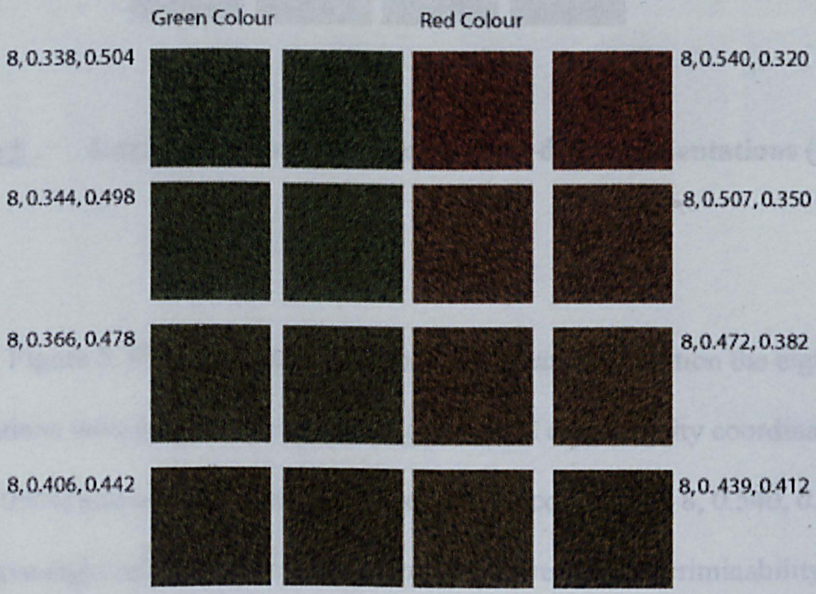


Figure 4. **CIE chromaticity coordinates (L.x.y.) of the psychologically equi-distant colours (j.n.d. = 75%).**

Figure 4. illustrates that in the multi-colour condition the eight colours were paired with orientation 1 (left, -33) and orientation 8 (right, 35).

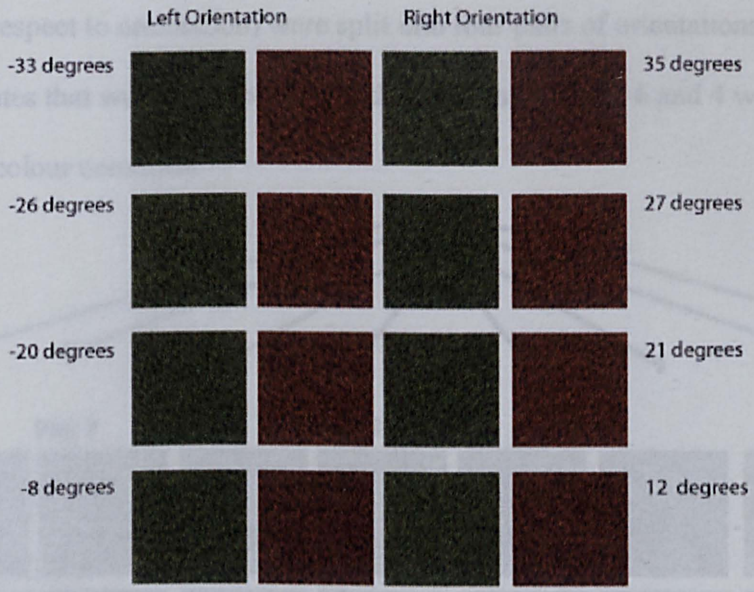


Figure 5 . **Angles of the psychologically equi-distant orientations (j.n.d. = 75%)**

Figure 5. illustrates that in the multi-orientation condition the eight orientations were paired with colour 1 (green, CIE chromaticity coordinates 8, 0.338, 0504) and colour 8 (red, CIE chromaticity coordinates 8, 0.540, 0.320). This gave eight red and eight green stimuli of decreasing discriminability (with respect to orientation) in the multi-orientation condition and eight left and eight right stimuli of decreasing discriminability (with respect to colour) in the multi-colour condition. Thus as in Experiment 1 four categorizations were possible: *green-right*, *green-left*, *red-right* and *red-left*.

For the multi-colour condition the 16 stimuli of decreasing discriminability (with respect to colour) were split into four pairs of colours. In the multi-orientation condition the 16 stimuli of decreasing discriminability (with respect to orientation) were split into four pairs of orientations. Figure 6. illustrates that we paired colour 1 with 8, 2 with 7, 3 with 6 and 4 with 5 in the multi-colour condition.

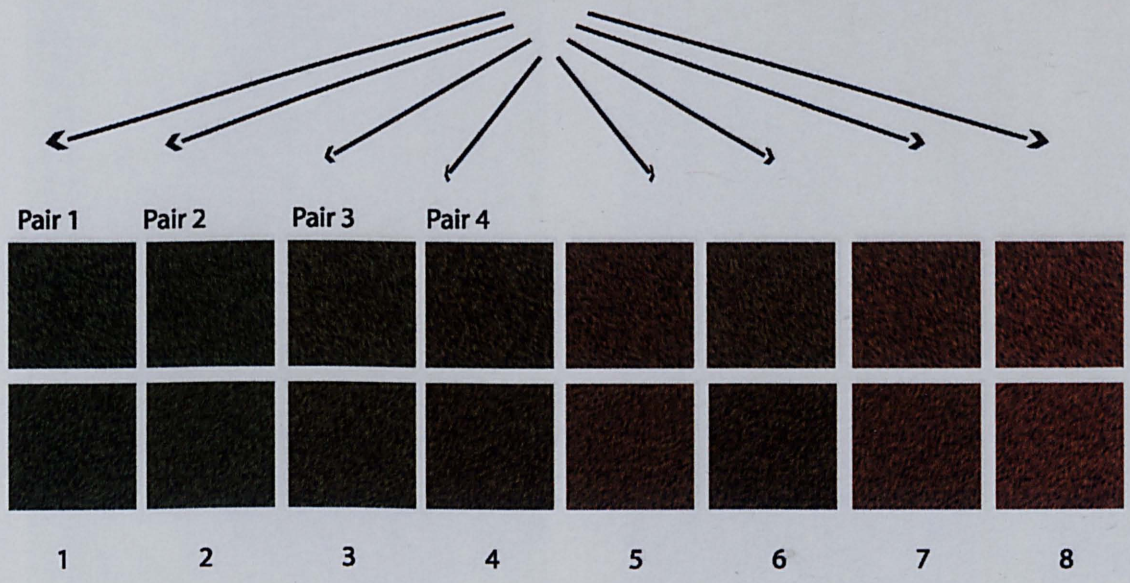


Figure 6. **Multi-colour pairs, we paired colour 1 with 8, 2 with 7, 3 with 6 and 4 with 5. The orientations employed were orientations 1 (left) and 8 (right).**

Figure 7. illustrates that we paired orientation 1 with 8, 2 with 7, 3 with 6 and 4 with 5 in the multi-orientation condition. From Figure 8 it is clear that the stimuli with extreme colours (pair 1, colours 1 and 8) in the multi-colour condition were physically identical to the stimuli with the extreme orientations (pair 1, orientations 1 and 8) in the multi-orientation condition. Therefore, for the purpose of our analysis data from these trials could be compared directly.

There were 28 stimuli in total. For each condition each colour-orientation pair was employed, and randomly presented, in the paradigm described in Experiment 1.

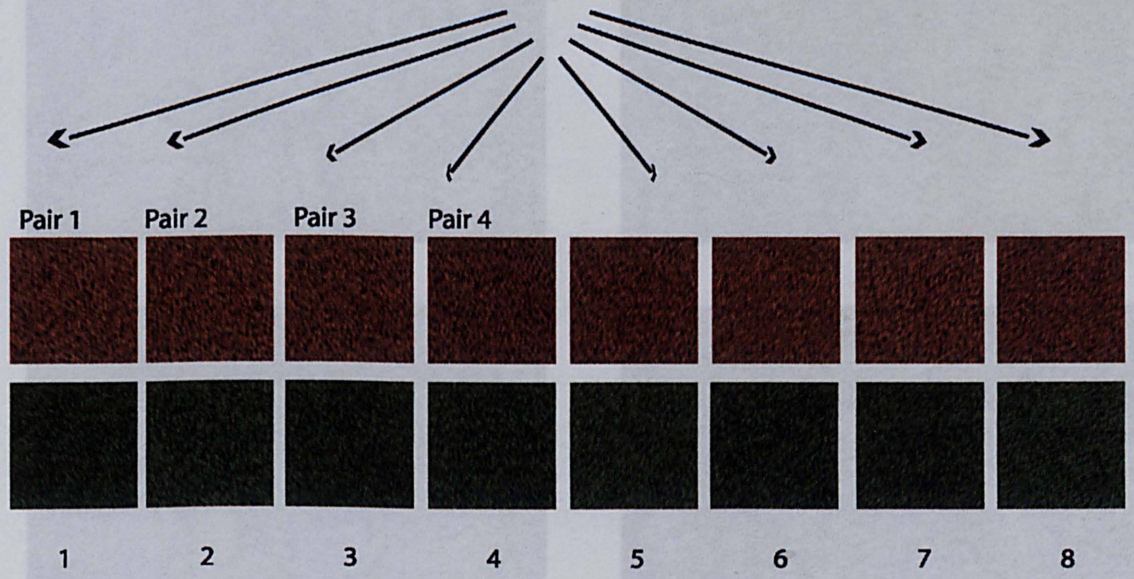
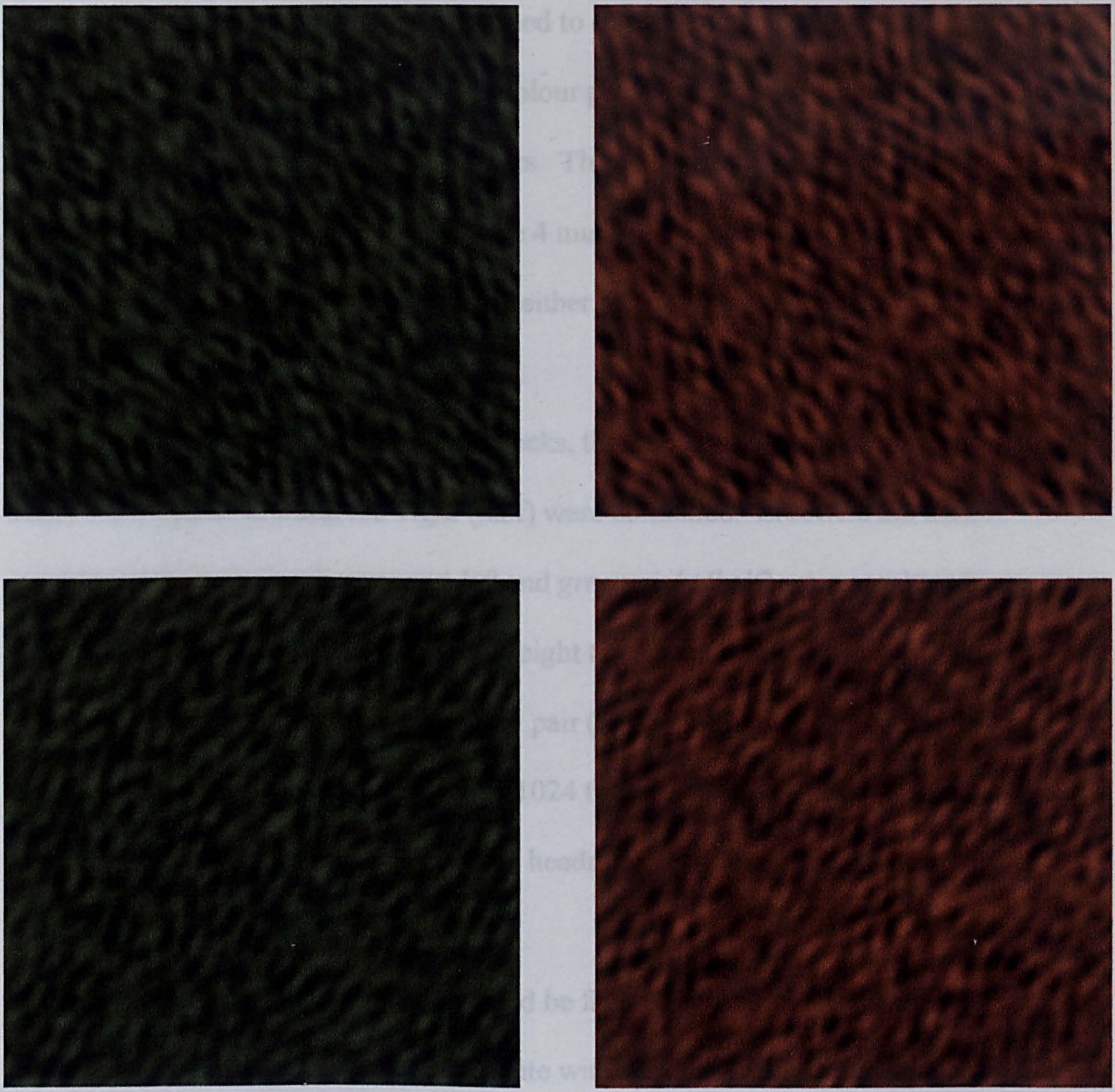


Figure 7. **Multi-orientation pairs, we paired orientation 1 with 8, 2 with 7, 3 with 6 and 4 with 5. The colours employed were colours 1 (green) and 8 (red).**



<u>Figure 8.</u> This figure depicts the stimuli employed in Pair 1 in both the multi colour and multi orientation conditions. This pair was identical across conditions.

<u>Procedure.</u> The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab (Brainard, 1997; Simoncelli, 1997; Pelli, 1997)

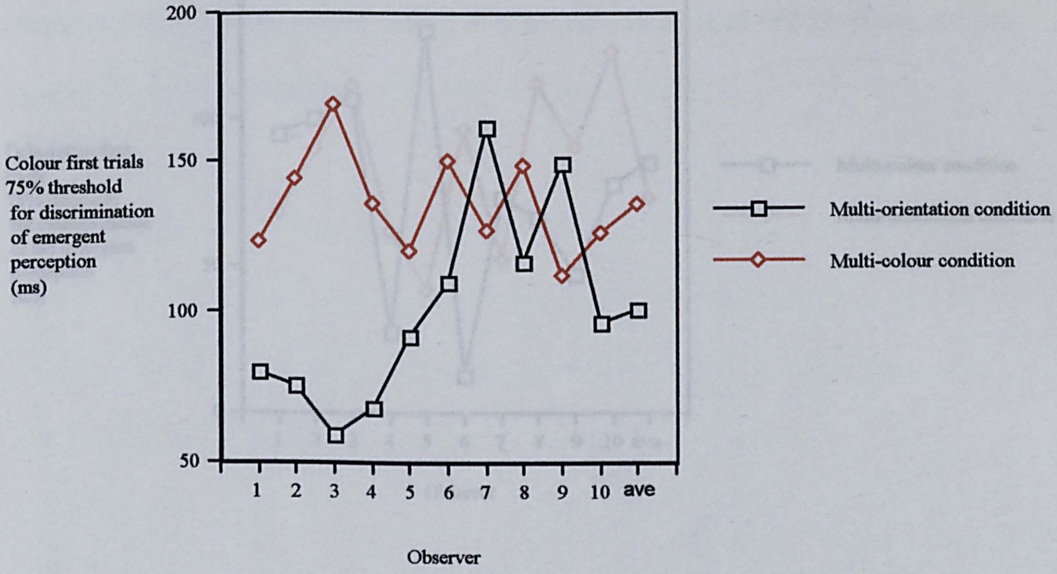
Participants were randomly assigned to one of two conditions (multi-colour or multi-orientation). The multi-colour participants were shown the 16 stimuli comprising the 4 multi-colour pairs. The multi-orientation participants were shown the 16 stimuli comprising the 4 multi-orientation pairs. In a 2-AFC task, participants had to indicate whether either a *red-left* or a *green-right* or either a *green-right* or a *red-left* appeared.

Participants were tested in two blocks, the trials in which the target stimuli were *green-left* and *red-right* (half) were combined. Likewise the trials in which the target stimuli were *red-left* and *green-right* (half) were combined. There were 16 repetitions for each of the eight temporal lags (16*8=128). This was replicated for each colour-orientation pair (4*128=512). Colour First and Form First trials were interleaved giving 1024 trials in total. Participants were instructed to guess if they were unsure. A headrest maintained viewing distance at one metre.

We predicted that observers should be faster at processing the attribute which is easier to discriminate (the attribute with only two values) than the attribute which is difficult to discriminate (the attribute with multiple values). Consequently, observers should require less time to perceive the emergent perception when it results from the integration of a new value of the easily discriminable attribute with an old value of the less discriminable attribute. In addition, if the requirements of the task modulate the perceptual processing for colour and spatial frequency by an unequal amount then the perceptual asynchrony between these attributes should also be modulated.

Results

Data from stimuli Pair 1 (i.e. when the stimulus was identical across experimental condition) in each condition was extracted for analysis. For 20 participants, we fitted a cumulative Gaussian curve to this temporal asynchrony data to determine the 75% threshold detection of the emergent perceptions separately for colour and orientation first trials. We then averaged the critical lags derived across participants for both the multi-colour and the multi-orientation conditions. Figure 9. illustrates that for colour first trials participants required 101 ms to discriminate the emergent perception in the multi-orientation condition and 136 ms in the multi colour condition.



<u>Figure 9.</u> 75% threshold discrimination of the emergent perception for colour first trials for 10 participants in the multi-orientation and multi-colour conditions.

For orientation first trials participants required 73 ms to discriminate the emergent perception in the multi-orientation condition and 85 ms in the multi colour condition (see Figure 10.).

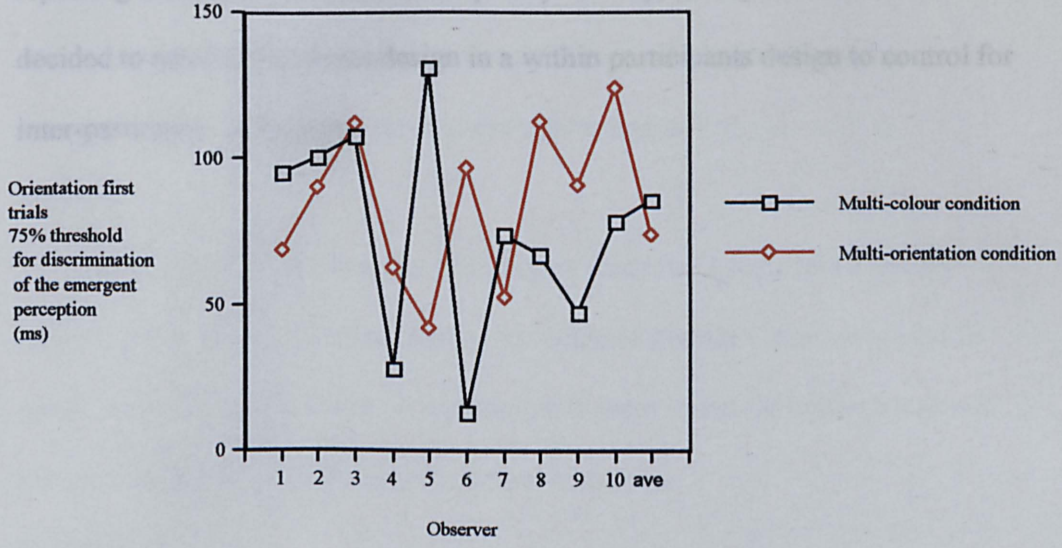


Figure 10. **75% threshold discrimination of the emergent perception for orientation first trials for 10 participants in the multi-orientation and 10 participants on the multi-colour condition.**

However, an ANOVA revealed no significant interaction between the experimental conditions $F(1, 18) = 1.479$, $p = 0.23$.

Discussion

We found no significant interaction between experimental conditions. From the data there does seem to be a general trend for an increased perceptual lag in colour first trials in the multi colour condition. However, there is clearly no such trend for orientation first trials. In retrospect it seems plausible that on orientation first trials, apparent motion may have arisen from changes in the value of orientation between stimuli which participants could have used to complete the task. We attempted to overcome this confound in Experiment 4 by replacing orientation with spatial frequency. Firstly, in Experiment 3, we decided to employ the above design in a within participants design to control for inter-participant variability.

Experiment 3

Investigating the effect of task requirements on the temporal integration of colour and orientation in a within participants design.

In Experiment 3 we replicated Experiment 2 in a within participants design in an attempt to control the variability between participants.

Methods.

Participants. 4 University of Glasgow students (1 male and 3 female under 35 years of age) with normal or corrected to normal vision were paid to participate in the experiment. All participants were tested for colour blindness using the standard Ishihara tests for colour-blindness.

Procedure.

The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab (Brainard, 1997; Simoncelli, 1997; Pelli, 1997).

This experiment differed from Experiment 2 only in that the same participants were tested in both the multi orientation and the multi colour conditions. Half of the participants were tested in the multi colour condition first and the remaining participants were tested in the multi orientation condition first. Therefore, there were 2048 trials in total (1024 multi orientation and 1024 multi colour trials).

Results

For each participant, we fitted a cumulative Gaussian curve to the temporal asynchrony data to determine the 75% threshold detection of the emergent perceptions separately for colour and orientation first trials. We then averaged the critical lags derived across participants. For orientation first trials (see Figure 11) participants required 36 ms to discriminate the emergent perception in the multi-orientation condition and 35 ms in the multi colour condition. Clearly, there was no increase in the time required to integrate a new colour value with an existing orientation value between experimental conditions.

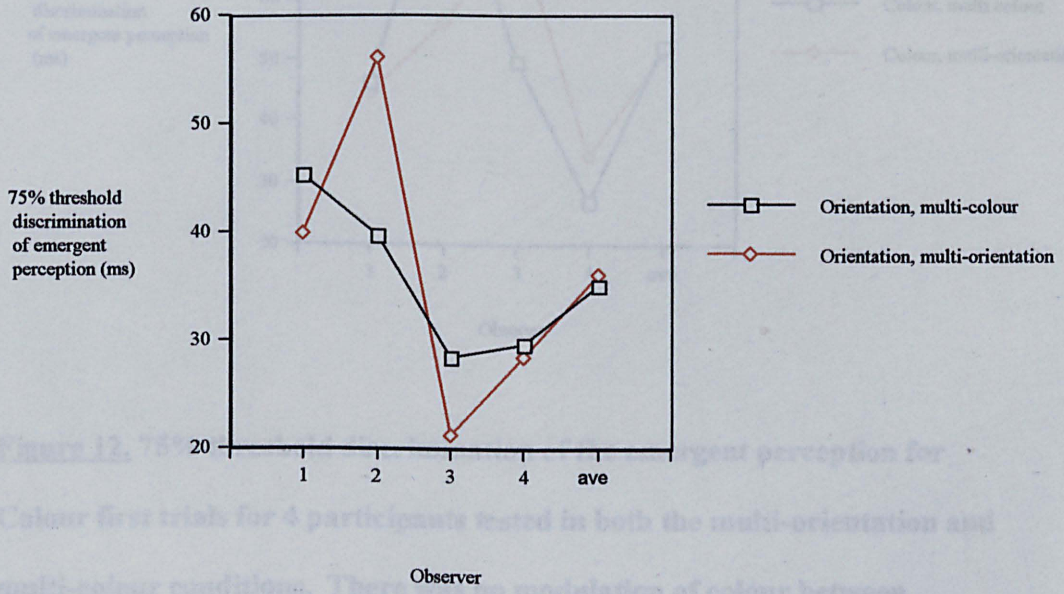


Figure 11. 75% threshold discrimination of the emergent perception for Orientation first trials for 4 participants tested in both the multi-orientation and multi-colour conditions. There was no modulation of orientation between conditions.

For colour first trials (see Figure 12) participants required 51 ms to discriminate the emergent perception in the multi-orientation condition and 52 ms in the multi colour condition. Again, there was clearly no increase in the time required to bind a new orientation value with an existing colour value between experimental conditions.

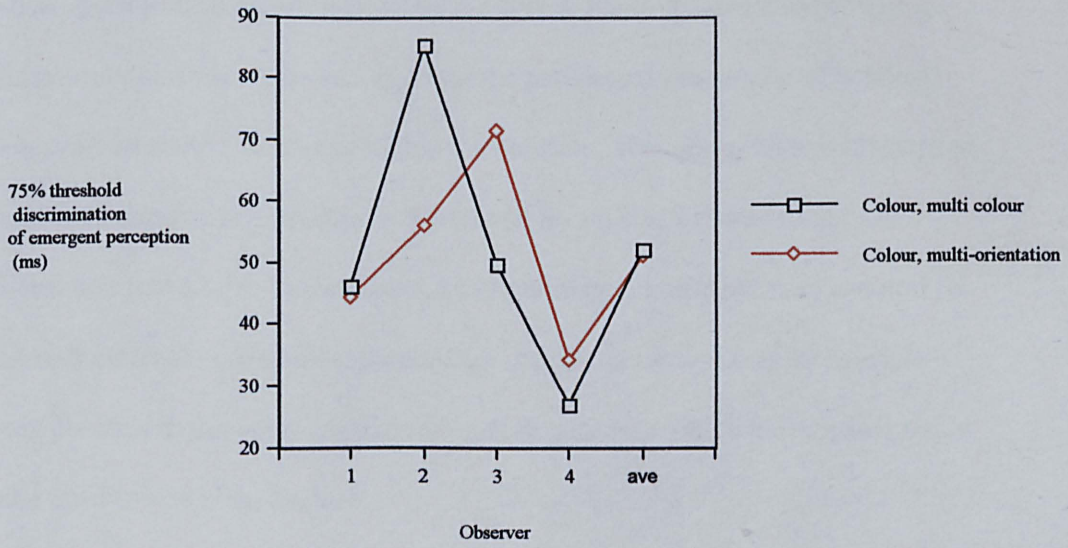


Figure 12. **75% threshold discrimination of the emergent perception for Colour first trials for 4 participants tested in both the multi-orientation and multi-colour conditions. There was no modulation of colour between conditions.**

Discussion

Clearly the integration of colour and orientation was not modulated by the experimental task. In retrospect because participants were sensitised to one dimension (e.g. colour) and then a second dimension (e.g. orientation) the null effect may have arisen from cross over effects induced by testing the same participants in both tasks. Specifically an observer that initially learned to use colour to perform the task (multi orientation condition) may continued to rely more on colour when subsequently tested in the condition (multi colour condition) where we would expect them to rely more on orientation.

Experiment 4

In Experiment 4 we examined whether the perceptual asynchrony in binding two sources of information can be modulated by task requirements. In Experiment 2 we found that the integration of a new colour value with an existing orientation value was significantly modulated by the task at hand. It seems likely that the attentional demands of the task sped up the perceptual processing of colour when this attribute was more reliable for the task. Therefore, feature integration was accelerated in this condition. However, no such effect was found for orientation first trials. In retrospect, an experimental confound may account for this null effect for orientation processing. Apparent motion may have arisen from changes in the value of orientation across stimuli which participants could have used to complete the task.

In Experiment 4 we set out to override this methodological problem. Here, we replicated Experiment 2 however the multi-orientation condition was replaced by a multi-spatial frequency condition.

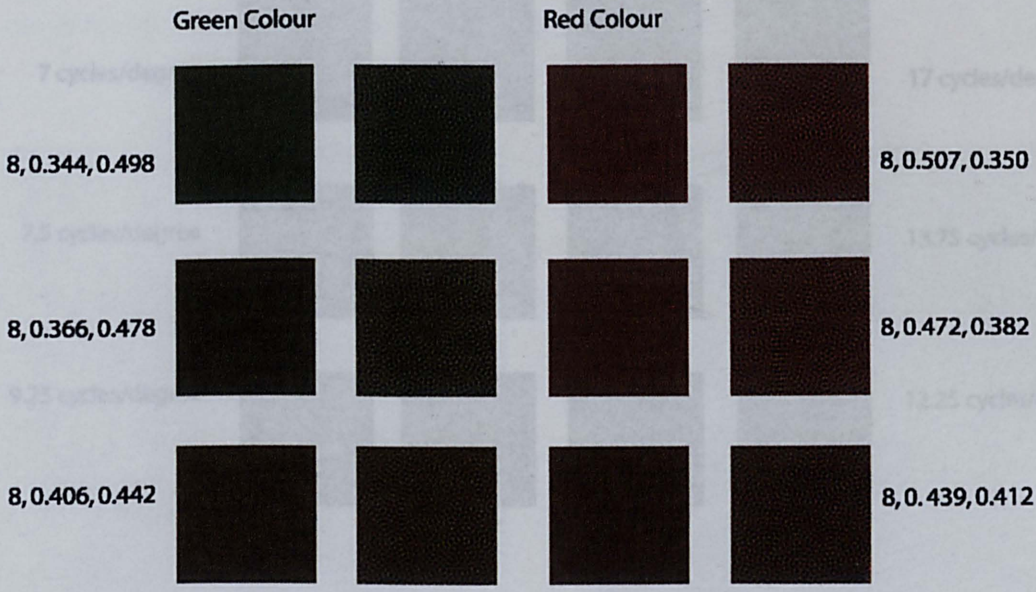
Method

Participants. 16 University of Glasgow students (5 male and 11 female under 35 years of age) with normal or corrected to normal vision were paid to participate in the experiment. All participants were tested for colour blindness using the Ishihara tests for coloured blindness (1978).

Stimuli. Stimuli spanned 4 x 4 degrees of visual angle. Once more stimuli were generated from 2D white noise using a rectangular filter (i.e. without attentuation). 7 possible temporal asynchronies ranging from 13 ms to 93 ms by equal increments—the 8th asynchrony was 200 ms were investigated using the paradigm developed in Experiment 1.

To investigate the effect of task requirements on perceptual asynchrony we employed this paradigm in two conditions, one in which we decreased the discriminability of spatial frequency (multi-spatial frequency condition) and one in which we decreased the discriminability of colour (multi-colour condition).

Six of the eight psychologically equi-distant colours employed in Experiment 2 were used in the current experiment. In addition, using QUEST six psychologically equi-distant spatial frequencies were calibrated for a threshold performance of 75%. Figures 12 and 13. display the CIE chromaticity coordinates of the six colours and the low-pass cut-off for each of the six orientations employed respectively. The six colours and six spatial frequencies were equally divided into red or green and fat or thin attribute values respectively.



<u>Figure 13.</u> **CIE chromaticity coordinates (L.x.y.) of the psychologically equi-distant colours (j.n.d. = 75%).**

Figure 13. illustrates that in the multi-colour condition the six colours were paired with spatial frequency 2 (cut-off at 7.5 cycles per degree) and spatial frequency 5 (cut-off at 13.75 cycles per degree).

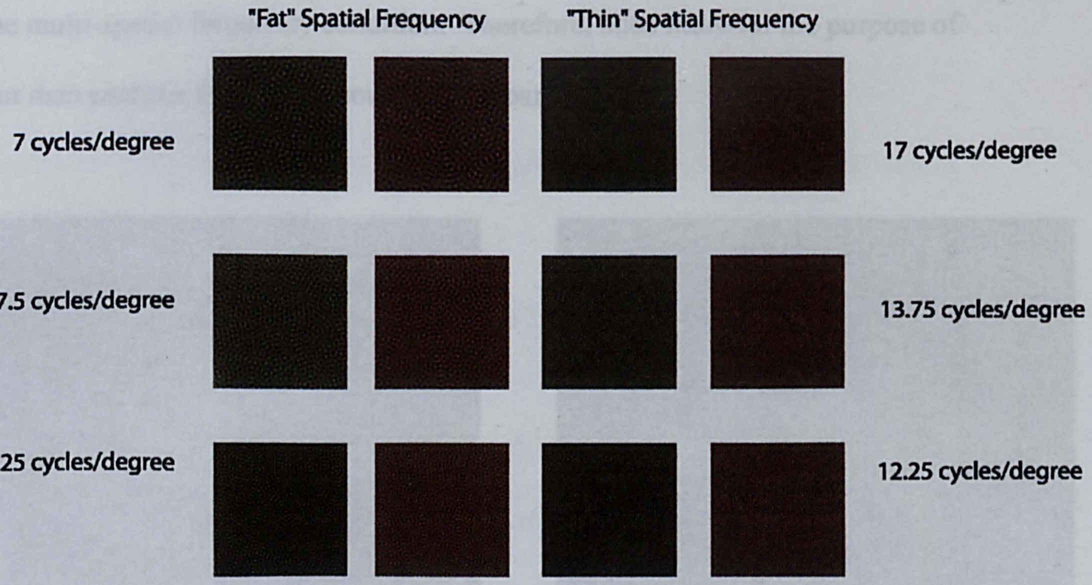


Figure 14. **Low pass cut-off for each of the psychologically equi-distant spatial frequencies (j.n.d. 75%).**

Figure 14. illustrates that in the multi-spatial frequency condition the six spatial frequencies were paired with colour 2 (green, CIE chromaticity coordinates 8, 0.366, 0.478) and colour 5 (red, CIE chromaticity coordinates 8, 0.472, 0.382). This gave six red and six green stimuli of decreasing discriminability (with respect to spatial frequency) in the multi-spatial frequency condition and six fat and six thin stimuli of decreasing discriminability (with respect to colour) in the multi-colour condition. Thus as in previous the experiments four categorizations were possible: *fat-green*, *thin-green*, *fat-red* and *thin-red*. Figure 15 illustrates that the stimuli with extreme colours (pair 2, colours 2 and 5) in the multi-colour condition were physically identical to the

stimuli with the extreme spatial frequencies (pair 2,spatial frequency 2 and 5) in the multi-spatial frequency condition. Therefore, once more for the purpose of our data analysis these trials could be compared directly.

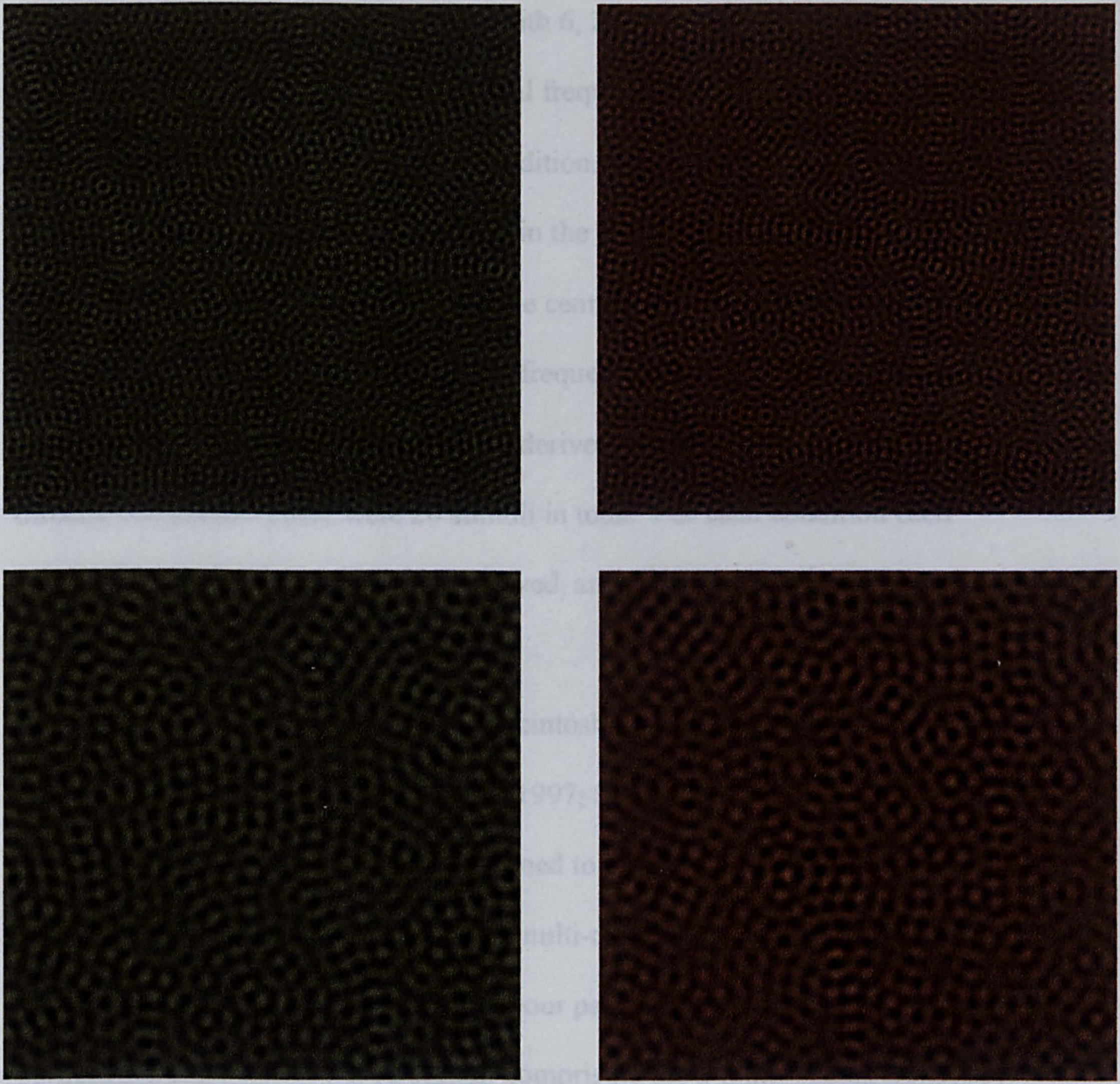


Figure 15 **This figure depicts the stimuli employed in Pair 2 in both the multi colour and multi spatial frequency conditions. This pair was identical across conditions.**

For the multi-colour condition the 12 stimuli of decreasing discriminability (with respect to colour) were split into three pairs of colours. In the multi-spatial frequency condition the 12 stimuli of decreasing discriminability (with respect to spatial frequency) were split into three pairs of spatial frequency. We paired colour 1 with 6, 2 with 5, and 3 with 4 in the multi-colour condition. We paired spatial frequency 1 with 6, 2 with 5, and 3 with 4 in the multi-spatial frequency condition. Note that the stimuli with central colours, (pair 2, colours 2 and 5) in the multi-colour condition were physically identical to the stimuli with the central spatial frequency (pair 2, orientations 2 and 5) in the multi-spatial frequency condition. Thus once more for the purpose of our data analysis data derived from these trials could be directly compared. There were 20 stimuli in total. For each condition each colour-spatial frequency pair was employed, and randomly presented, in the paradigm described in Experiment 1.

Procedure. The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab (Brainard, 1997; Simoncelli, 1997; Pelli, 1997)

Participants were randomly assigned to one of two conditions (multi-colour or multi-spatial frequency). The multi-colour participants were shown the 12 stimuli comprising the 3 multi-colour pairs. The multi-spatial frequency participants were shown the 12 stimuli comprising the 3 multi-spatial frequency pairs. In a 2-AFC task, participants had to indicate whether either a *thin-red* or a *fat-green* or either a *thin-green* or a *fat-red* appeared.

Participants were tested in two blocks, the trials in which the target stimuli were *thin-red* and *fat-green* (half) were combined. Likewise the trials in which the target stimuli were *thin-green* and *fat-red* (half) were combined. There were 32 repetitions for each of the eight temporal lags (32*8=256). This was replicated for each colour-spatial frequency pair (3*256=768). Colour First and Form First trials were interleaved giving 1536 trials in total. Participants were instructed to guess if they were unsure. A headrest maintained viewing distance at one metre.

Results

For 16 participants, we fitted a cumulative Gaussian curve to the temporal asynchrony data to determine the 75% threshold detection of the emergent perceptions separately for colour and spatial frequency first trials. We then averaged the critical lags derived across participants for both the multi-colour and the multi-spatial frequency conditions.

Figure 16. illustrates that for colour first trials participants required 49 ms to discriminate the emergent perception in the multi-spatial frequency condition and 76 ms in the multi colour condition.

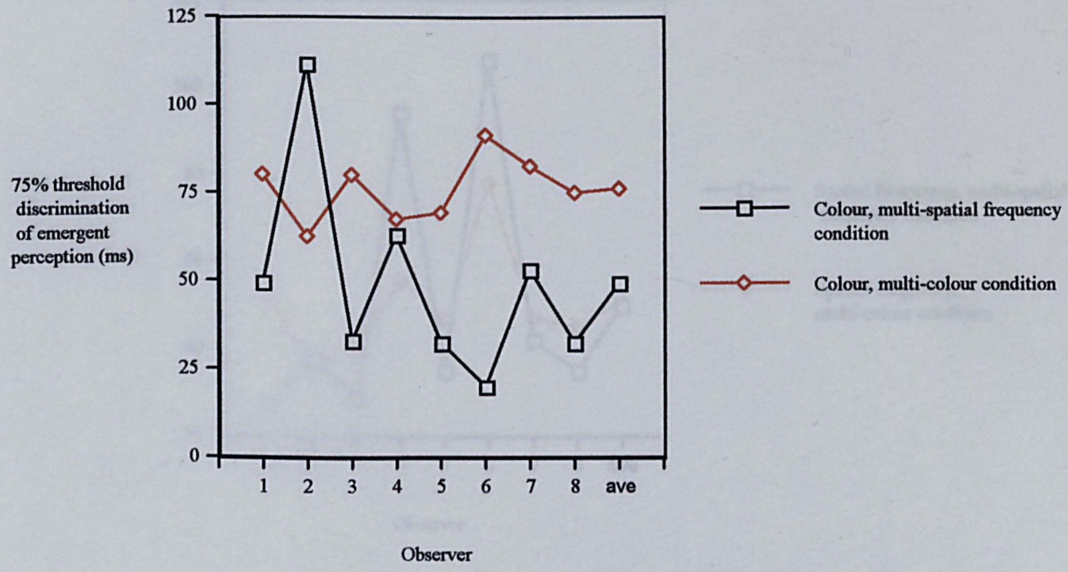


Figure 16. **75% threshold discrimination of the emergent perception for colour first trials for 16 participants in the multi-spatial frequency and the multi-colour conditions.**

Figure 17. illustrates that for spatial frequency first trials participants required 50 ms to discriminate the emergent perception in the multi-spatial frequency condition and 51 ms in the multi colour condition.

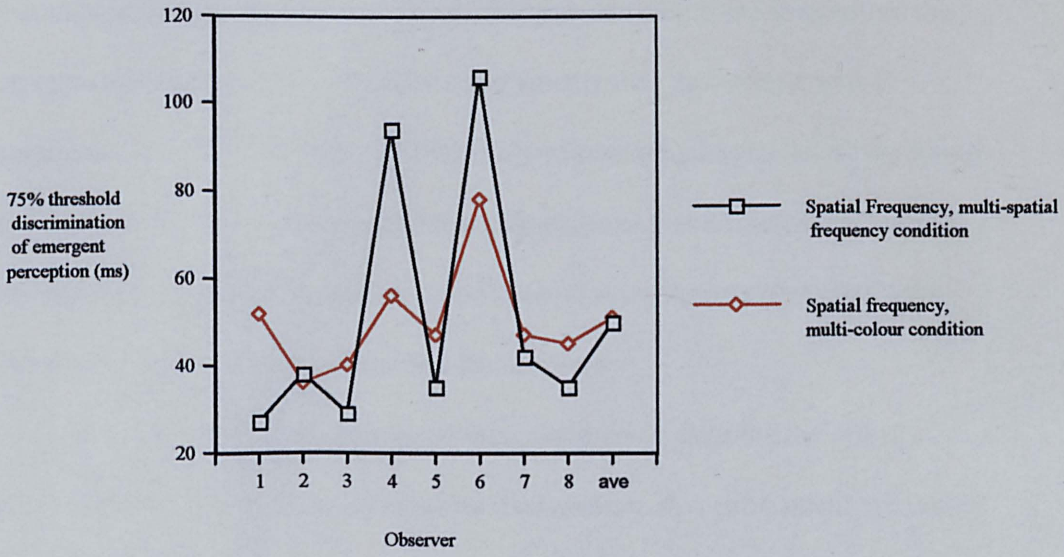


Figure 17. 75% threshold discrimination of the emergent perception for spatial frequency first trials for 16 participants in the multi-spatial frequency and the multi-colour conditions.

Once more an ANOVA did not reveal a significant interaction between the two experimental conditions, F(1, 14) = 2.4, $p = 0.14$.

Discussion

Once more we found no significant interaction between experimental conditions. Again, there does seem to be a general trend for an increased perceptual lag in colour first trials in the multi colour condition. However, there is clearly no such trend for spatial frequency first trials. Therefore, it seems plausible that a for spatial frequency first trials there may be a residual confound of apparent motion.

General Discussion

In Experiment 1 we developed a novel paradigm to examine the temporal dynamics of feature integration. This technique was employed to examine the perceptual asynchrony between colour and orientation. In contrast with Moutoussis and Zeki's (1997a; 1997b) study of perceptual asynchrony we found no asynchrony between these attributes. We propose that a flexible account of attribute processing and consequently perceptual asynchrony may explain the discrepancy between our findings and these results.

In Experiment 2 we developed this paradigm to examine the effect of task requirements on feature integration. However, in this experiment we found no significant interaction between experimental conditions. There did seem to be a general trend for increased temporal lag in colour first trials between conditions. However, we found no such trend for orientation (in Experiment 2) or spatial frequency (in Experiment 4). In retrospect, this null effect may have. been produced by an experimental confound. Namely, on a given trial presenting a sequence of changing orientations or spatial frequencies may have given rise to apparent motion.

In Experiment 3 no effect of the task on the integration of colour and orientation was found. It seems likely that testing the same participants in both conditions produced cross over effects.

Chapter 3

Investigating the influence of attention on feature integration.

In Chapter 2 we examined how the requirements of the task modulate the perceptual asynchrony between two attributes to be bound into a unitary perception. Presumably any such modulation would arise because observers selectively attend to the attribute that is more informative for the task at hand. In Chapter 3 we examined the influence of attention on perceptual asynchrony directly.

Several lines of evidence converge to suggest that attention plays an important role in the integration of functionally processed information (Treisman and Gelade, 1980; Reynolds and Desimone, 1999; Yershurun and Carrasco, 1998). However, exactly how attention modulates the temporal integration of information remains unclear. Studies suggest that attention speeds up the processing of attended information (Posner *et al*,1980; Stelmach and Herdman, 1991; Carrasco and McElree, 2001). Presumably attention can operate on each processing dimension independently. Therefore, attention could potentially modulate perceptual asynchrony by differentially speeding up the processing of each dimension. In other words, attention may enhance temporal integration by decreasing the perceptual asynchrony between attributes. Alternatively, attention may speed up the perceptual processing of each attribute by an equal amount thereby having no effect on perceptual asynchrony.

Using the paradigm developed in Chapter 2, in Chapter 3 we examined how attention modulates the integration of color and form into a unitary perception in an attempt to tease apart these possible influences of attention on feature integration. In Experiment 5 we examined the influence of attention on 6 stimuli arranged in a line. In Experiment 6 we extended this study to stimuli arranged radially across the visual field.

Results suggest that attending to the location of an object decreases the time that observers require to integrate its defining attributes. In addition, we found a perceptual advantage for form over colour in both attended and unattended conditions. Consequently, the perceptual asynchrony between these attributes was not significantly modulated by attention. We conclude that attending to the location of an object enhances the integration of its defining attributes by speeding up the perceptual processing of each attribute. Moreover, the perceptual asynchrony between attributes remains constant across attended and unattended conditions because attention seems to offer each processing dimension an equal processing advantage.

Experiment 5

Investigating the influence of attention on the integration of colour and form.

To examine the possible influence of attention on feature integration we employed the methodology developed in Chapter 2 for 6 stimuli arranged in a line. Here, we were interested in how attention modulates the integration of colour and form.

Using the paradigm developed in Chapter 2 we derived the temporal asynchrony observers required to discriminate the emergent perception independently for each stimulus location. Two variables were manipulated. The first variable was the leading attribute, (colour vs form). The second variable was spatial attention (left and right of the line of stimuli). Consequently, we could compute the influence of attention on each attribute independently. Moreover, we can compute any perceptual advantage that attention offers to either dimension by comparing these conditions.

Methods

Participants Twenty observers (under 30 years of age), with normal or corrected to normal vision participated in the experiment. All observers were tested for colour blindness using the standard Ishihara tests for color blindness.

Materials. The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab (Brainard, 1997; Simoncelli, 1997; Pelli, 1997).

In Experiment 5 we examined how spatial attention modulates the integration of form and color, using the paradigm we developed in Chapter 2 (illustrated in Figure 18). This paradigm was employed independently in each of the six shape positions.

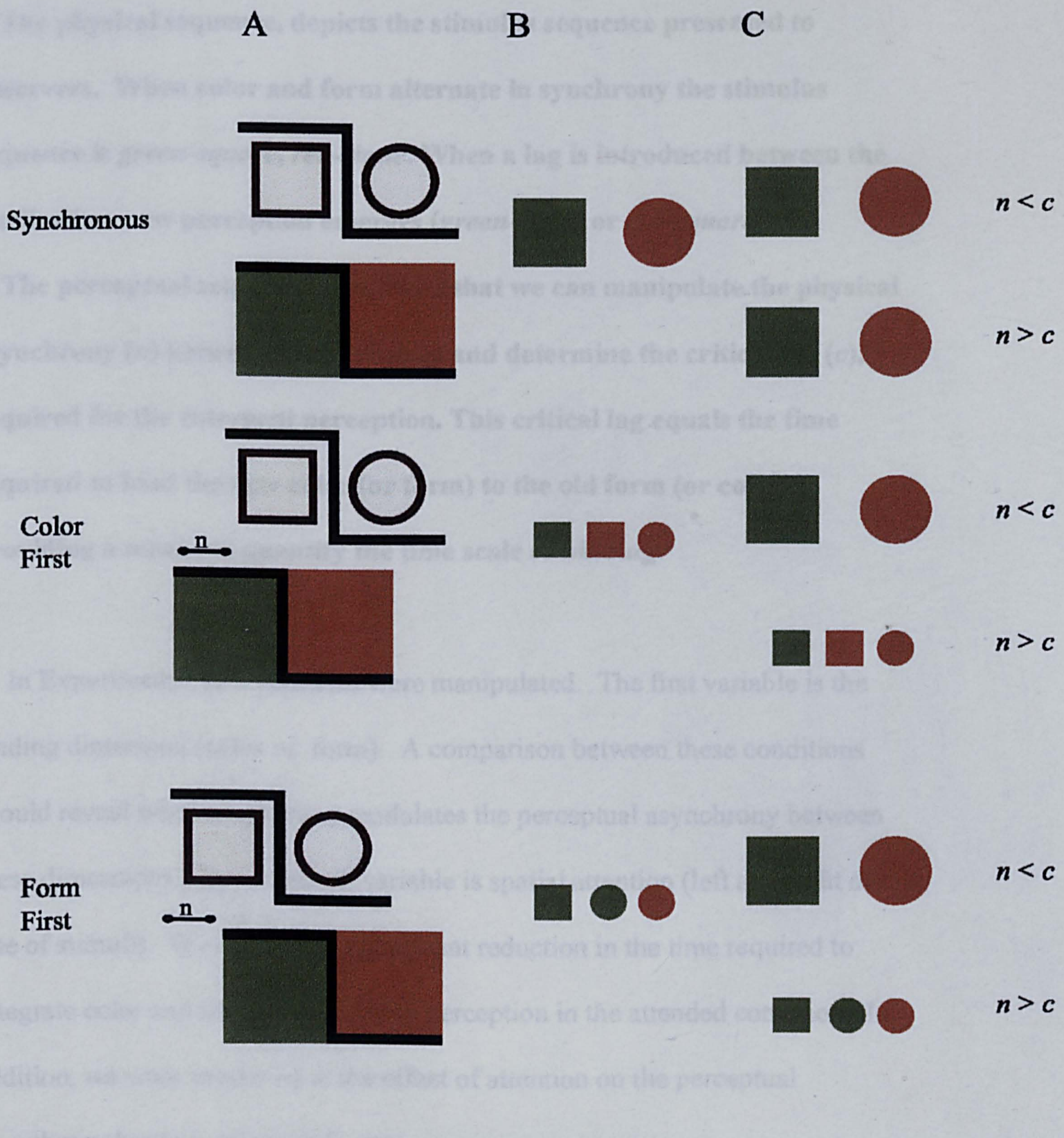


Figure 18. **The Emergence of a Perception from Binding.**

A depicts the two attributes to be bound (color, alternating between green and red and form, alternating between square and circle). CIE chromaticity coordinates: green [L= 8, x = 0.338, y = 0.504] and red [L = 8, x = 0.540, y = 0.320].

B The physical sequence, depicts the stimulus sequence presented to observers. When color and form alternate in synchrony the stimulus sequence is *green-square, red-circle.* When a lag is introduced between the attributes a new perception emerges (*green-circle* or *red-square*).

C The perceptual sequence, illustrates that we can manipulate the physical asynchrony (*n*) between the attributes and determine the critical lag (*c*), required for the emergent perception. This critical lag equals the time required to bind the new color (or form) to the old form (or color) providing a means to quantify the time scale of binding.

In Experiment 5 two variables were manipulated. The first variable is the leading dimension (color vs. form). A comparison between these conditions should reveal whether attention modulates the perceptual asynchrony between these dimensions. An additional variable is spatial attention (left and right of the line of stimuli). We expected a significant reduction in the time required to integrate color and form into a unitary perception in the attended condition. In addition, we were interested in the effect of attention on the perceptual asynchrony between these attributes.

The test stimuli (spanning 7.4 x.69 degrees of visual angle) comprised 6 equidistant shapes (spanning 0.69 x 0.69 degrees of visual angle) arranged in a line. Each shape comprised two attributes (here, color and form) with two possible values (red or green and square or circle) to form the four basic *red-square*, *red-circle*, *green-square* and *green-circle* stimuli (see Figure 19).

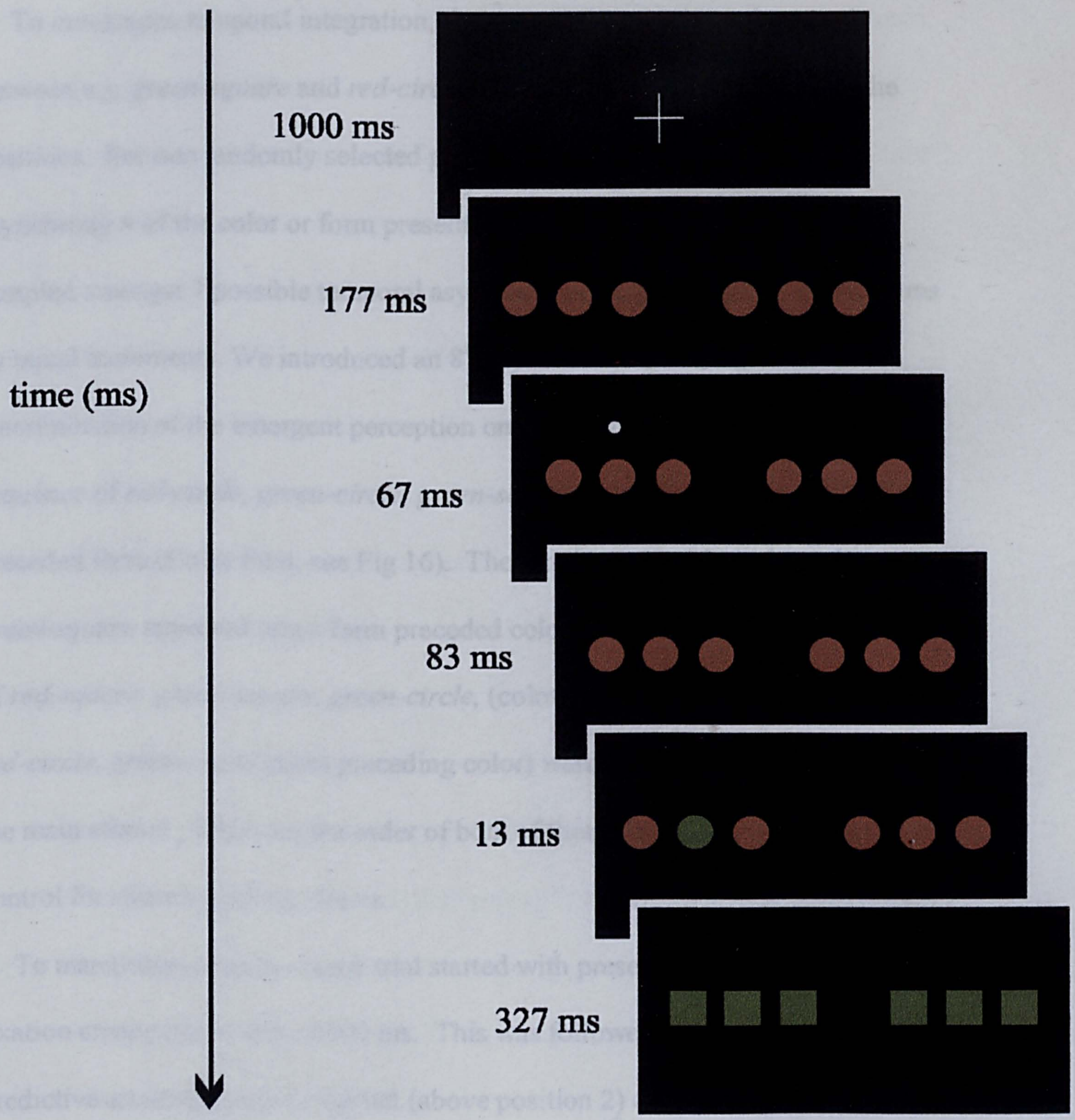


Figure 19. **A sample trial for which second shape was asynchronous. This element is removed for a randomly selected lag, *n* (here, 13 ms) in the middle of each trial (lasting a total of 667 ms). A cue (here, to the left) is presented for 67 ms, 150 ms prior to asynchrony onset.**

To investigate temporal integration, the shapes alternated synchronously between e.g. *green-square* and *red-circle* over a 667 ms interval in five of the positions. For one randomly selected position we changed the temporal asynchrony *n* of the color or form presented in this location. We randomly sampled amongst 7 possible temporal asynchronies ranging from 13 ms to 93 ms by equal increments. We introduced an 8th asynchrony of 200 ms to ensure discrimination of the emergent perception on at least one trial. To illustrate, the sequence of *red-circle, green-circle, green-square,* appeared when color preceded form (Color First, see Fig 16). The sequence of *red-circle, red-square, green-square* appeared when form preceded color (Form First). The sequence of *red-square, green-square, green-circle,* (color preceding form) or *red-square, red-circle, green-circle* (form preceding color) were included to counterbalance the main stimuli. Likewise the order of both of these conditions was reversed to control for stimulus driven effects.

To manipulate attention, each trial started with presentation of a central fixation cross presented for 1000 ms. This was followed by a 67ms non-predictive attentional cue to the left (above position 2) or to the right (above position 5), presented 150 ms prior the onset of the asynchrony, to prevent a saccadic eye movement to the cue[5]. The cue measured 5 pixels in radius (the monitor resolution was 1280 by 1024 pixels) and 1.83 candelas per square metre. Observers were tested in two blocks, the trials in which the target stimuli

---

[5] This cue to stimulus latency is consistent with previous studies of visual attention (e.g. Yeshurun and Carrasco, 1998; 1999; Carrasco and McElree, 2001)

were *green-square* and *red-circle* (half) were combined. Likewise the trials in which the target stimuli were *red-square* and *green-circle* (half) were combined. Again, this gave a 2-AFC task in which observers either had to indicate either whether a *red-square* or a *green-circle* appeared or they had to indicate whether a *green-square* or a *red-circle* appeared. For both colour and form first trials, there were 4 repetitions for each of the eight temporal lags (2*4*8=64). This was replicated for each position (6*128=384) and for each cue type (384*2=768) giving 768 trials in total. Color First and Form First trials were interleaved. Observers were instructed to guess if they were unsure and to attend to the cues without eye movement. A headrest maintained viewing distance at one meter.

Results

For each observer, and for each stimulus position, we fitted a cumulative Gaussian curve to the temporal asynchrony data to determine the 75% discrimination threshold of the emergent perceptions (the critical lag), separately for left and right conditions of attentional cueing (see Figure 20). We then averaged the critical lags derived for each observer and position, in the left and right cueing conditions. For our analysis we collapsed and compared trials in which the cue appeared at the same side as the target stimuli (cue concurrent) with trials in which the cue appeared at the opposite side to the target (cue non-concurrent). A t-test[6] comparing the difference between cue concurrent with element position (51 ms) vs non-concurrent with element position (62 ms) reveals a significant enhancement of cueing $t(119) = 3.59, p < .001$.

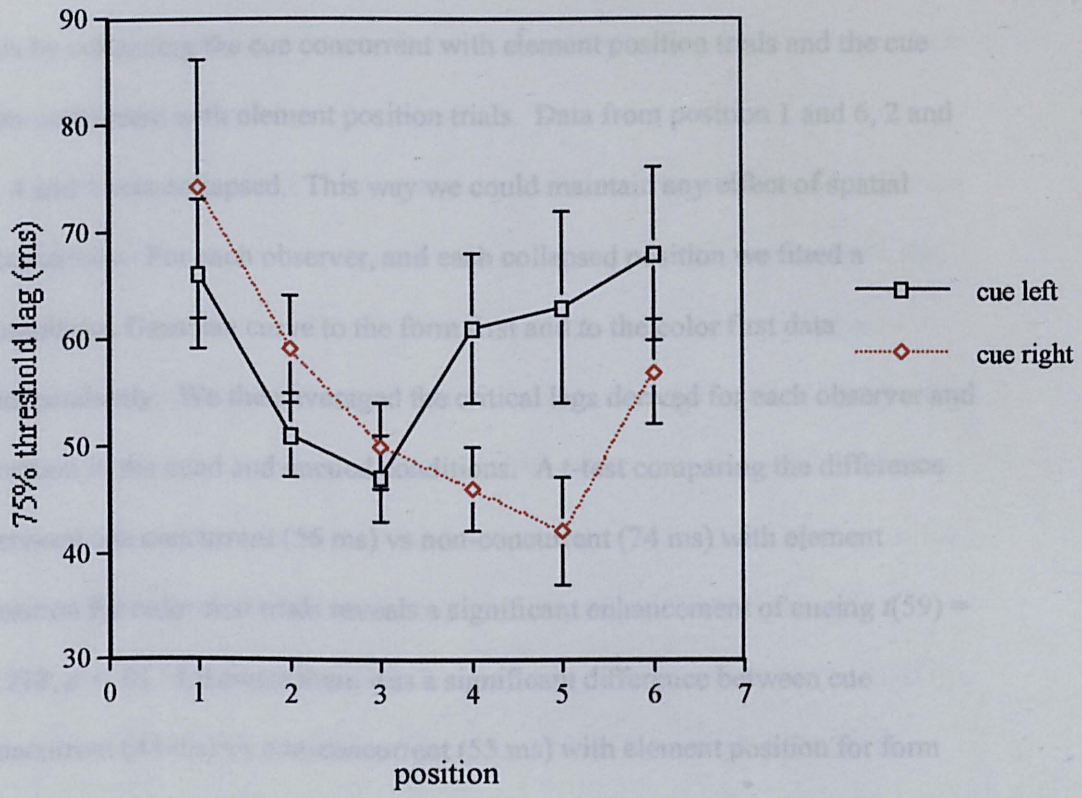


Figure 20. **Attention modulates the critical lag required for emergent perception. This figure depicts the critical lag required for the emergent perception across 20 observers for each position (left, position 1,2 and 3; right positions 4,5 and 6), by cueing condition (left and right).**

To examine the influence of attention on color and form in more detail we analysed the data from color leading and form leading trials independently. Splitting the data into colour and form trials for independent analysis obviously reduced the number of trials by half. This did not provide enough trials to fit a

---

[6] All t-tests condicted in this thesis were 1-tailed.

cummulative Gaussian curve to. Therefore, we had to collapse the data. We did this by collapsing the cue concurrent with element position trials and the cue non-concurrent with element position trials. Data from position 1 and 6, 2 and 3, 4 and 5 was collapsed. This way we could maintain any effect of spatial eccentricity. For each observer, and each collapsed position we fitted a cumulative Gaussian curve to the form first and to the color first data independently. We then averaged the critical lags derived for each observer and position in the cued and uncued conditions. A t-test comparing the difference between cue concurrent (56 ms) vs non-concurrent (74 ms) with element position for color first trials reveals a significant enhancement of cueing $t(59) = 2.218, p < .01$. Likewise there was a significant difference between cue concurrent (44 ms) vs non-concurrent (55 ms) with element position for form first trials $t(59) = 1.924, p = .03$. In addition, we found a significant perceptual advantage for form first trials in both attended (12 ms) $t(59) = 3.242, p < .001$ and unattended (19 ms) conditions $t(59) = 2.133, p = 0.02$. This asynchrony was not significantly reduced by attention.

From this data it seems that attention enhances the integration of color and form. However, it does not significantly reduce the perceptual asynchrony between them.

Discussion

We set out to disentangle the influence of attention on the integration of two information sources into a unitary perception. These results demonstrate that attention enhances the integration of two information sources into a unitary perception. Attention decreases the time that observers require to bind for example, a color attribute (e.g. red) to a shape attribute (e.g. square) to produce the unitary perception of a *red square.*

From our results it seems that attention does not enhance the integration of attribute information by decreasing the perceptual asynchrony between the attributes comprising the stimuli. Observers were faster at perceiving an emergent perception that resulted from a change in form (form first trials) in both attended and unattended conditions. Thus attention must enhance feature integration either by speeding up the perceptual processing time of each attribute by an equal magnitude or by speeding up an additional "binding stage". Evidence converges to support the former theory (Carrasco and McElree, 2001; Hiosaka *et al*, 1992; Stelmach and Herdman, 1991; Posner *et al*,1980). In particular, Carrasco and McElree (2001) demonstrated that attention accelerates processing time and improves accuracy for conjunction targets using the speed-accuracy trade-off procedure (SAT).

We found a significant perceptual advantage of form with respect to color in both attended and unattended conditions. As discussed earlier, Moutoussis and Zeki (1997a; 1997b) reported a 50 ms perceptual advantage of color with respect to form. In addition, Viviani and Aymoz (2001) reported no such perceptual synchrony between these attributes. We propose that the discrepancy between these findings and our results may reflect the fact that the task, more specifically, the attentional requirements of a task, can modulate the perceptual processing of stimulus dimensions. Thus, the perceptual processing of dimensions appears to be flexible, rather than fixed. In particular, it seems likely that perceptual asynchrony between dimensions will depend on the relative salience of these dimensions.

Nishida and Johnston (2002) provide an alternative to the processing delay account of perceptual asynchrony. These authors contend that temporal coding is time locked to events. Perception of temporal order is achieved by comparing temporal markers (transitions, first order changes requiring measurement at two points in time versus turning points second order, requiring measurements at three points in time). At high alteration rates (250ms) asynchronies arise because transitions (of e.g. color) are more salient than turning points (of e.g. motion). However, we report perceptual asynchrony between two temporal markers of the same type (as did Moutoussis and Zeki, 1997) (transitions). Thus to account for these findings the temporal marker hypothesis must explain temporal asynchrony between temporal markers of the same type.

The idea that attention enhances binding is not new (Reynolds & Desimone, 1999; Treisman & Gelade, 1980) indeed this proposal is the main contention of Treisman's Feature Integration Theory. However, our studies provide a direct measure to quantify modulation of perceptual processing. This modulation could explain the intervention of attentional mechanisms in binding the separate attributes of an object into unified perceptions.

Experiment 6

Investigating the influence of attention on the integration of colour and form across the visual field.

Previous literature suggests that attention does not operate symmetrically across the visual field. In particular, a recent study mapped visual attention using a change detection paradigm (Tse, in preparation). In this study, change blindness, the failure of the visual system to detect changes in a scene that occur with blank interferences was exploited to map attention. Results from this study suggest that attention is biased to the horizontal axis. Therefore, we decided to examine the influence of attention across the visual field. In particular, in the current experiment we replicated Experiment 5 for stimuli arranged radially across the visual field.

Method

Participants Two observers (under 30 years of age), with normal or corrected to normal vision participated in the experiment. Both observers were tested for colour blindness using the standard Ishihara tests for color blindness.

Materials. The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab and the Matlab Pyramid Toolbox (Brainard, 1997; Simoncelli, 1997; Pelli, 1997).

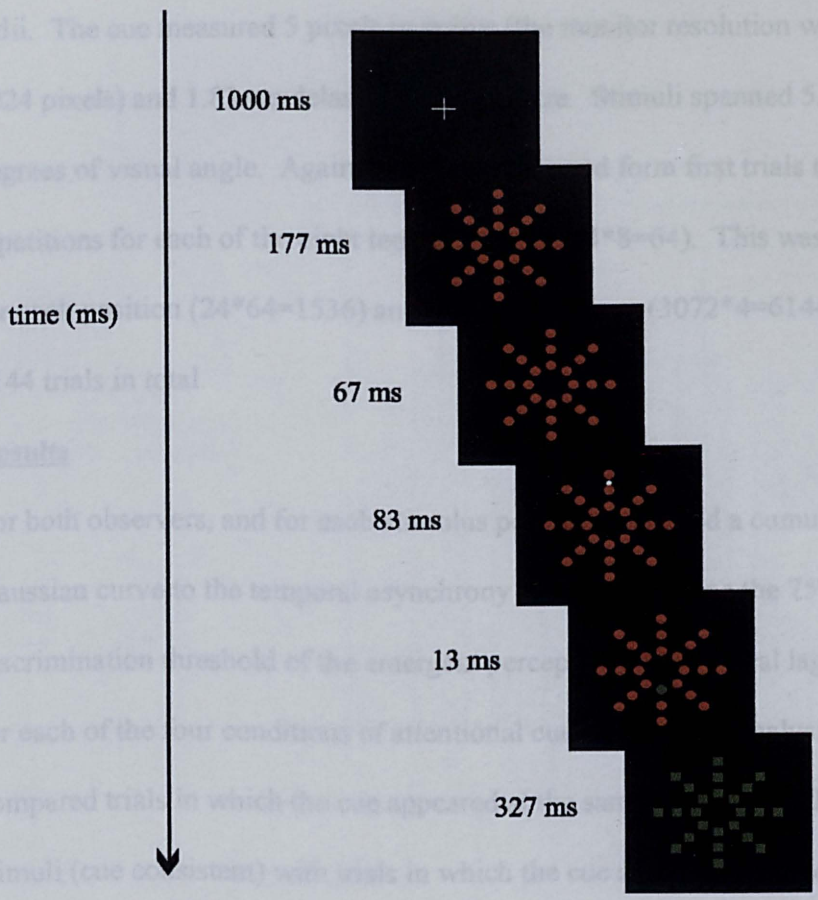


Figure 21. **A sample trial for which second shape was asynchronous. This element is removed for a randomly selected lag, *n* (here, 13 ms) in the middle of each trial (lasting a total of 667 ms). A cue (here, to the left) is presented for 67 ms, 150 ms prior to asynchrony onset.**

Figure 21 illustrates that in Experiment 6 we extended Experiment 5 radially across the visual field. The same experimental design was employed for 24 positions and 4 types of cue (north, south, east and west). Specifically, the cue was located above the second element of the north, south, east and west radii. The cue measured 5 pixels in radius (the monitor resolution was 1280 by 1024 pixels) and 1.83 candelas per square metre. Stimuli spanned 5.3 by 5.3 degrees of visual angle. Again, for both colour and form first trials there were 4 repetitions for each of the eight temporal lags (2*4*8=64). This was replicated for each position (24*64=1536) and for each cue type (3072*4=6144) giving 6144 trials in total.

Results

For both observers, and for each stimulus position, we fitted a cumulative Gaussian curve to the temporal asynchrony data to determine the 75% discrimination threshold of the emergent perceptions (the critical lag), separately for each of the four conditions of attentional cueing. For our analysis we compared trials in which the cue appeared at the same direction as the target stimuli (cue consistent) with trials in which the cue appeared at the opposite side to the target (cue non-consistent) for north versus south and east versus west cueing conditions.

Figure 22. illustrates that for one observer cueing reduced the time required to perceive the emergent perception. A t-test comparing the difference between cue concurrent with element position vs non-concurrent reveals a significant enhancement of cueing $t(11) = 3.24, p = 0.008$.

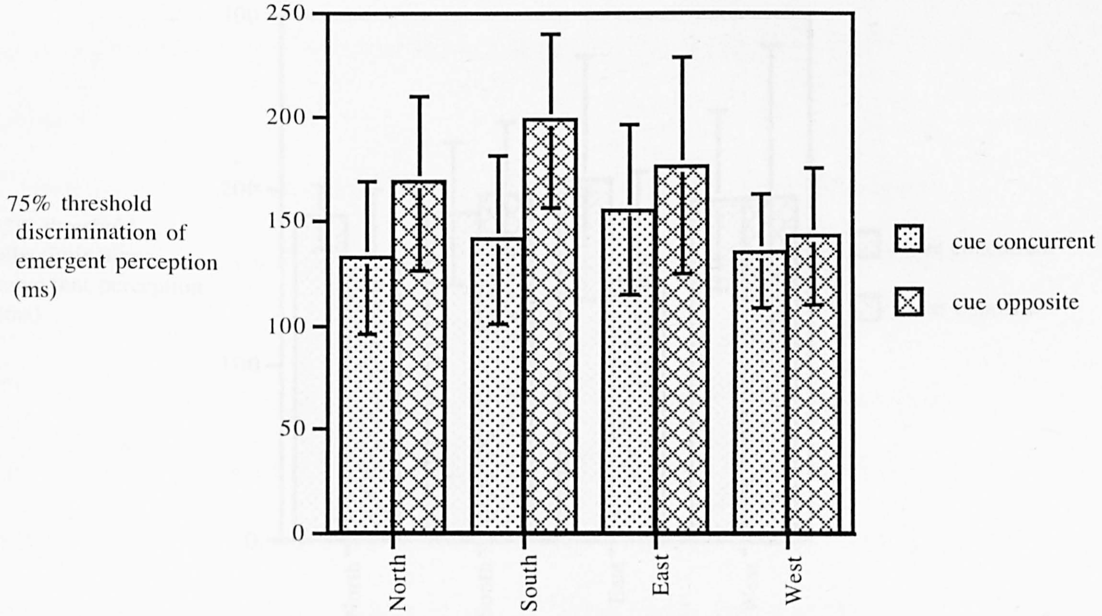


Figure 22. **Observer 1, this figure depicts the critical lag required for the emergent perception averaged across 9 positions when cueing is concurrent versus opposite emergent perception position. Clearly, cueing enhanced feature integration for this observer.**

However, Figure 23 illustrates that for a second observer there was not significant enhancement of cueing $t(11) = 0.57, p = 0.58$.

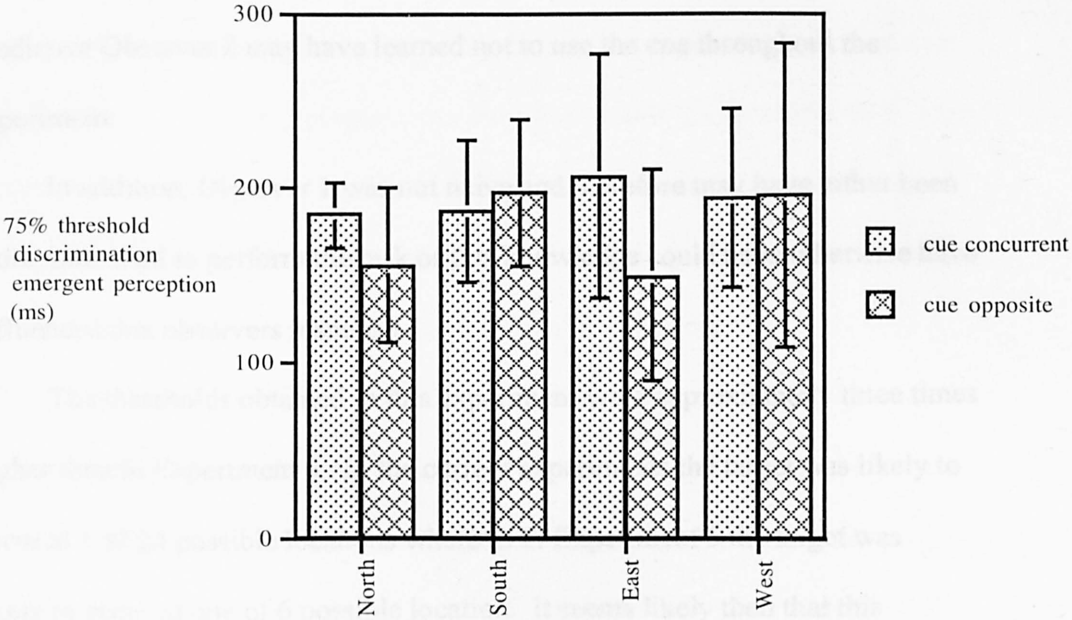


Figure 23. Observer 2, this figure depicts the critical lag required for the emergent perception averaged across 9 positions when cueing is concurrent versus opposite emergent perception position. However, cueing did not enhance feature integration for this observer.

Discussion

For observer 1 we found that attention enhances the integration of form and colour into a unitary perception. Consistent with Experiment 5 attention decreases the time required to bind a colour attribute (e.g. red) to a shape attribute (e.g. square) to produce the unitary perception of a *red-square*.

However, this effect was not found in Observer 2's data. It seems possible that the large number of trials may account for the results from this experiment. For each observer there were 6144 trials in total. Because the cue was non-predictive Observer 2 may have learned not to use the cue throughout the experiment.

In addition, Observer 1 was not naive and therefore may have either been more motivated to perform the task or this knowledge could have otherwise have influenced this observers response.

The thresholds obtained in this experiment were approximately three times higher than in Experiment 5. In the current experiments the target was likely to occur at 1 of 24 possible locations where as in Experiment 5 the target was likely to occur at one of 6 possible location. It seems likely then that this fourfold increase in the possible location of the target caused the increase in discrimination threshold.

General Discussion

In this Chapter we set out to disentangle the influence of attention on the integration of two information sources into a unitary perception. The results from Experiment 1 demonstrated that attention enhances the integration of two information sources into a unitary perception for stimuli arranged in a line. This result was replicated across the visual field for an observer in Experiment 2. However, it seems possible that the large number of trials prevented this result from being replicated for a second observer in this experiment.

The results from Experiment 1 suggest that attention does not enhance the integration of attribute information by decreasing the perceptual asynchrony between the attributes comprising the stimuli. Observers were faster at perceiving an emergent perception that resulted from a change in form (form first trials) in both attended and unattended conditions. From the attentional literature (Carrasco and McElree, 2001; Hiosaka *et al*, 1992; Stelmach and Herdman, 1991; Posner *et al*,1980) it seems likely that attention enhances feature integration by speeding up the perceptual processing time of each attribute by an equal magnitude

In addition to the findings from Chapter 2 the current experiments add weight to our proposal that perceptual processing of dimensions appears to be flexible, rather than fixed. Consequently, the perceptual asynchrony between feature attributes should also be flexible.

Chapter 4

Investigating the influence of attention on the integration of information across the visual field.

We have established that attention speeds up the processing of attended information. To recap studies of reaction time (Posner, 1980), temporal order (Stelmach and Herdman, 1991) and using the speed-accuracy trade-off procedure (Carrasco and McElree, 2001) have revealed a temporal processing advantage for attended information. In particular, in Chapter 3 we examined the influence of attention on the perceptual asynchrony between two information sources (e.g. colour and form). However, in Chapter 1 we also noted that the selective acceleration of attended information presents a problem of temporal integration across the visual field. Specifically, attention to a portion of the visual field speeds up the processing of information within its focus resulting in temporal asynchrony between attended and unattended information. Because it is the nature of our visual experience it is often assumed that vision reduces such asynchronies to construct a temporally veridical perception of the input. However, perhaps our perceptions mirror the temporal asynchronies that result from the allocation of attention. It is this possibility that is considered here.

Experiment 7

Investigating the influence of attention on the integration of information into a line stimulus.

To investigate the influence of attention on the integration of information across the visual field we desynchronised in time the segments forming a line. We then cued either the left or right of the line and examined the gradient of temporal asynchrony tolerated by the visual system around the focus of attention. We propose that if the attentional acceleration of visual information processing is mirrored in perception then gradient of asynchrony for left versus right elements of the line should depend on where attention is directed. Conversely, if the asynchronous nature of visual processing is compensated for then the elements comprising the line should be uniformly integrated regardless of attentional focus. Results suggest that attention does modulate the integration of information comprising the line. As a consequence, the observers' perception depends on where their attention is focused.

Method

Participants. 12 University of Glasgow students (under 30 years of age) with normal or corrected to normal vision were paid to participate in the experiment.

Materials. The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab and the Matlab Pyramid Toolbox (Brainard, 1997; Simoncelli, 1997; Pelli, 1997).

Four juxtaposed elements making a line were randomly desynchronised when attention was directed to a cue (to the left, or right above the line).

Observers had to indicate whether they perceived a continuous, or a discontinuous line (see Figure 24). To investigate the gradient of temporal asynchrony tolerated around the focus of attention we tested 8 temporal asynchronies at four spatial locations (one per element of a line). The critical variable is the cued location (left vs. right for the line). Specifically, the cue was located above the line either one or three quarters along it. Again the cue measures 5 pixels in radius (the monitor resolution was 1280 by 1024 pixels) and 1.83 candelas per square metre.

Specifically, we predicted that if the visual system accurately integrates information across the visual field then observers should require the same temporal asynchrony, for any given element, to perceive discontinuity regardless of the focus of attention. However, if the visual system does not compensate for attentional processing advantages then attention should modulate the asynchrony required for perception of discontinuity.

Stimuli. On any given trial, a line was constructed from 3 synchronous elements presented simultaneously throughout the trial, and one asynchronous element. This element comprised one quarter of the line selected at random. The temporal lag was randomly sampled from 7 temporal lags ranging from 27 ms to 187 ms by equal increments of 27 ms--the 8th lag was 400 ms (see Figure 24 for two examples of trials with an asynchronous second element of the line). The randomly selected element was removed for the randomly selected lag, (in Figure 24, 27ms) in the middle of each trial (lasting a total of 667 ms). The stimuli spanned 5.45 x 5.43 degrees of visual angle. They were generated from

2D white noise and were low-passed (cut-off of at 2 cycles per degree). They were composed of a centred greyscale horizontal line (subtending 1.36 x .57 degrees of visual angle). The stimulus measured 7.04 candelas per square metre.

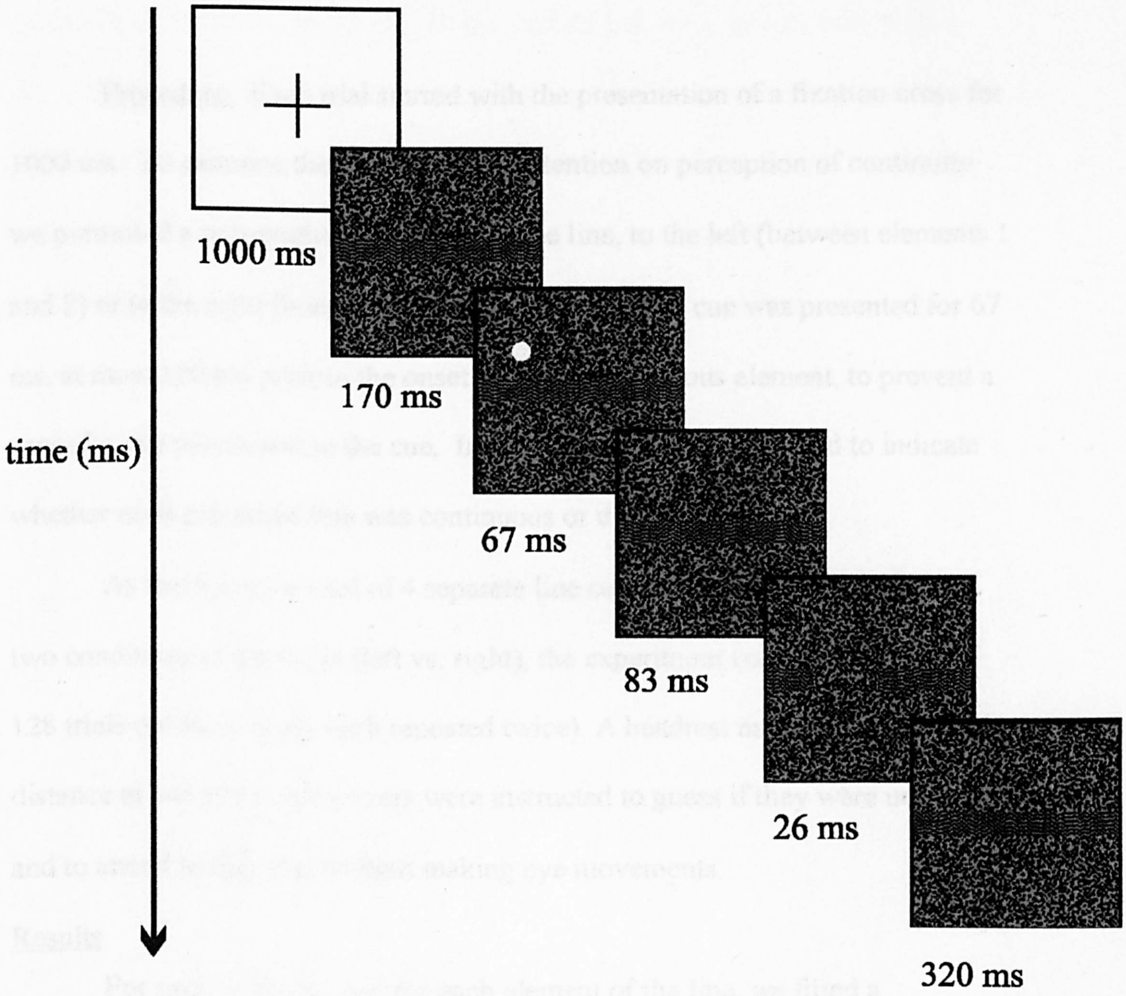


Figure 24. This figure illustrates a sample trial from Experiment 7. Here, the second element is asynchronous, this element is removed for a randomly selected lag, (here, 27ms) in the middle of each trial (lasting a total of 667 ms). A cue (here, to the left) is presented for 67 ms, 150 ms prior to asynchrony onset.

Procedure. Each trial started with the presentation of a fixation cross for 1000 ms. To examine the modulation of attention on perception of continuity we presented a non-predictive cue above the line, to the left (between elements 1 and 2) or to the right (between elements 3 and 4). The cue was presented for 67 ms, at most 150 ms prior to the onset of the asynchronous element, to prevent a saccadic eye movement to the cue. In a 2-AFC task, observers had to indicate whether each presented line was continuous or discontinuous.

As there were a total of 4 separate line segments, 8 temporal lags, and two conditions of attention (left vs. right), the experiment comprised a total of 128 trials (64 basic trials each repeated twice). A headrest maintained viewing distance at one meter. Observers were instructed to guess if they were unsure, and to attend to the cues without making eye movements.

Results

For each observer, and for each element of the line, we fitted a cumulative Gaussian curve to the lag data to determine the critical temporal lag for 75% threshold discrimination of discontinuity, separately for the left and right conditions of attentional cueing.

We then averaged the temporal lag across observers, for each line element, in the left and right cueing conditions. Figure 25. illustrates that to perceive a discontinuous line, observers cued to the left required, on average, temporal asynchronies of 50 ms, 29 ms, 45 ms, and 92 ms for elements one to four, respectively. When cued to the right, the temporal asynchronies required by observers were 72 ms, 54 ms, 30 ms, and 65 ms, for elements one to four, respectively. A t-test on the difference between cue concurrent (e.g. elements 1 and 2 in the cue left condition and elements 3 and 4 in the cue right condition) with element position vs non-concurrent (e.g. elements 1 and 2 in the cue right condition and elements 3 and 4 in the cue left condition) with element position reveals a significant enhancement of cueing $t(47) = 3.17, p < .003$.

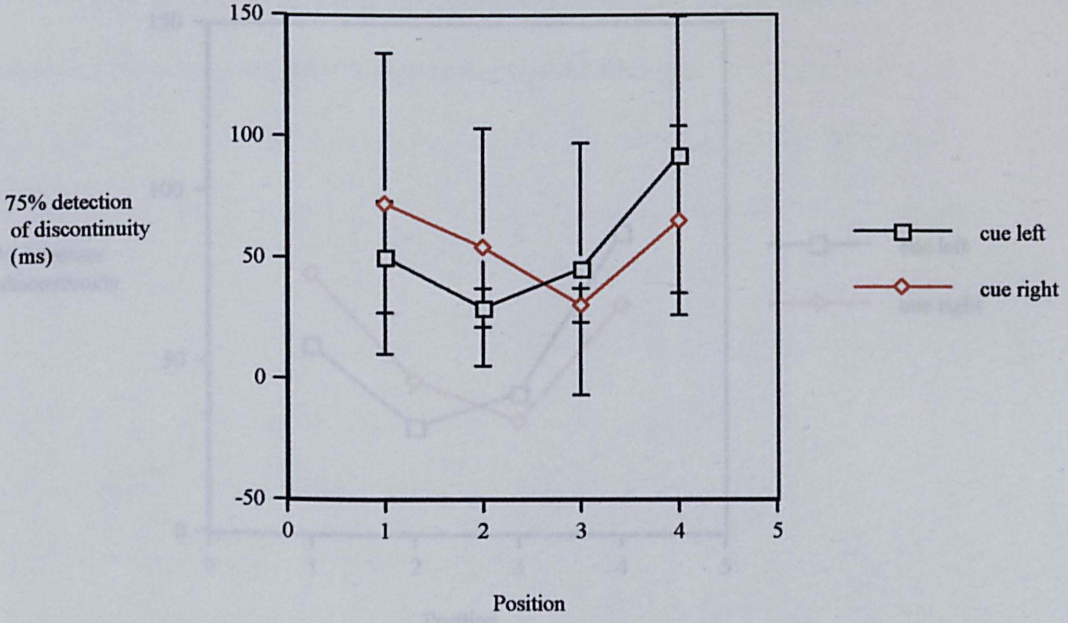


Figure 25. The mean temporal lag across 12 observers, for each line element (left, position 1 and 2; right positions 4 and 5), for right and left cueing conditions of Experiment 7 is depicted.

There were only 2 repetitions of each type of trial for each observer therefore to ensure that the curve fitting was reliable we also analysed the data by pooling the data across the observers. For each element of the line we fitted a cumulative Gaussian curve to this pooled lag data to determine the critical temporal lag for 75% threshold discrimination of discontinuity, separately for the left and right conditions of attentional cueing. Figure 26 illustrates that this analysis produces the same effect as the previous analysis.

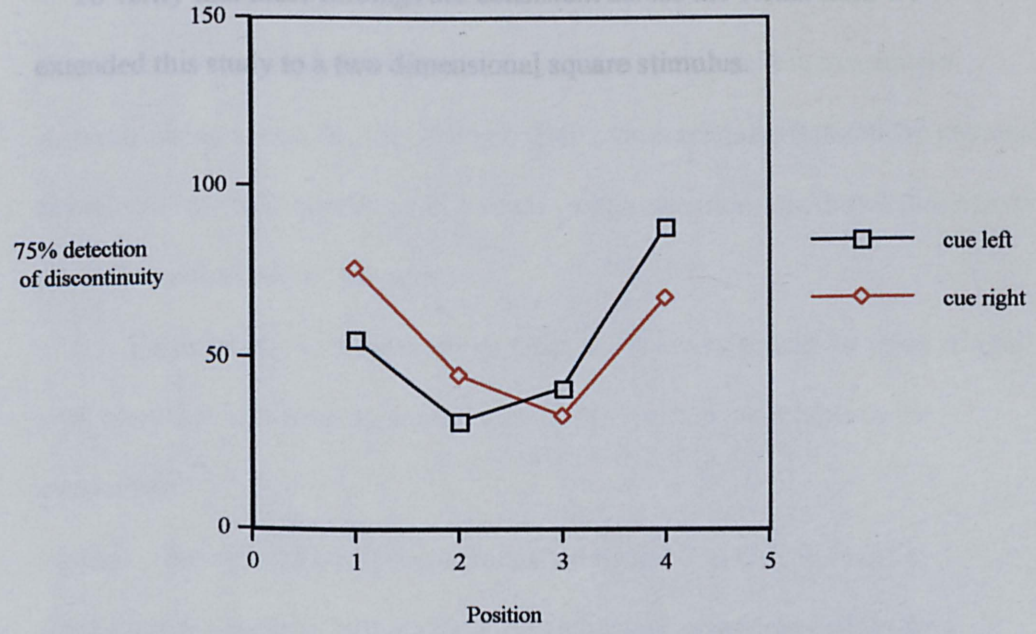


Figure 26. The temporal lag, for each line element (left, position 1 and 2; right positions 4 and 5), for right and left cueing conditions derived from pooled data across all 12 observers.

These results reveal that attention does modulate the integration of the elements of a line. The visual system integrates the elements of a line orthogonally depending on whether attention is directed to the left or to the right.

Discussion

These results suggest that the visual system does not compensate for attentional acceleration of information processing. Rather, they imply that perception mirrors the selective processing advantage offered by attention. Because there was less than 150 ms between the cue and asynchrony onset it is unlikely that these results could have arisen because of an eye movement to the cued location.

To verify that these findings are consistent across the visual field we extended this study to a two dimensional square stimulus.

Experiment 8

Investigating the influence of attention on the integration of information into a square stimulus.

Experiment 8 extended the design of Experiment 7 from a line to a square stimulus, using a similar methodology. Here, we randomly changed the physical asynchrony of the four corners of a square when attention was directed to a non-predictive cue to one of the corners.

Participants. 11 University of Glasgow students (under 30 years of age) with normal or corrected to normal vision were paid to participate in the experiment.

Stimuli. This experiment differed from Experiment 7 in only the spatial dimension, because we manipulated the perceptual asynchrony of the four corners of a square (see Figure 26). We presented non-predictive attentional cues at the top-left, top-right, bottom-left and bottom-right corners of the square. The cue measured 10 pixels in radius (the monitor resolution was 1280 by 1024 pixels) and 1.83 candelas per square metre.

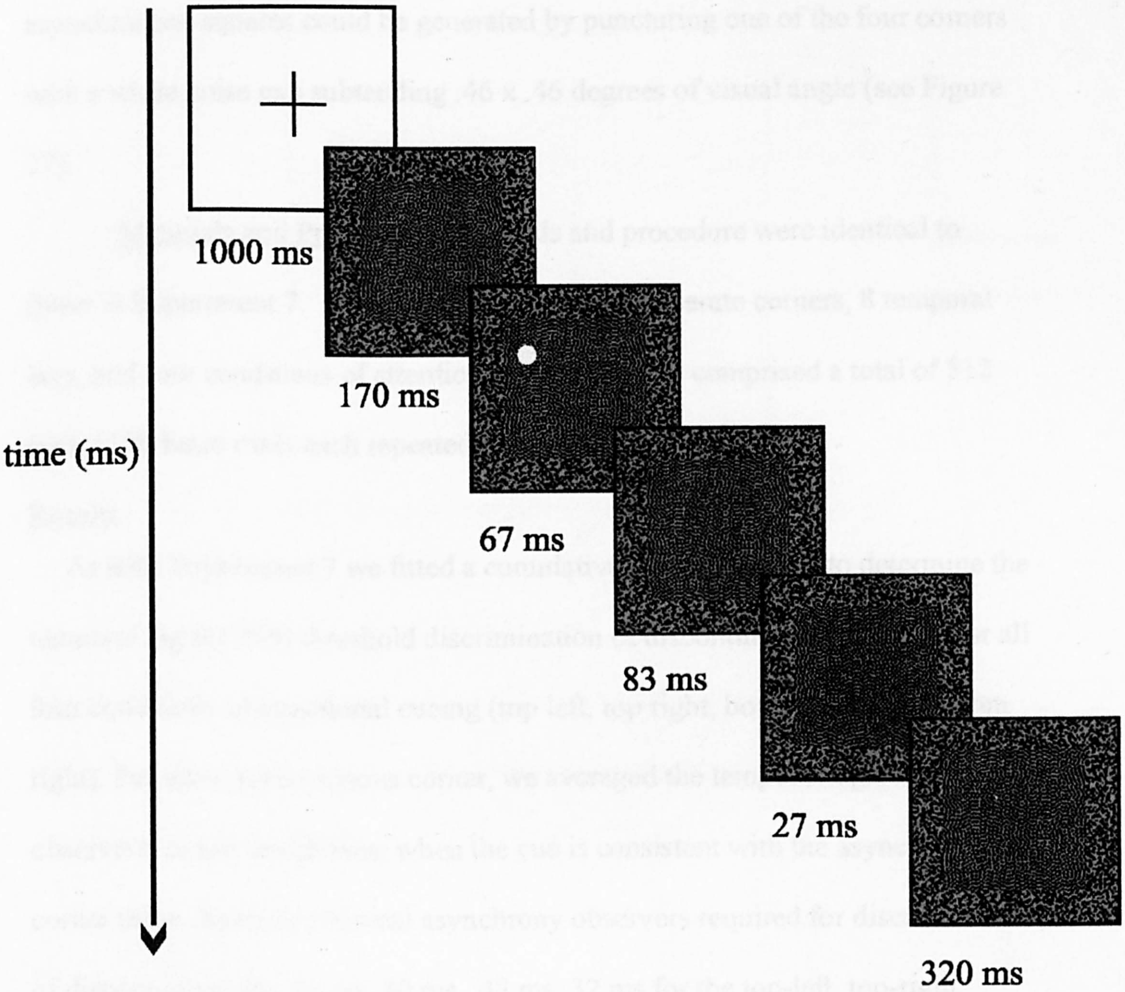


Figure 27. A sample trial from Experiment 8. Here, the top-right element of the square is asynchronous. The experimental sequence is identical to Experiment 7. However, in this experiment, it is the four corners of the square that are randomly desynchronised.

Stimuli (subtending 5.43 x 5.43 degrees of visual angle) comprised low-pass spatially filtered white noise (cut-off of at 2 cycles per degree) and a square (subtending 3.7 x 3.7 degrees of visual angle) located in the centre of the image. The stimulus measured 7.53 candelas per square metre. Four types of asynchronous squares could be generated by puncturing one of the four corners with a white noise gap subtending .46 x .46 degrees of visual angle (see Figure 27).

Materials and Procedure. Materials and procedure were identical to those in Experiment 7. As there were a total of 4 separate corners, 8 temporal lags, and four conditions of attention, the experiment comprised a total of 512 trials (128 basic trials each repeated four times).

Results

As with Experiment 7 we fitted a cumulative Gaussian curve to determine the temporal lag for 75% threshold discrimination of discontinuity, separately for all four conditions of attentional cueing (top left, top right, bottom left and bottom right). For each asynchronous corner, we averaged the temporal lags, across observers, in two conditions: when the cue is consistent with the asynchronous corner (here the mean physical asynchrony observers required for discrimination of discontinuity was 45 ms, 40 ms , 48 ms, 32 ms for the top-left, top-right, bottom-left and bottom-right corners, respectively) and when the cue is diagonally opposite to the asynchronous corner (here the mean physical asynchrony observers required was 69 ms, 46 ms, 67 ms, 45 ms for the top-left, top-right, bottom-left and bottom-right corners, respectively). These findings are illustrated in Figure 28. A t-test comparing the difference between cue concurrent vs non-concurrent with element changed reveals a significant enhancement of cueing $t(43) = 4.92, p < .001$.

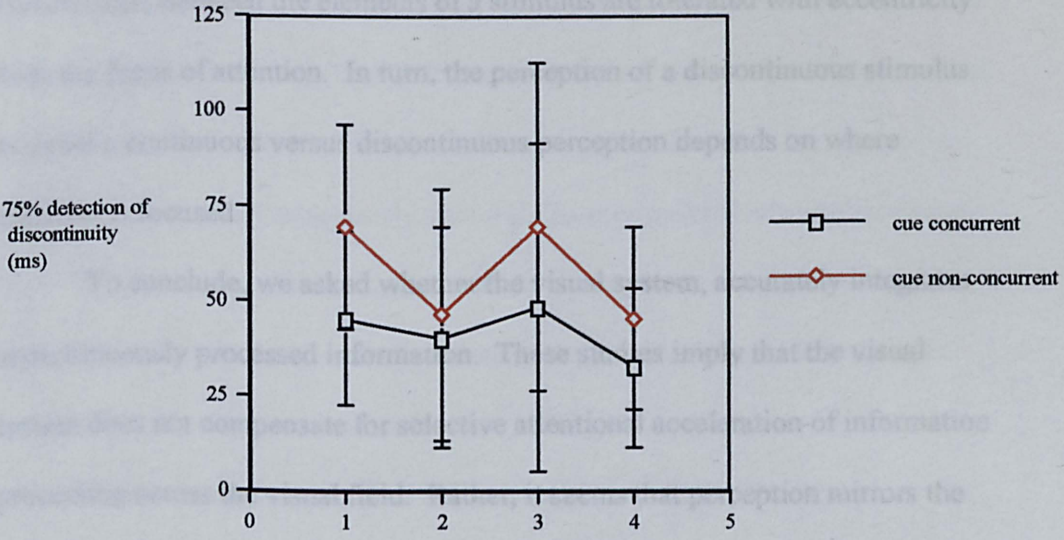


Figure 28. The mean temporal lag across 11 observers, for cue concurrent with element discontinuity and cue non-concurrent with discontinuity for Experiment 8 is depicted.

Discussion

These results confirm that the findings of Experiment 7. Attention modulates the integration of elements into a square. Consistent with the results from Experiment 7 these results imply that rather than compensating for attentionally induced temporal asynchrony across the visual field the visual system yields a temporally asynchronous perception.

General Discussion

By desynchronising a stimulus we found that increasing temporal asynchronies between the elements of a stimulus are tolerated with eccentricity from the focus of attention. In turn, the perception of a discontinuous stimulus as either a continuous versus discontinuous perception depends on where attention is focused.

To conclude, we asked whether the visual system, accurately integrates asynchronously processed information. These studies imply that the visual system does not compensate for selective attentional acceleration of information processing across the visual field. Rather, it seems that perception mirrors the increase in processing time with eccentricity from the focus of attention.

These studies suggest that our visual system provides us with a temporally non-veridical perception. This finding is in agreement with other studies revealing asynchronous integration of functionally processed feature information, for example color, form and motion (Moutoussis and Zeki, 1997a, Moutoussis and Zeki, 1997b).

In addition, these results support current theory about the motion line illusion (Hiosaka *et al*,1993). When attention is directed to a cue presented above a line observers perceive motion propagated from the cued location. Our findings support the hypothesis that this illusion occurs because motion centres seem to construct a motion sensation from the asynchronously processed information around the attentional focus.

The temporal dynamics of perception remain for the most part neglected (Walsh, 2002) yet these results yield many interesting implications that only future research can resolve. For example, besides the motion-line illusion what other failures of perception can be induced by the asynchronous nature in which information is processed? In addition, the categorization literature has established that people selectively attend to features to resolve complex object categorizations. Our results suggest that the perceptions of complex objects could themselves be temporally processed around the attributes that are most diagnostic in the task considered (Schyns, 1998).

However, in retrospect there were several methodological problems with the studies in the present chapter. Firstly, in an attempt to measure the threshold of temporal asynchrony tolerated around an attentional cue we introduced a discontinuity in our stimulus for a randomly selected lag. However, observers may have resolved this task simply by detecting the gap in the stimulus.

Moreover, the target discontinuity was removed in the middle of each trial and the cue was presented 150ms before in an attempt to control for saccadic eye movements. However, this also meant that there was different latencies to cue onset which may have influenced the results.

The Experiments in Chapter 5 were developed in an attempt to overcome these methodological problems.

Chapter 5

Investigating the temporal dynamics of an attentionally induced bias.

To recap, we have established that attention speeds up the processing of attended information (Posner, 1980; Stelmach and Herdman, 1991; Carrasco and McElree, 2001). In Chapter 4 we set out to examine whether the visual system compensates for temporal asynchrony that arises between attended and unattended information versus whether this asynchrony is mirrored in perception. In particular, in Chapter 4 we found that by desynchronising a stimulus (a line and a square) increasing temporal asynchronies between the elements of a stimulus were tolerated with eccentricity from the focus of attention. Therefore, an observer's perception of a discontinuous stimulus as either a continuous versus discontinuous perception depends on where attention is focused. Thus we concluded that the temporal asynchronies, induced by selectively accelerating information processing, are not compensated for by the visual system. Rather they seem to be revealed in perception.

In the current chapter we extended the work described in Chapter 4. Because a detection paradigm was employed in the experiments conducted in Chapter 4 it is possible that detection of the asynchrony may account for the results derived in these experiments rather than an attentional modulation of perception. Therefore, in the current chapter we set out to replicate the findings from this study.

Specifically, in Experiment 9 we examined whether we can induce orthogonal perceptions, despite presenting observers with an identical stimulus, by manipulating the cueing condition. In Experiment 10 we extended this methodology to examine whether these orthogonal perceptions are time-dependent around the focus of attention.

Experiment 9

Biasing the observers' response with an attentional cue.

To examine whether attention modulates perception we desynchronised a stimulus that would induce orthogonal perceptions depending on which elements of the stimulus were perceived first. By employing such a stimulus it is possible to examine whether the accelerated processing offered to attended information modulates perception. If attended information is processed first and this perceptual advantage is mirrored in perception then despite being presented with an identical stimulus observers should report orthogonal perceptions depending on where their attention is focused. Crucially then attention will induce a perceptual bias depending on its focus. However, if the processing advantage offered to attended information is not mirrored in perception then we should expect no such bias.

To this end, we desynchronised in time the line segments forming the number "eight". To investigate the influence of attention on the observers' perceptions we cued one of four possible locations, top-left, top-right, bottom-left, bottom-right. If attentional acceleration of information processing is mirrored in perception then we would expect orthogonal perceptions depending on the attention focus. For example, when the stimulus is cued at the top-left information in this position should enjoy the processing advantage. Moreover, from Experiments 7 and 8 we might expect that the time required to process information would increase with distance from this position. Therefore, this processing advantage should be revealed by a perceptual bias. Because the top-left element discriminates a “five” from a “two” we might expect a biased response of “five” when the cue is in this location (or when cued bottom-right). Likewise, we would expect observers to respond “two” when the cue occurs at the top-right or bottom-left. However, if attentional acceleration of information processing is compensated for at some stage of visual processing then the observers’ response should not be biased by cueing.

Results suggest that observers’ perceptions were directly correlated with the location of the cue. That is, observers were significantly more likely to respond “two” (vs. “five”) when cued to the top-right and bottom-left (vs. top-left and bottom-right) elements. Thus, rather than compensating for processing asynchronies across the visual field these orthogonal perceptions indicate a time-dependent integration of information for the perception of two numbers induced by the location of the attentional cue.

Method

Participants. 3 University of Glasgow students (under 30 years of age) with normal or corrected to normal vision were paid to participate in the experiment.

Materials. The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab (Brainard, 1997; Simoncelli, 1997; Pelli, 1997).

Stimuli. On any given trial, observers were presented with a desynchronised “two” and “five” stimuli superimposed to create an “eight” stimulus (see Figure 29). Stimuli spanned 5.1 by 6.8 degrees of visual angle.

Two variables were manipulated. The sequence of line segments comprising the stimulus appeared desynchronized from either top to bottom or vice versa. Secondly, to examine the influence of attentional cueing on the observer's perception a cue was presented in one of four locations, top-left, top-right, bottom-left or bottom right.

Procedure. Each trial started with the presentation of a fixation cross for 1000 ms. To examine the effect of attention on the observers perception we presented a non-predictive cue to either the top-left, top-right, bottom-left or bottom right of the stimulus. The cue measured 10 pixels in radius (the monitor resolution was 1280 by 1024 pixels) and 1.83 candelas per square metre. The cue was presented for 27 ms and presentation of the randomly desynchronised stimulus began 13 ms after cue onset. The desynchronised elements of the stimulus were presented sequentially over five frames from the top to bottom or vice versa (see Figure 28). Each frame was presented for 13 ms and the total duration of each trial was 67 ms. Therefore, there was less than 150 ms between the onset of the cue and offset of the stimulus preventing a saccadic eye movement to the cued location. In a 2-AFC discrimination task, observers responded either "two" or "five".

As there were a total of four conditions of attention, 2 orders of presentation and 15 repetitions the experiment comprised a total of 120 trials. A headrest maintained viewing distance at one metre. Observers were instructed to guess if they were unsure, and to attend to the cues without making eye movements.

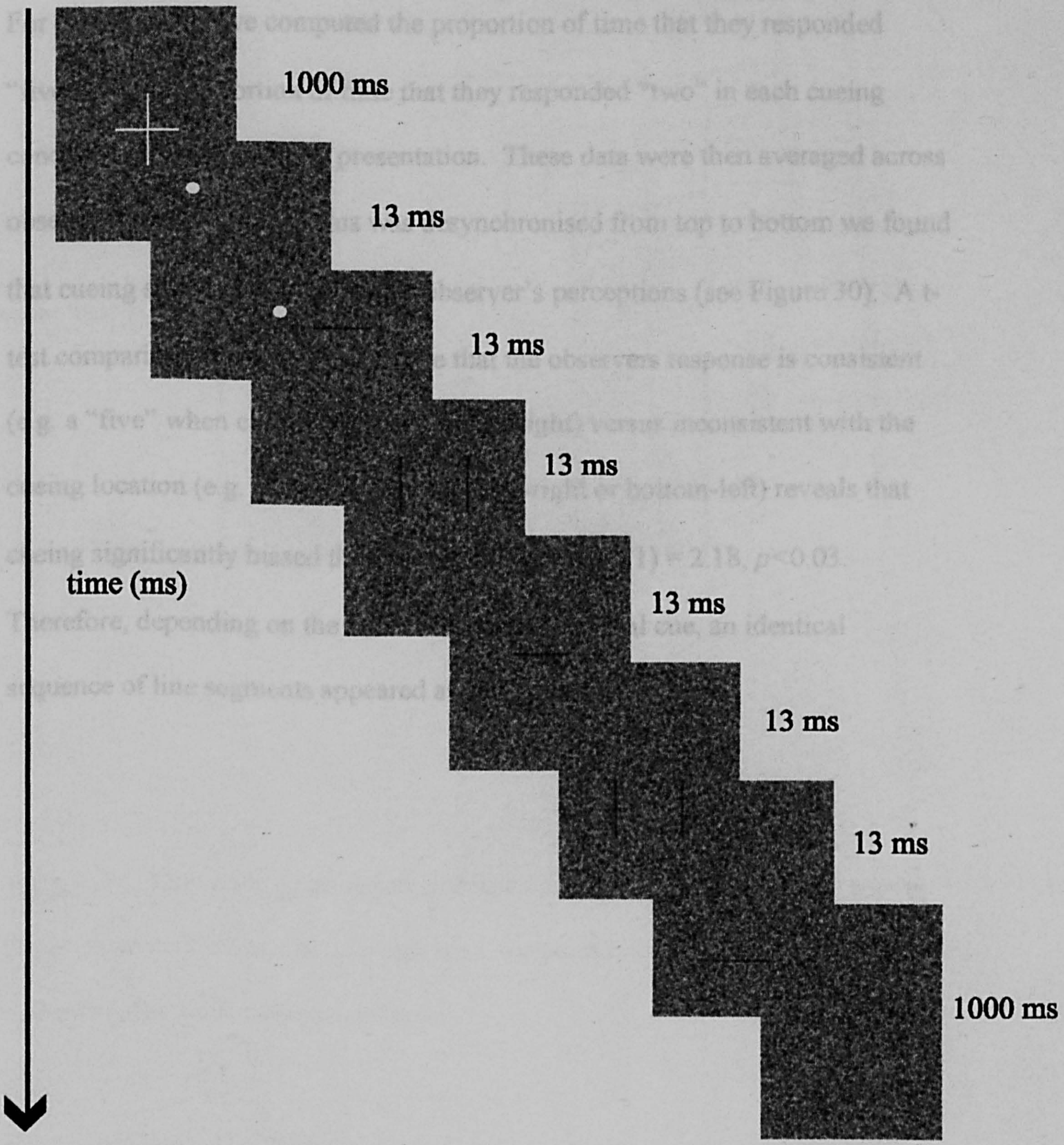


Figure 29. **A sample trial from Experiment 9, here a cue was presented to the top-left and the stimulus ("eight") was presented in a desynchronised sequence from the top to the bottom.**

Results

For each observer we computed the proportion of time that they responded "five" and the proportion of time that they responded "two" in each cueing condition for both orders of presentation. These data were then averaged across observers. When the stimulus was desynchronised from top to bottom we found that cueing significantly biased the observer's perceptions (see Figure 30). A t-test comparing the proportion of time that the observers response is consistent (e.g. a "five" when cued top-left or bottom-right) versus inconsistent with the cueing location (e.g. a "two" when cued top-right or bottom-left) reveals that cueing significantly biased the observers response $t(11) = 2.18, p<0.03$. Therefore, depending on the location of the attentional cue, an identical sequence of line segments appeared as a "two" or a "five".

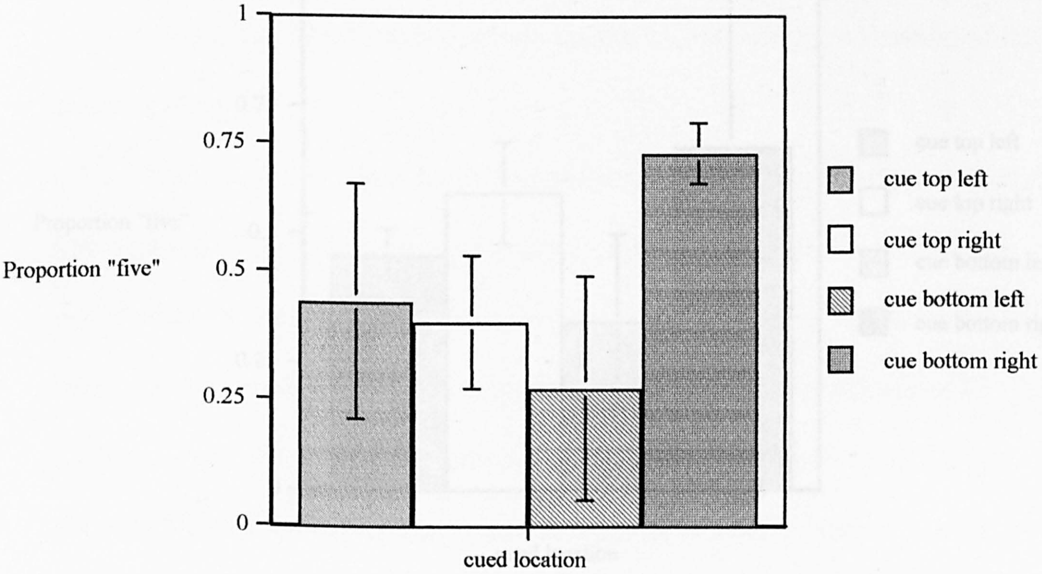


Figure 30. The mean proportion of responding "two" versus "five" across three observers when the stimulus was temporally desynchronised from top to bottom for each cueing condition.

However, Figure 31. illustrates that when the stimulus was desynchronised from the bottom to the top cueing did not significantly bias the observer's response $t(11) = 1.03, p = 0.3$.

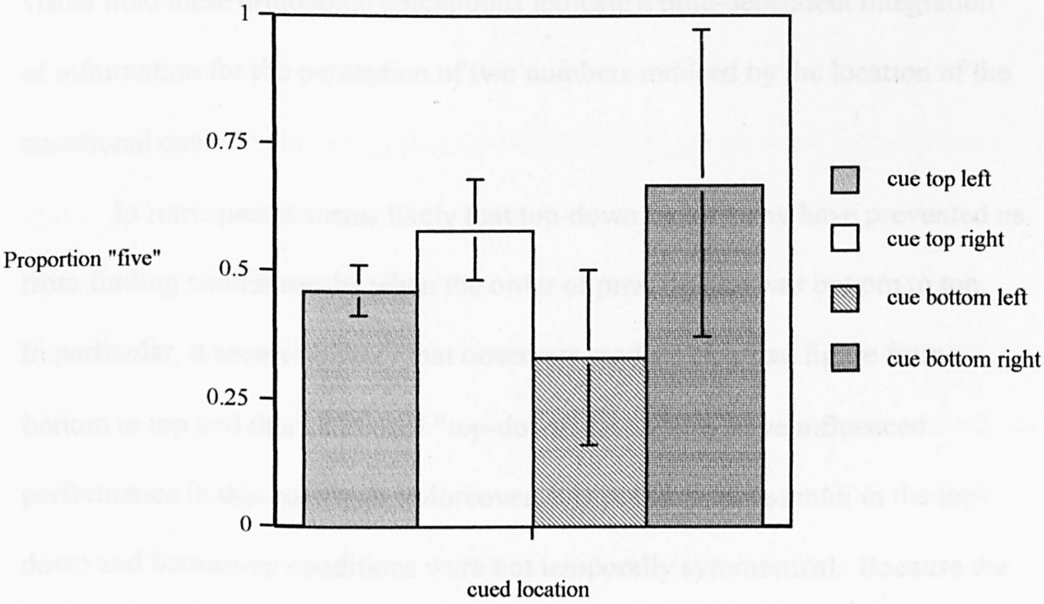


Figure 31. The mean proportion of responding “two” versus “five” for 3 observers when the stimulus was temporally desynchronised from bottom to top for each cueing condition.

Discussion

When the stimulus was temporally desynchronised from top to bottom the results suggest that the observer’s perceptions were directly correlated with the location of the cue. Observers were significantly more likely to respond “two” (vs. “five”) when cued to the top-left and bottom-right (vs. top-right and bottom-left) elements. Thus, these results add weight to the findings from

Chapter 4 that rather than compensating for processing asynchronies across the visual field these orthogonal perceptions indicate a time-dependent integration of information for the perception of two numbers induced by the location of the attentional cue.

In retrospect it seems likely that top-down factors may have prevented us from finding similar results when the order of presentation was bottom to top. In particular, it seems unlikely that observers read a numerical figure from bottom to top and this additional "top-down" factor may have influenced performance in this condition. Moreover, it is possible that stimuli in the top-down and bottom-up conditions were not temporally symmetrical. Because the bottom of the screen is drawn last the temporal gap in the bottom-up condition would have been less than in the top-down condition (Robson and Carpenter, 1997).

Experiment 10

Experiments 7, 8 and 9 suggest that the visual system does not compensate for temporal asynchronies between attended and unattended information. Rather than accounting for the processing advantage offered to attended information it seems that perception mirrors this temporal asynchrony of information processing across the visual field. Consequently presentation of an identical stimulus can induce orthogonal perceptions depending on the focus of attention. In Experiment 7 and 8 a discontinuous line and square stimuli were perceived as either continuous or discontinuous depending on where attention was focused. Moreover, Experiment 9 demonstrated that orthogonal perceptions of a "two" versus "five" were induced by orthogonal cueing despite presentation of an identical desynchronised stimulus.

The results from these studies indicate a time-dependent integration of information around the focus of attention. The present study sets out to examine how attention modulates the temporal integration of information into a unitary perception in more detail. Here we examined how attention modulates the temporal asynchronies required between the elements of a randomly desynchronised stimulus to induce orthogonal perceptions.

In particular, we randomly desynchronised in time the stimulus presented in Experiment 9 (a figure "eight") to derive the optimal onset timing required for each element to induce orthogonal perceptions. Recall that this stimulus should induce orthogonal perceptions depending on which elements of the stimulus are perceived first. For example, if information in the top-left enjoys the perceptual processing advantage observers should perceive a "five". This is because the top-left discriminates a "five" from a "two" (i.e. the top-left element). Thus, if attention speeds up information processing then we would expect that cueing the top-left will bias the observer's response to a "five". Indeed this bias was found in Experiment 9.

In addition to biasing the observer's response cueing should induce orthogonal temporal asynchronies between the elements comprising the stimulus. To illustrate when cued at the top-left information in this location should be processed first. Therefore, the observer's response bias should be optimal when information in this location appears earlier than the information in a spatial location that is further from the cue (e.g. bottom-right). Because two diagonally opposite elements are diagnostic for perception of a "five" (top-left and bottom-right) and a "two" (top-right and bottom-left) we can compare the optimal temporal onset for these two diagonally opposite elements to examine whether the integration of information is time-dependent around the focus of attention. Specifically, the observer's perception should be optimally biased when the diagnostic element nearest the cue appears before the diagonally opposite element. However, if attention does not modulate perception then we should find no such pattern in the temporal asynchrony between these elements.

Method

Participants. 3 University of Glasgow students (under 30 years of age) with corrected to normal vision were paid to participate in the experiment.

Materials. The experiment ran on a Macintosh G4 using the Psychophysics and Pyramid Toolbox for Matlab and the Matlab Pyramid Toolbox (Brainard, 1997; Simoncelli, 1997; Pelli, 1997).

Stimuli. On any given trial, observers were presented with a randomly desynchronised "two" and "five" stimuli superimposed to create an "eight" stimulus. Each element of this stimulus was desynchronised giving seven desynchronised elements in total. To examine the influence of attentional cueing on the observers perception a cue was presented in one of four locations, top-left, top-right, bottom-left or bottom right. Stimuli spanned 5 x 6.8 degrees of visual angle.

Procedure. Each trial started with the presentation of a fixation cross for 1000 ms. To examine the modulation of attention on the observers perception we presented a non-predictive cue to either the top-left, top-right, bottom-left or bottom right of the stimulus. The cue measured 10 pixels in radius (the monitor resolution was 1280 by 1024 pixels) and 1.83 candelas per square metre. The cue was presented for 27 ms and presentation of the randomly desynchronised stimulus began 13 ms after cue onset. Each of the seven desynchronised elements of the stimulus were presented at one of seven randomly selected lags, ranging from 13 ms to 91 ms in equal increments, for 13 ms. Therefore, there was always less than 150 ms between the onset of the cue and offset of the stimulus preventing a saccadic eye movement to the cued location.. In a 2-AFC discrimination task, observers responded either "two" or "five".

As there were a total of four conditions of attention and 140 repetitions the experiment comprised a total of 560 trials. A headrest maintained viewing distance at one meter. Observers were instructed to guess if they were unsure, and to attend to the cues without making eye movements.

Results

To examine the temporal integration of information into each of the orthogonal perceptions we computed the proportion of time observers responded "two' versus "five" for each of the seven temporal lags independently for each of the seven elements in each of the cueing conditions.

Firstly, to examine whether attentional cueing biased the observers' response we computed the proportion of time that observers responded "two" versus "five" for each condition of attentional cueing. The proportion of time observers responded "two" and "five" was averaged across each of the seven temporal lags and across the seven desynchronised elements (see Figure 32 to 34).

Figure 32. illustrates that Observer 1's perceptions were consistent with the cueing location. In other words, this observer's response was biased by attentional cueing. This observer was more likely to respond "five" when cued to the bottom-right. Whereas cueing the top-right and the bottom-left was more likely to induce a "two" response. However, cueing the top-left did not bias this observers response.

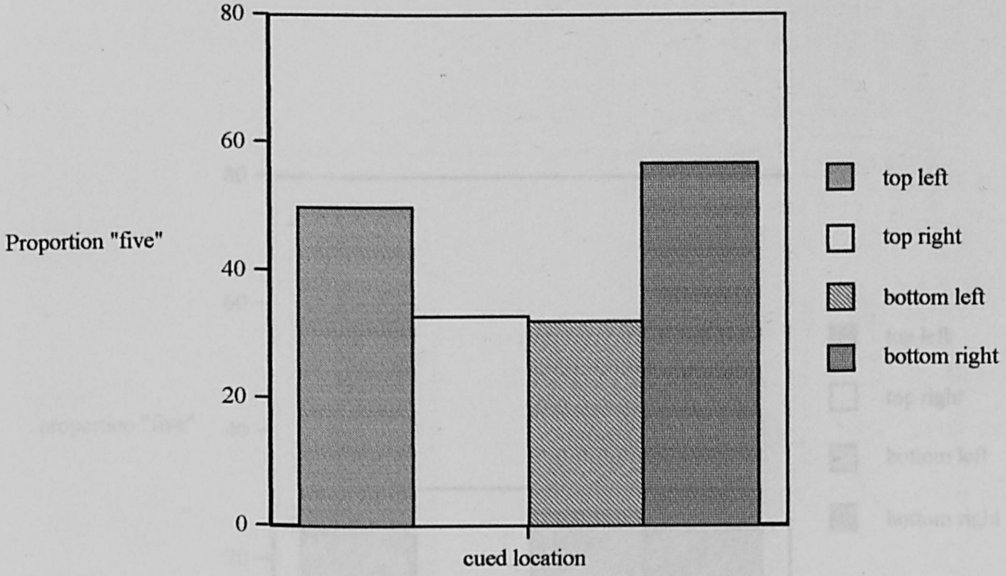
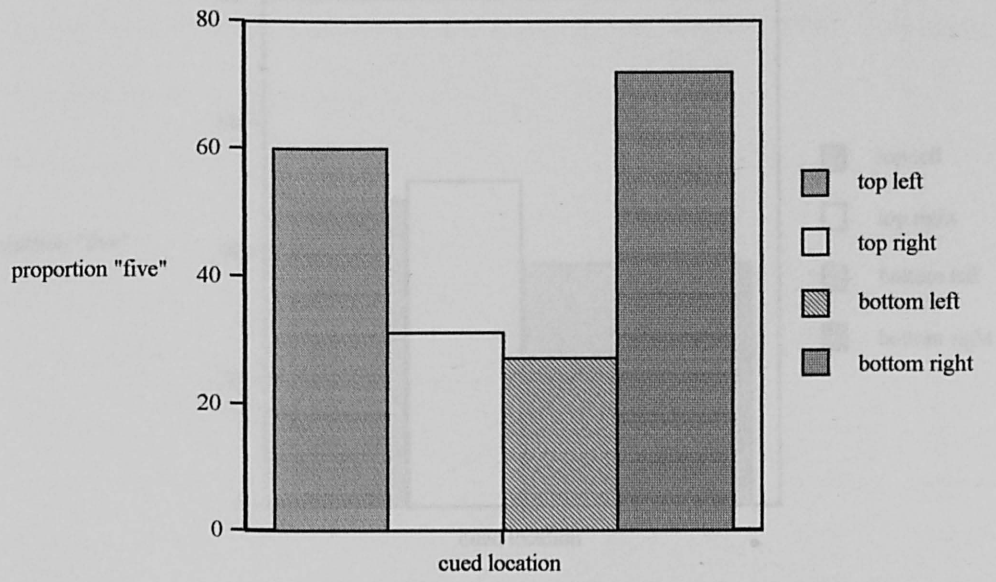


Figure 32. The proportion of time that Observer 1 responded "two" and "five" averaged across all seven temporal lags and the seven elements that comprised the stimulus. This observer was biased by the condition of attentional cueing. Cueing the top-right or the bottom-left were more likely to induce a "two" response whereas this observer was more likely to respond "five" when cued to the bottom-right.

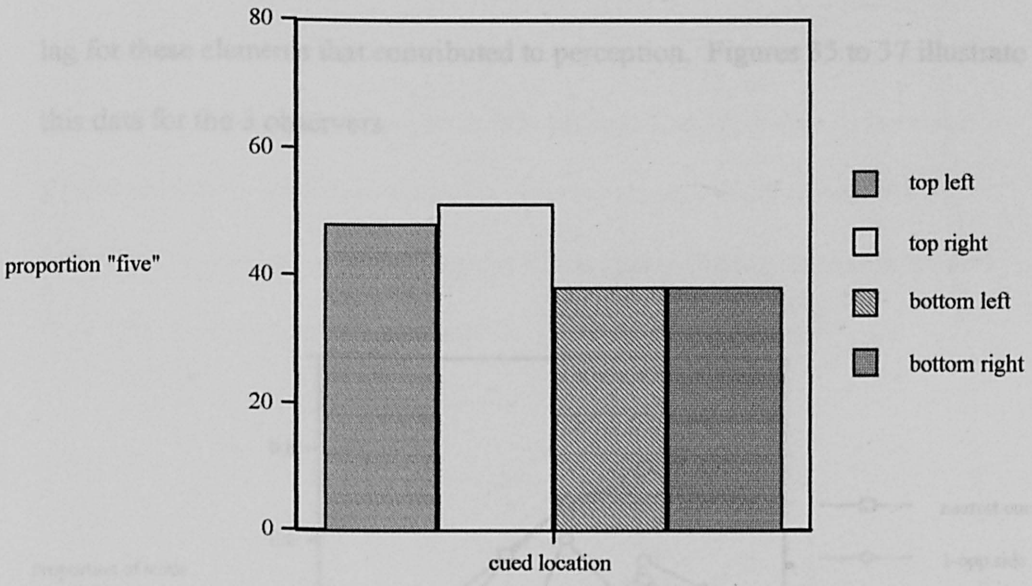
Figure 33. illustrates that Observer 2's response was also biased by the condition of attentional cueing. This Observer was more likely to respond "five" when cued to the top-left and bottom-right. Whereas cueing the top-right and the

bottom-left was more likely to induce a "two" response. The bias in these data was even more pronounced than that observed in Observer 1's data.



<u>Figure 33.</u> The proportion of time that Observer 2 responded "two" and "five" averaged across all seven temporal lags and the seven elements that comprised the stimulus. This observer was also biased by condition of attentional cueing. Cueing the top-right or the bottom-left were more likely to induce a "two" response whereas this observer was more likely to respond "five" when cued to the top-left or the bottom-right.

However, Figure 34. illustrates that Observer 3's response was not biased by attentional cueing.



<u>Figure 34.</u> The proportion of time that Observer 3 responded "two" and "five" averaged across all seven temporal lags and the seven elements that comprised the stimulus. This observer was not biased by condition of attentional cueing.

To further examine the data for each observer we pooled the temporal lag data across cueing conditions for the diagnostic elements. We did this as a function of distance from the cued location. In particular, we pooled the trials into four groups: when the cue occurred nearest to the element, at the opposite side, below and diagonally opposite the element. Furthermore, because the elements at the opposite side and below the cue contribute to perception when they are off we took the difference between these proportions and 1 to derive the lag for these elements that contributed to perception. Figures 35 to 37 illustrate this data for the 3 observers.

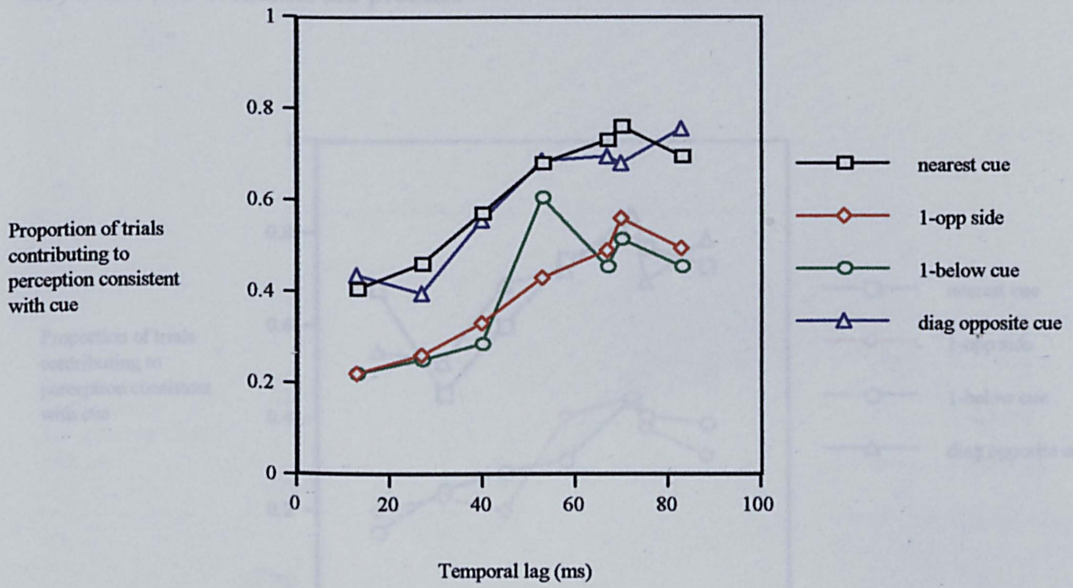


Figure 35. **For observer 1 the temporal lag data pooled according to distance from the cue.**

Figure 35 illustrates that for observer 1 the elements that contribute to perception (nearest cue and diagonally opposite cue) both reach an asymptote at about 67 ms. Because both of these elements seem to optimally contribute to perception at the same time there does not seem to be an effect of distance from the cue for this observer. The elements that contribute to perception when they are absent seem to be less important for perception because they never reach the same proportion as the other two elements. Moreover, they seem to optimally contribute to perception when they are off at approximately the same time as they other two elements are present.

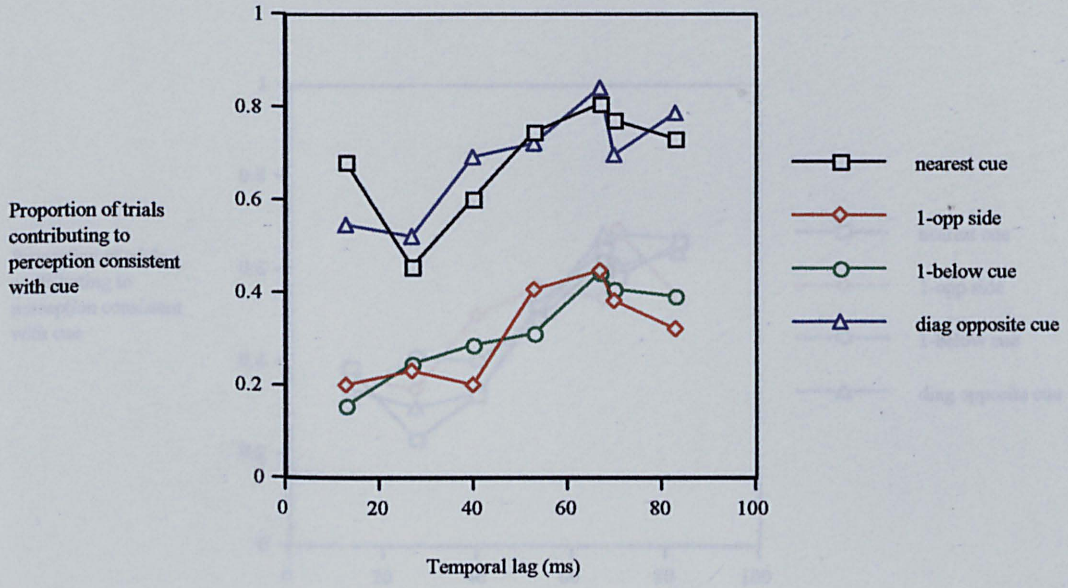


Figure 36. Observer 2 the temporal lag data pooled according to distance from the cue.

Figure 36 illustrates that for observer 2 the elements that contribute to perception (nearest cue and diagonally opposite cue) also both reach an asymptote at about 67 ms. Once more because both of these elements seem to optimally contribute to perception at the same time there does not seem to be an effect of distance from the cue for this observer. Likewise, the elements that contribute to perception when they are absent seem to be less important for perception because they never reach the same proportion as the other two elements. Moreover, one again they seem to optimally contribute to perception when they are off at approximately the same time as they other two elements are present.

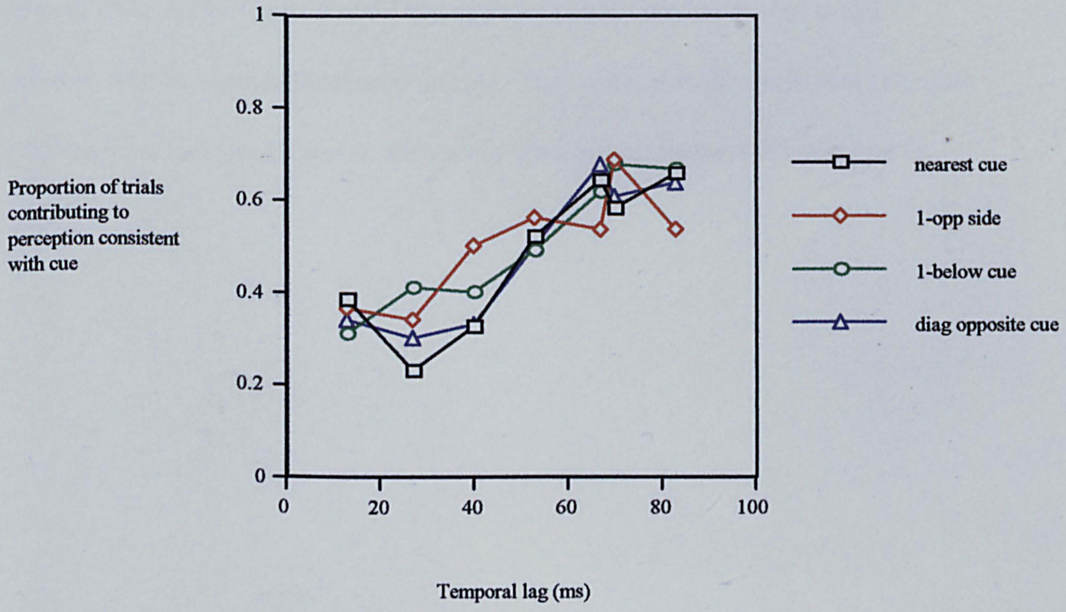


Figure 37. **Observer 3 the temporal lag data pooled according to distance from the cue.**

Figure 37 illustrates that for observer 3 once again the elements that contribute to perception (nearest cue and diagonally opposite cue) reach an asymptote at about 67 ms. So once again because both of these elements seem to optimally contribute to perception at the same time there does not seem to be an effect of distance from the cue for this observer. However here, the elements that contribute to perception when they are absent seem as important for perception because reach approximately the same proportion as the other two elements. Moreover, they seem to optimally contribute to perception if they are off at approximately the same time as they other two elements are off.

Discussion

Generally these results suggest an optimal onset time for elements should be present perception to contribute to perception and offset time for elements that should be absent to contribute to perception. This time seems to be around 67ms. However, because this time is common across all elements there does not seem to be an effect of spatial distance from the cued location. Rather it seems that optimal performance is reached when the onset and offset of the relevant elements is synchronous.

It is possible that temporal constraints may have contributed to this null effect for spatial distance. In particular, the temporal scale of the experiment may have imposed limitations on our design. We searched 7 temporal lags ranging from 13 to 91 ms to find the optimal lag for each element under different conditions of attentional cueing. However, it is possible that attention operates on a finer and shorter time scale than our equipment allowed us to examine.

General Discussion

Experiment 9 suggests that the visual system does not compensate for processing asynchronies across the visual field. Instead, attention can induce orthogonal perceptions depending on its focus. This finding is consistent with the results from Experiment 7 and 8.

However, the results from Experiment 10 suggest that the integration of information into a unitary perception is not time dependent around the focus of attention. It seems likely that mapping the temporal dynamics of attention requires a more sensitive measure than the current methodological constraints would allow. Future research, employing a more refined temporal scale are required to examine how attention modulates the temporal integration of information across the visual field.

Chapter 6

Discussion

1. Aim of Thesis.

In brief, the primary aim of this thesis was to examine how the visual system constructs a seemingly unified and veridical representation from temporally asynchronous information. Physiological, clinical and empirical studies suggest that visual input is functionally segregated (e.g. Livingstone and Hubel, 1988, Zeki, 1973). Moreover, this functional processing results in concurrently presented feature attributes being processed and perceived at different times (Moutoussis and Zeki, 1997). However, findings from the attentional and categorisation literature call into question a fixed account of feature processing. In particular, previous research has demonstrated a processing advantage for attended information (e.g. Carrasco and McElree, 2001). From this literature it seems likely that the enhanced saliency of an attribute will accelerate the processing time of this dimension and consequently should modulate any perceptual asynchrony between concurrently presented features. Moreover, if attention offers a selective processing advantage this should induce processing asynchrony between attended and unattended information across the visual field.

In an attempt to consider the temporal dynamics of perception, the present research set out to examine the influence of task demands and attention on feature processing (Chapter 2 and 3) and how attention modulates perceptual processing across the visual field (Chapter 4 and 5).

2. Chapter Summaries.

2.1. Chapter 2.

In Experiment 1 we developed a novel paradigm to examine the temporal dynamics of feature integration. We employed this method to examine the perceptual asynchrony between colour and orientation. In contrast with Moutoussis and Zeki's (1997a; 1997b) study of perceptual asynchrony we found no asynchrony between these attributes. Consequently, we propose that a flexible account of attribute processing and consequently perceptual asynchrony may explain the discrepancy between our findings and these results.

In the remainder of Chapter 2 we developed this paradigm to investigate this proposal directly. In Experiment 2 and 4 we examined the effect of task requirements on feature integration. However, we found no significant interaction between the experimental conditions. In retrospect, this null effect may have been produced by an experimental confound. Namely, on a given trial presenting a sequence of changing orientations or spatial frequencies may have given rise to apparent motion.

In Experiment 3 we found no effect of the task on the integration of colour and orientation. It seems likely that testing the same observers in both conditions produced cross over effects in this experiment.

2.2. Chapter 3.

In this Chapter we set out to disentangle the influence of attention on the integration of two information sources into a unitary perception. The results from Experiment 5 demonstrated that attention enhances the integration of two information sources into a unitary perception for stimuli arranged in a line. This result was replicated across the visual field for an observer in Experiment 6. However, it seems likely that the large number of trials prevented this result from being replicated for a second observer in this experiment.

The results from Experiment 5 suggest that attention does not enhance the integration of attribute information by decreasing the perceptual asynchrony between the attributes comprising the stimuli. Observers were faster at perceiving an emergent perception that resulted from a change in form (form first trials) in both attended and unattended conditions. From the attentional literature (Carrasco and McElree, 2001; Hiosaka *et al*, 1992; Stelmach and Herdman, 1991; Posner *et al*,1980) it seems likely that attention enhances feature integration by speeding up the perceptual processing time of each attribute by an equal magnitude

The findings from these experiments add weight to our proposal that perceptual processing of independent feature dimensions appears to be flexible, rather than fixed.

2.3. Chapter 4.

In Chapter 4 we examined the influence of attention on the integration of information across the visual field. By desynchronising a line (Experiment 7) and a square (Experiment 8) stimulus we found that increasing temporal asynchronies between the elements of a stimulus are tolerated with eccentricity from the focus of attention. In turn, the perception of a discontinuous stimulus as either a continuous or discontinuous perception depends on where attention is focused.

These studies imply that the visual system does not compensate for selective attentional acceleration of information processing across the visual field. Rather, it seems that perception mirrors the increase in processing time with eccentricity from the focus of attention. These studies suggest that our visual system provides us with a temporally non-veridical perception.

2.4. Chapter 5.

In Chapter 5 we set out to extend the findings from Chapter 4. The findings from Experiment 9 also suggests that the visual system does not compensate for processing asynchronies across the visual field. Instead, attention can induce orthogonal perceptions depending on its focus a finding that is consistent with the results from Chapter 4.

However, the results from Experiment 10 suggest that the integration of information into a unitary perception is not time dependent around the focus of attention. It seems likely that mapping the temporal dynamics of attention requires a more sensitive measure than the current methodological constraints would allow. Future research, employing a more refined temporal scale are required to examine how attention modulates the temporal integration of information across the visual field.

3. Methodological Problems

In Chapter 1 we developed a novel paradigm to examine the time to integrate attributes into a new perception. However, it should be noted that the temporal measure that we derive might include not only the time required to integrate attributes but also the time required to "unbind" previously bound attributes and the time required for binding itself if such a stage occurs. As yet we do not know whether such separate stages are involved in feature integration and a more refined measure would be required to determine if this is the case. Therefore, at present we had to content ourselves with a general temporal measure of the binding process.

Moreover, using this paradigm we attributed any modulation in the threshold required to perceive the emergent perception as arising from a modulation in the perceptual processing of the leading attribute. However, it could be argued that modulation might reflect a change in decision criterion rather than perceptual processing. Using the current paradigm it is impossible to disentangle these possible effects.

The temporal characteristics of the equipment employed presented a consistent problem throughout our studies. Because observers make saccadic eye movements in around 150 ms the temporal distance between cue onset and asynchrony offset had to be less than this time. However, the frame rate of the monitor employed was 75Hz (13.3 ms). Therefore, only around 10 temporal points could be sampled within this range to determine the temporal dynamics of perceptual processing. This imposed a considerable constraint on our studies that no doubt had consequences for our results.

In addition, there seem to be large differences between temporal measures between observers. This finding is consistent in literature studying temporal perception (e.g. Moutoussis and Zeki, 1997a; 1997b) and throughout each of the experiments conducted in this thesis. As such it seems likely that the latter experiments carried out in Chapter 5 did not have enough observers to overcome this problem. Moreover, the Experiments carried out in Chapter 4 did not have enough trial repetitions to account for such discrepancies.

Finally, in the paradigm employed in Chapter 1 and 2 a stimulus is presented in the same location as the target both before and after its presentation. This could lead to both forward and backward masking. Generally, masking is the reduction of performance when a bright field is presented in the same location as the target (Sperling, 1960). This effect is commonly attributed to erasure of iconic memory. Recent work suggests that low level factors (e.g. luminance) and higher level factors such as attention contribute to this effect (Di Lollo *et al* 2001). To illustrate possible masking effects in the current experiments consider a trial when the stimulus asynchronously alternate between *red-left* and *green-right* with colour preceding orientation. Here, there may be forward masking of the colour of the target (*green-left*) with the initial stimulus and backward masking of orientation of the target with the final stimulus. However, any such effect would be consistent across all conditions therefore would be a constant variable. In the current experiments we were interested in the flexibility of processing under different experimental conditions rather than a definitive and fixed processing time. Therefore, any such constant variable does not seem relevant.

4. Conclusions.

Three major points have emerged from the findings of the experiments reported. Firstly, these experiments add weight to the proposal that visual processing is not synchronous and that this asynchrony is revealed in perception. Temporal asynchrony between different visual attributes (e.g. colour and orientation) and across the visual field was a consistent finding across the experiments we conducted. Secondly, because this asynchrony is revealed in perception it seems that the visual system fails to account for processing asynchrony between feature information. In addition, the visual system does not appear to compensate for processing asynchrony across the visual field. Rather it seems our mistake lay in assuming that the visual system achieves a temporally veridical representation. Finally, any asynchrony between information processing does not appear to be fixed. Instead the experimental or attentional demands of the task seem to modulate the perceptual processing time of feature (or localised) information. Consequently, any temporal asynchrony between information can also be modulated

5. Theoretical Implications.

To return to our point of enquiry, how does the visual system provide us with a phenomenologically unified perception from asynchronous information? This question seems even more relevant in the light of the present observations. However, if we turn our findings on their head it seems plausible that the unified perception that is our experience arises as a consequence of processing flexibility. Perhaps, factors such as attention and categorisation serve to conceal the temporal constraints of the visual system. These factors may provide the visual system with a representation that is "temporally veridical enough" for the beholder to successfully interact with the environment it evolved to represent. Of course an extensive program of future research examining the temporal dynamics of perception is required to qualify this proposal.

This conclusion is reminiscent of literature concerned with the spatial properties of visual perception. Here, it is well known that the visual system does not construct a veridical perception. Recent phenomena, for example, inattentional blindness (Most *et al*, 2001) and the failure of perception demonstrated in change detection tasks ("change-blindness") (O'Regan, 1992; Phillips and Singer, 1974; Rensink, 1999; Singer and Phillips, 1974) reveal the limitations of visual perception.

In particular, future research is required to examine the effect of categorisation on perceptual processing in more detail. Future studies are also required to investigate whether for example, task requirements and colour categorisation modulate the speed with which attributes are processed. If these factors do modulate perceptual processing then how does this influence feature integration?

In addition, we need to clearly establish whether attention can modulate perceptual asynchrony. For example, if attention is drawn to one attribute can the perceptual asynchrony between feature attributes be modulated? Moreover, do factors that increase salience modulate perceptual asynchrony in a similar way?

It would also be interesting to examine the extent to which perceptual asynchrony between object information results in "illusory conjunctions". If attention or salience increase perceptual processing and consequently modulates the perceptual asynchrony between different attribute features do these factors also induce "illusory conjunctions"?

Moreover, temporal processing across the visual field warrants future examination. From our studies it seems that an attentional cue can induce orthogonal perceptions depending on its location. However, a finer temporal scale is required to directly measure the temporal dynamics of information processing across the visual field.

Finally, this thesis, in retrospect somewhat naively, considered what seemed to be a unique quandary concerning the temporal integration of visual information. However, it is now clear that this issue incorporates a host of theoretical questions that merit empirical study. For example, Which factors modulate perceptual processing? How do these factors influence perceptual asynchrony and perhaps conversely feature integration? What is the relationship between perceptual asynchrony and feature integration? These problems must be addressed independently and no doubt each one will lead to a generation of questions of their own.

It seems that vision science has dedicated itself primarily to understanding how the visual system processes information across space perhaps at the cost of understanding the temporal dynamics of perception (Walsh, 2002).

However, understanding the "when" of perception may prove to be as much of a challenge.

References

Arnold, D. H., Clifford, C.W.G., and Wenderworth, P. (2001) Asynchronous processing in vision: Color leads motion. *Current Biology*, **11**, 600.

Bartels, A., and Zeki, S. (2000) The architecture of the colour centre in the human visual brain: new results and a review. *European Journal of Neuroscience*, **12**, 172-193.

Bartels, A., and Zeki, Z. (1998) The Theory of multistage integration in the visual brain. *Proc R Soc Lond* B, **265**, 2527-2332.

Bender, M.B., and Feldmen, M. (1972) The so-called visual agnosias. *Brain*, **95**, 173-186.

Brainard, D. H. (1997) The Psychophysics Toolbox. *Spatial Vision*, **10**, 433-436.

Campbell, F.W., and Maffei, L. (1981) The influence of spatial frequency and contrast on the perception of moving patterns. *Vision Research*, **21**, 713-721.

Carrasco, M., and McElree, B. (2001) Covert attention accelerates the rate of visual information processing. *PNAS*, **98**, 5363-5367.

Cavanagh, P., Tyler, C.W., and Favreau, O.E. (1984) Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America*, **1**, 893-899.

Cumming, B. G. and DeAngelis, G.C. (2001) The Physiology of Stereopsis. *Annual Review of Neuroscience*, **24**, 203-238.

DeValois and DeValois (1990) Spatial Vision. Oxford University Press.

Di Lollo, V., Enns, J., and Rensink, R.A. (2000) Competition for consciousness among visual events: The psychophysics of re-entrant visual processes. *Journal of Experimental Psychology: General*, **129**, 481-507.

Farah, M. (2000) The Cognitive Neuroscience of Vision. Blackwell Publishers.

Gegenfurtner, K.R. (2001) Color in the cortex revisited. *Nature Neuroscience*, **4**, 339-340.

Gegenfurtner, K.R. (1997) Colouring the cortex. *Nature*, **388**, 23-24.

Gegenfurtner, K.R., and Hawken, M.J. (1996) Interaction of motion and color in the visual pathways. *Trends in Neuroscience*, **19**, 394-401.

Gegenfurtner, K. R., Kiper, D.C., and Fenstemaker, S.B. (1996) Processing of color, form, and motion in macaque area V2. *Visual Neuroscience*, **13**, 161-172.

Gegenfurtner, K.R., and Sharpe, L.T. (2001) Color Vision: From Genes to Perception. Cambridge University Press.

Goldstone, R. (1994) Influences of Categorisation on Perceptual Discrimination. *Journal of Experimental Psychology: General*, **123**, 178-200.

Hiosaka, O., Miyauchi, S., and Shimojo, S. (1992) Focal visual attention produces illusory temporal order and motion sensation. *Vision Research*, **33**, 1219-1240.

Holcombe, A.O., and Cavanagh, P. (2001) Early Binding of feature pairs for visual perception. *Nature Neuroscience*. 4, 127-128.

Hubel, D. H., and Livingstone., M.S. (1987) Segregation of Form, Color and Stereopsis in Primate Area 18. *The Journal of Neuroscience*, **7**, 3378-3415.

Johnson, E.N., Hawken, M.J., and Shapley, R. (2001) The spatial transformation of color in the primary visual cortex of the macaque monkey. *Nature Neuroscience*, **4**, 409-416.

Kingdom, F.A.A., and Simmons, D. (2000) The Relationship between Colour Vision and Stereoscopic Depth Perception. *Journal of the society for 3D Broadcasting and Imaging*, **1**, 10-19.

Livingstone, M., and Hubel, D. (1988) Segregation of Form, Color, Movement, and Depth: Anatomy, Physiology, and Perception. *Science*, **240**, 740-749.

Lu, C., and Fender, D.H. (1972) The Interaction of Colour and Luminance in Stereoscopic Vision. *Investigative Opthalmology*, **11**, 482-490.

Morrison, D, J. and Schyns, P.G. (2001) Usage of spatial scales for the categorisation of faces, objects, and scenes. Psychonomic Bulletin & Review, 8, 454-469.

Most, S.B., Simons, D.J., Scholl, B.J., Jimenez, R., Clifford, E., and Chabris, C.F. (2001) HOW NOT TO BE SEEN: The Contribution of Similarity and Selective Ignoring to Sustained Inattentional Blindness. *Psychological Science, 12,* 9-17

Moutoussis, K., and Zeki, S. (1997a) Functional segregation and temporal hierarchy of the visual perceptive systems. *Proceedings of the Royal Society of London*. B. **264**, 1407-1414.

Moutoussis, K., and Zeki, S. (1997b) A direct demonstration of perceptual asynchrony in vision. *Proceedings of the Royal Society of London*. B. **264**, 393-399.

Nishida, S., and Johnston, A. (2002) Marker Correspondence, Not Processing Latency, Determines Temporal Binding of Visual Attributes. *Current Biology*, Vol 12, 359-368.

Nishida, S., and Johnston, A. (2001) Time Perception: Brain time or event time. *Current Biology*, **11**, R427-R430.

Oliva, A., and Schyns, P. (1997) Flexible, diagnosticity-driven, rather than fixed, perceptually determined scale selection in scene and face recognition. *Perception*, **26**, 1027-1038.

Oliva, A., and Schyns, P. (2000) Diagnostic Colors Mediate Scene Recognition. *Cognitive Psychology*, **41**, 176-210.

O'Regan, J.K. (1992) Solving the "real" mysteries of visual perception: the world as an outside memory. *Canadian Journal of Psychology* **46**, 461-468.

Özgen, E., and Davies, I.R. (2002) Acquisition of Categorical Color Perception: A Perceptual Learning Approach to the Linguistic Relativity Hypothesis. *Journal of Experimental Psychology: General*, **131**, 477-493.

Pashler, H. E. (1999) The Psychology of Attention. The MIT Press.

Pelli, D.G. (1997) The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, **10**, 437-442.

Phillips, W.A., and Singer, W. (1974) Function of On and Off Transients in

Vision. Psychophysics. *Experimental Brain Research* **19**, 493-506.

Poggio, G.F. (1995) Mechanisms of stereopsis in monkey visual cortex. *Cerebral Cortex*, **3**, 193-204.

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.

Rensink, R.A., O'Regan, J.K., and Clark, J.J. (1999) The Need for Attention to Perceive Changes in Scenes. *Psychological Science* **8**, 368-373.

Reynolds, J.H., and Desimone, R. (1999) The Role of Neural Mechanisms of Attention in Solving the Binding Problem. *Neuron*, **24**, 19-29.

Rizzo, M., and Vecera, S.P. (2002) Psychoanatomical substrates of Bálint's syndrome. *Journal of Neurological and Neurosurgical Psychiatry*, **72**, 162-178.

Robson, J.G., and Carpenter, R.H.S. (1997) Vision Research: A practical approach. Oxford University Press.

Sacks, O. (1995) An Anthropologist on Mars. Picador.

Shafritz, K. M., Gore, J.C., and Marois, R. (2002) The role of the parietal cortex in visual feature binding. *PNAS*, **99**, 10917-10922.

Schyns, P.G. and Oliva, A. (1999) Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition*, **69**, 243-265.

Simoncelli, E.P. (1997). Image and Multi-scale Pyramid Tools [Computer software] NewYork: Author.

Singer, W., and Phillips W.A. (1974) Function of On and Off Transients in

Vision. *Experimental Brain Research* **19**, 507-521

Stelmach, L.B., and Herdman, C.M. (1991) Directed Attention and Perception of Temporal Order. *Journal of Experimental Psychology, Human Perception and Performance*. **17**, 539-550.

Sowden, P.T, Özgen, E, Schyns, P.G., and Daoutis, C. (in Press) Expectancy effects on spatial frequency processing. Vision Research.

Sperling, G. (1960) The information available in brief visual presentations. *Psychological Monographs*, **74** (11).

Tanaka, J., Weiskopf, D., and Williams.P. (2001) The role of colour in high-level vision. *TRENDS in Cognitive Sciences*, **5**, 211-215.

Tootell, R.B., Hadjikhani, N.K., Vanduffel, W., Liu, A.K., Mendola, J.D., Serenno, M., and Dale, A.M. (1995) Functional analysis of primary visual cortex (V1) in humans. Proceedings of Natural Academy Science, 95, 811-817.

Treisman, A. (1996) The binding problem. *Current Opinion in Neurobiology*, **6**, 171-178.

Treisman, A., and Schmidt, H. (1982) Illusory Conjunctions in the perception of Objects. *Cognitive Psychology*, **14**, 107-141.

Treisman, A., and Gelade, G. (1980) A feature integration theory of attention. *Cognitive Psychology*, **12**, 97-136.

Tse, P. U. (in preparation) Mapping the distribution of spatial attention using change blindness as a probe. *Special Issue of Cognitive Science* on behavioural techniques for visualising information about information processing (Schyns, P.G. and Gosselin, F editors).

Viviani, P., and Aymoz, C. (2001) Color, form and motion are not perceived simultaneously. *Vision Research*, **41**, 2909-2918.

von der Malsburg, C. (1981) The Correlation Theory of Brain Function. MPI Biophysical chemistry report 81-82. Reprinted in E., Domay, J.L, vanHemmen, & K. Schulten. (1994). *Models of Neural Networks II (1994)* (Eds.), (pp. 95-119) Berlin: Springer.

Walsh, V. (2002) Vision. The When of Perception. *Current Biology*, **12**, R355-R356.

Wandell, B.A. (2003) Computational Neuroimaging of Human Visual Cortex. *Annual Reviews Neuroscience*, **22**, 145.

Watson, A.B., and Pelli, D.G. (1979) QUEST; A Bayesian adaptive psychometric method. *Perception and Psychophysics*, **33**, 2, 113-120.

Weiskranzt, L. (1990) Blindsight: A Case Study and Implications. Oxford University Press.

Yeshurun, Y., and Carrasco, M. (1999) Spatial attention improves performance in spatial resolution tasks. *Vision Research*, **39**, 293-306.

Yeshurun, Y., and Carrasco, M. (1998) Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, **396**, 72-75.

Zeki, S.M. (2001) Localization and Globalization in Conscious Vision. *Annual Review of Neuroscience*, **24**, 57-86.

Zeki, S.M. (1997) The Colour and Motion Systems as Guides to Conscious Visual Perception. *Cerebral Cortex*, **12**, 777-809.

Zeki, S.M. (1993) A Vision of the Brain. Blackwell Science.

Zeki, S.M. (1990a) Parallelism and Functional Specialization in Human Visual Cortex, *Cold Spring Harbour Symposia on Quantitative Biology*, **LV**, 651-661.

Zeki, S.M. (1990b) A century of cerebral achromatopsia, *Brain*, **113**, 1721-1777.

Zeki, S.M., (1980). The response of cells in the anterior bank of the superior temporal sulcus in macaque monkeys. *Journal of Physiology*, **308**, 85.

Zeki, S.M, (1973). Colour coding in rhesus monkey prestriate cortex. *Brain Research*, **53**, 422-427.

Zeki, S.M,, Aglioti, S., McKeefry, D., and Berlucchi, G. (1999) The neurological basis of a conscious color perception in a blind patient. *PNAS*, **96**, 14124-14129.

Zeki, S.M,, and Bartels, A. (1999) Toward a Theory of Visual Consciousness. *Consciousness and Cognition*, **8**, 255-259.

Zeki, S.M., and Marini.L. (1998) Three cortical stages of colour processing in the human brain. *Brain*, **121**, 1669-1685.

Zeki, S.M., and Bartels, A. (1998a) The autonomy of the visual systems and the modularity of conscious vision. *Philisophical Transactions of the Royal Society of London B*, **353**, 1911-1914.

Zeki, S.M., and Bartels, A. (1998b) The asynchrony of consciousness. *Proc R Soc Lond* B, **265**, 1583-1585.

Zihl, J., Von Cramon, D., and Mai, N. (1983) Selective disturbance of movement vision after bilateral brain damage, *Brain*, **106**, 313-340.