Response latencies to chromatic and achromatic visual stimuli

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Abstract

There has been considerable debate about how visual information is processed for the perception of stimuli and the generation of motor responses to the same stimuli. While there are well-documented differences in conduction latencies of the luminance and chromatic pathways, it is unclear if information that is integrated from these pathways is used in a similar way across motor and perceptual tasks. Key aspects of human behaviour have different requirements in terms of the spatial and temporal resolution required to complete the task. Certain tasks may therefore rely on processing of information that has spatial or temporal characteristics that are most informative for that specific task. Three studies examined tasks with different task demands; a simple reaction time task, three perceptual asynchrony tasks and a reaching task. Differences in processing for perceptual and motor responses were investigated by measuring differences in the relative response latencies to chromatic and luminance stimuli in these tasks.

In the first study, I investigated ways to equate the contrast of different chromatic and luminance stimuli. I then measured RTs to these stimuli as a function of contrast. RTs to luminance stimuli were approximately 45 and 60 ms shorter than RTs to L-M and S-cone stimuli respectively. RTs decreased as a function of contrast more rapidly to luminance stimuli than to chromatic stimuli.

In the second study, I used three tasks to investigate relative latencies with which chromatic and luminance stimuli were perceived to appear. I demonstrated that two of the existing tasks typically used to investigate

perceptual asynchrony were unsuited for this comparison. I then developed a task that determined the minimum backmask onset delays that allowed participants to accurately locate stimuli. The differences in the delays between the pathways indicated the differences in the latencies in when the stimuli appeared to participants. The temporal advantage for the luminance pathway was only approximately 9 and 14 ms over the L-M and S-cone pathways respectively.

In the final study, I examined the delays in correcting rapid reaches to luminance and chromatic stimuli. The temporal advantage for the luminance pathway was approximately 15 and 20 ms over the L-M and S-cone pathways respectively.

The temporal advantage found for the luminance pathway in the RT task may be larger than the advantage that would be predicted on the basis of differences in conduction latencies alone. Thus, the relatively rapid decrease in RT with contrast for the luminance pathway, and the large dissociation in the response latencies measured in the RT and perceptual tasks, is consistent with there being separate decision making processes for RT and perception, with the RT response being relatively more reliant on luminance information. The reaching correction response however appears to rely on a similar contribution from the pathways to the perception of the stimuli. It is discussed how these stimuli and results could be readily utilised to extend these comparisons to further develop understanding of commonality and differences in processing visual information for different visual tasks.

Contents

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Abbreviations

(in order of appearance)

L-M	L-M opponent or parvocellular retino-geniculate pathway
S-cone	S-cone opponent or koniocellular retino-geniculate pathway
RT	Simple reaction time
VEP	visually evoked potential
TOJ	temporal order judgement
SJ	simultaneity judgement
AFC	alternative forced choice
MOA	mask-onset asynchrony
L	long wavelength photoreceptive cone
M	medium wavelength photoreceptive cone
S	short wavelength photoreceptive cone
LGN	lateral geniculate nucleus
MT	middle temporal
PPC	posterior parietal cortex
MB-DKL	MacLeod, Boynton, Derrington, Krauskopf & Lennie colour space
CRT	cathode ray tube
RMS	Root mean square
MDT	Multiples of detection threshold
PA	perceptual asynchrony
SOA	stimulus onset asynchrony
ART	anticipatory reaction time

1. Introduction

1.1. Do the different visual pathways have similar contributions to different visual functions?

Humans have an achromatic (luminance) geniculate pathway, and chromatic L-M and S-cone pathways that convey visual information from the retina to higher brain areas. In this thesis, I explore the degree to which chromatic and luminance pathways contribute to different functions of human vision such as forming a perception of the environment or controlling motor responses. For example, humans have evolved to eat ripe vegetation and this simple action involves different tasks such as first identifying ripe vegetation amongst foliage, and then guiding a hand to it (Bompas, Kendall, & Sumner, 2013). But in theory, these two tasks may require different aspects of visual information in order for performance to optimised. The selection of ripe vegetation amongst the foliage requires considerable chromatic information. The task of selecting fruit (Sumner & Mollon, 2003) and foliage (Dominy & Lucas, 2001) itself has been proposed to be a driving force in the evolution of primate trichromacy. Clearly, the task requires sufficient chromatic information to clearly see differences in shades of red through to green that are relatively close to each other on the visible spectrum.

The accurate guidance of reaching to objects involves continuous feedback about the locations of the hand and target (see Wolpert, Ghahramani, & Jordan, 1995; van Beers, Baraduc, & Wolpert, 2002; Saunders & Knill, 2004; Ma-Wyatt & McKee, 2007). The luminance pathway has a faster neural conduction rate than the chromatic pathways (Nowak, Munk, Girard, & Bullier, 1995; Cottaris & De Valois, 1998; Maunsell *et al.*, 1999; Reid & Shapely, 2002). Therefore, the visual system could have evolved to primarily use the faster luminance information when guiding the hand as errors could be

detected sooner, and so online corrections could also occur faster. So, is it the case that humans perceive their environment with a system that relies heavily on chromatic information, while reaching guidance uses a system that relies relatively heavily on luminance information? A separation in processing would seem to allow better performance on the two tasks. However, an alternative might be that the visual brain combines information from the different pathways, and then uses the same combined information to both perceive the appearance of targets and to guide reaches to them. This latter system is suggested to be more parsimonious (Miller & Schwarz, 2006).

A similar question that lends itself more to direct experimental comparison can be framed in terms of the simple reaction time (RT) task. In this task, a participant is told to press a button, and release it when they see a stimulus appear. A lay participant may assume that they will consciously perceive the stimulus, and then release the button as a consequence. However, while the participant may both perceive the target appearing, and release the button, it is unclear how a subjective perception could play a causative role in the release of the button. A testable question is whether the processing that identifies the appearance of the stimulus that leads to the percept of it, is the exact same processing that leads to the release of the button. Alternatively, the processing that leads to the percept of the stimulus and to the RT response could have been separated earlier in the processing hierarchy, before the stage where the appearance of the stimulus is identified. If so, it could be that the RT response relies relatively heavily on the faster luminance information to support faster responses, as was suggested for the reaching correction responses above.

I examined the similarity of neural processing for perceiving stimuli and reacting to stimuli. Understanding whether these tasks use common processing or different processing will provide insight into the broader principles underlying neural processing. To explore this question, I determined how participants respond to luminance, L-M and

S-cone stimuli in three different types of tasks. The first publication examines simple RTs to chromatic and luminance stimuli over a range of contrasts. The second publication focuses on when the chromatic and luminance stimuli are affected by masking. The third publication examines the speed and accuracy with which participants reached to a target that changed location in mid-flight. The exegesis includes a discussion of what the differences in responses to chromatic and luminance stimuli across these tasks suggests about the processing of visual information for these tasks.

1.2. Responses require neural decision making

It is commonly assumed that responses to the appearance of stimuli require the stimulus to be detected by a neural decision making system. This assumption is supported by neurally inspired models of the neural mechanisms underlying RT responses, such as Shadlen, Britten, Newsome, and Movshon's (1996) model or Smith and Ratcliff's (2004) diffusion model. Smith and Ratcliff's (2004) model is illustrated in Figure 1.

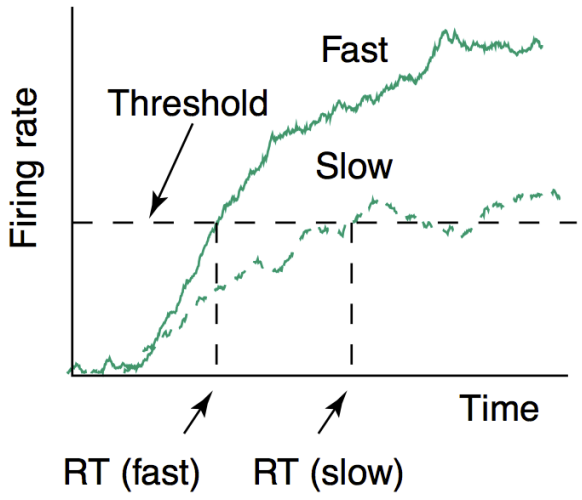

Figure 1. RT modeled as function of contrast. RT (fast) is the response to a high contrast stimulus and RT (slow) is the response to a low contrast stimulus. RT is determined by a firing rate reaching a criterion threshold. This firing rate increases faster when there is more information input into the system (from Smith & Ratcliff, 2004).

In this model, RTs can be predicted with two key parameters; the rate of information accumulation and the threshold criterion. The rate of accumulation is thought to reflect the accrual of information towards the decision and therefore varies with changes to a stimulus that change the amount of information present, such as stimulus contrast or motion coherence levels. Accumulation starts as soon as the stimulus is presented. Information about the presence of the stimulus continues to accumulate in the system (while the stimulus is still present) by increasing the rate of activity of the decision making system as a stochastic process. This increase continues until the decision-making system reaches its decision threshold criterion. Reaching this level constitutes a decision that then activates the motor plan to execute the RT response. The level of this criterion then determines the amount of information that needs to be collected before the RT response is released, or the degree of certainty required that the stimulus exists. The higher this criterion level is, the less likely a participant is to release the button on a catch trial when no stimulus is presented.

It appears that a similar decision making process is involved in perceiving stimuli (Palmer, Huk, & Shadlen, 2005) and this is assumed in the perceptual tasks examined in the literature review below (e.g, Lee, Mollon, Zaidi, & Smithson, 2009). In this case, the participant would perceive a stimulus (or accurately indicate its location), when the decision making system reached its decision criterion. Similarly, in the reaching task, the visuomotor system may also begin to correct the path of a reach when a similar detection process occurs.

In this thesis, I explored whether these three visual tasks rely on a common processing or decision making system. In particular, is it likely that chromatic and luminance information is integrated in a stage before it goes into a single decision making system that is used for all of the tasks examined here? Or, alternatively, are different decision making systems used for different tasks. This is explored by

examining whether all of the tasks appear to be similar in how they use chromatic and luminance input.

2. Literature review

Colour vision is a key part of vision in many species. All Old World monkeys, apes and humans have trichromatic vision (Bowmaker, Astell, Hunt, & Mollon, 1991; Dulai, Bowmaker, Mollon, & Hunt, 1994; Jacobs, Neitz, Deegan, & Neitz, 1996; Hunt *et al.*, 1998; Dulai, von Dornum, Mollon, & Hunt, 1999; Jacobs & Deegan, 1999; Kainz, Neitz, & Neitz, 1998). As predicted by Young (1802; as cited in Solomon & Lennie, 2007), human (and catarrhine) trichromacy is based on there being three different types of photoreceptive cones in the retina. Light is absorbed and transduced by the long (L), medium (M) and short (S) wavelength cones which are most sensitive to light of approximately 560, 530 and 430 nm respectively.

The luminance, L-M and S-cone geniculate pathways described below, are named for how they combine the information from the L, M and S cones. These three pathways take information from the retina and convey it back to the lateral geniculate nucleus (LGN). The pathways remain distinct as they convey information to the different layers and sides of the LGN (Hubel & Wiesel, 1972). The different pathways remain separate until V1/V2, where information from the different pathways can then be combined as discussed in 2.2.

This segregation of the pathways though the LGN presumably has a function. It may require some continuation of this segregation to allow different areas to rely on different relative balances of chromatic and luminance information (e.g., MT and V4, Zeki, 1978). However, it is unclear how this difference in the balance of chromatic and luminance information used in some cortical regions, translates into functional differences in how perceiving and reacting to stimuli relies differently on chromatic and luminance information.

In the literature review below, I discuss the characteristics of the pathways in detail as a basis for considering how they may be suited to the tasks used in this thesis. While there has been much research characterising the morphology and responses of the pathways, the review below demonstrates that it is unclear how these different pathways might contribute to different visual tasks, and how the processing of information might differ between tasks.

2.1. The geniculate pathways

2.1.1. The achromatic or luminance pathway

The achromatic, luminance or magnocellular pathway conveys achromatic information as it has the same types of photoreceptors in both the excitatory and inhibitory parts of its receptive fields. Each part of the receptive field is comprised primarily of L and M, and a limited number of S wavelength cones (Lee, Pokorny, Smith, Martin, & Valberg, 1990; Chatterjee & Callaway, 2002). For this reason is it sometimes called the (L+M) or (L+M+S) pathway. The balance of inputs from the excitatory and inhibitory parts of their receptive fields is such that if the whole of the receptive field is illuminated, the excitatory and inhibitory responses roughly cancel out. However, if light were to strike the excitatory component of the receptive field, but only a part of the inhibitory component, then there would be an overall increase in luminance ganglion cell activity from baseline. Light falling differently on the two components of the receptive fields, or activity in the ganglion cells different to baseline, therefore indicates a region of luminance contrast.

The achromatic cells are more heavily myelinated than the chromatic pathways, giving them a relatively large diameter (Wiesel & Hubel, 1966) and a faster conduction

velocity. The achromatic response is also more transient (Schiller & Malpeli, 1978; Schwartz & Loop, 1982). Presumably, evolution has favored faster processing as faster motor responses have obvious benefits for survival. The reduced transmission latencies for the achromatic pathways translate into faster simple RTs to achromatic than to chromatic stimuli (McKeefry, Parry, & Murray, 2003; Smithson & Mollon, 2004; White, Kerzel, & Gegenfurtner, 2006, for example). However, the additional diameter of the achromatic cells also limits the numbers that fit into a given volume, which then affects the spatial resolution of a system for a given volume. The fact that this compromise is made suggests that the faster conduction velocity of this pathway still has an important role, possibly in controlling motor functions.

2.1.2. The L-M opponent pathway

Up to 35 million years ago, when primate colour vision may have only been dichromatic, there appears to have been a mutation in the opsin of the L cone that has lead to the evolution of the M cone (Nathans, Thomas, & Hogness, 1986). The parvocellular or L-M opponent pathway in catarrhines contrasts L and M cone responses. It compares the responses of one cone type in one component of its receptive field to the responses of the other cone type in the other component. This gives it a sensitivity to changes in chromaticity along a roughly red-green axis. The different possible combinations of cone types and excitatory and inhibitory responses means that the L-M pathway includes a range of red or green ‘on’ and ‘off’ ganglion cells. As the spectral sensitivities of the L and M cones are similar, the colour vision added by this pathway is over a narrow range when compared to the S-cone pathway. However, L-M cells out number the achromatic cells approximately 10 to 1 (Ahmad & Spear, 1993; Suner & Rakic, 1996). The greater relative abundance of L-M cells

overcomes the spectral overlap of the L and M cones, giving us great sensitivity between the reds, yellows and greens that are relatively close in wavelengths (Sumner & Mollon, 2003). The evolution of the L-M pathway may have been driven by our co-evolution with fruit (Sumner & Mollon, 2003) and foliage (Dominy & Lucas, 2001).

While the response of the L-M pathway depends on the chromaticity of a stimulus, this pathway may also facilitate high spatial resolution, including to achromatic stimuli. This is a consequence of having opposing excitatory and inhibitory responses from the two components of the receptive fields, and of having great numbers of cells. For this reason the L-M pathway may also have a role in spatial localisation, and was suggested as a candidate for explaining hyperacuity (Westheimer & Pettet, 1990); the finding that vernier acuity thresholds are smaller than the elements of the retinal mosaic (see Westheimer & McKee, 1977). The spatial resolution of this pathway is a characteristic that may be suited to either the planning or the correction of visually guided reaching. In particular, it would seem to offer some benefits where there was a requirement of the reach to be very precise, such as when threading a needle.

2.1.3. The S-cone pathway

Early studies of the primate geniculate pathways focused on the achromatic and L-M pathways, largely as they were more readily identified. In the review by Hendry and Reid (2000, pg. 128), they note that many early studies observed “extremely small and lightly stained” cells between the magnocellular and parvocellular layers in the LGN. These cells were smaller than the parvocellular cells and account for only approximately 10 of the retinal ganglion cells in the macaque (Rodieck, 1988; in Casagrande, 1994). The review by Casagrande (1994) argued that these cells formed what was named the koniocellular pathway by Kaas, Huerta, Weber and Harting (1978). This pathway

contrasts the activity of S cones against the activity of a combination of L and M cones, and so is also known as the S-cone opponent pathway. This means that the response of the S-cone ganglion cells is indicative of the balance of long and short wavelength light in its receptive field.

Unlike the centre-surround receptive fields described above, the receptive fields of the S-cone opponent system are arranged such that both excitatory and inhibitory information is collected from within a common area (for a review see Hendry & Reid, 2000). It therefore does not convey contrast information without additional processing. This suggests that most of the functionality added by this pathway is in processing colour information. Most of the cells of this pathway are 'S on' or 'blue on' cells (Mariani, 1984). The S-cone cells in the LGN are the only cells that receive connections from the superior colliculus (Harting, Huerta, Hashikaw, & van Lieshout, 1991) suggesting that it also plays a role in the regulation of eye movements (Raybourn & Keller, 1977). However, there is limited or no evidence to suggest that there is feedforward S-cone connections to the retinotectal pathway (e.g, Schiller & Malpeli, 1977; De Monasterio, 1978). But the S-cone pathway may still have a role in saccadic target selection, even if the information is not processed directly via the retinotectal pathway (Bompas & Sumner, 2009; White, Boehnke, Marino, Itti, & Munoz, 2009). S-cone information is also a small part of the input into area MT (Seidemann, Poirson, Wandell, & Newsome, 1999; Newsome, *et al*., 1999), suggesting that it also makes some contribution to the processing of motion for functions such as the perception of motion (Newsome & Pare, 1988) or the use of motion to guide smooth-pursuit eye movements (Komatsu & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988).

The responses of the S-cone cells have the lowest conduction velocity (Irvin, Norton, Sesma, & Casagrande, 1986; Cottaris & De Valois, 1998; Reid & Shapely,

2002) and the longest response duration (Brindley, Du Croz, & Rushton, 1966) of any of the three pathways.

2.2. Do different visual tasks use common processing or utilise required pathway characteristics?

There is physiological (Lennie, Krauskopf, & Sclar, 1990; Johnson, Hawken, & Shapley, 2001; Horwitz, Chichilnisky, & Albright, 2007; Goddard, Mannion, McDonald, Solomon, & Clifford, 2010) and psychophysical (de Valois, Cottaris, Elfar, Mahon, & Wilson, 2000; Conway, 2001; Clifford, Spehar, Solomon, Martin, & Zaidi, 2003) evidence that there are cells in V1 that integrate information from the different pathways. If cortical computation is costly (Lennie, 2003), it may be more efficient to have information from all of the pathways travel to an area such as V1, and be integrated before it becomes input for a decision making system that determines the presence of a stimulus in any of the three tasks examined here. Similarly, it is also possible that the information from the three pathways is integrated at a location other than V1 before it is used as input for these tasks.

Alternatively, it is known that some parts of the higher visual cortex use information that is not an evenly balanced integration of information from the three pathways. For example, the area MT in the rhesus (Zeki, 1978) or macaque (Seidemann *et al.*, 1999; Barberini, Cohen, Wandell, & Newsome, 2005) monkey or human MT (Ramachandran & Gregory, 1978; Wandell *et al.*, 1999; Liu & Wandell, 2005), involved in processing motion information, has primarily achromatic input. Zeki (1978) also found that 54% of the cells that he tested in V4 of the rhesus monkey had colour opponent responses.

A model of a decision making process that accumulates information over time predicts that a decision can be reached faster where the information input into the system is greater. In practice, visually evoked potentials (VEPs; Rabin, Switkes, Crognale, Schneck, & Adams, 1994) and RT (McKeefry *et al*., 2003; White *et al*., 2006) response latencies also decrease with increased contrast. However, it may not just be the firing rate of the input neurons that determines the volume or quality of the input. The quality of the signal received is also presumably related to the number of neurons wired to input information about the presence of a stimulus into the system. If the input into the decision making system was increased for a particular pathway, then the response latencies for that particular pathway would be expected to shorten relative to the other pathways. That is, if the RT and reaching correction tasks were more reliant on the faster luminance information, then this could be physically manifested as there being more neurons carrying luminance information into the decision making system for these tasks. If there are limitations on the neural resources that can be to allocated to this task, then it may not be as efficient to use the slower chromatic input for time-critical tasks such as locating a moving object one is trying to hit. If natural selection has favored reduced motor response times in primates, then it may have done so by altering the relative balance of chromatic and luminance input into the decision making process that facilitates these responses. If this were true then we would expect that the temporal advantage for the achromatic system was greater in the motor tasks than in equivalent perceptual tasks.

The dorsal visual stream appears to be more specialised in supporting motor functions (see Mishkin, Ungerleider, & Macko, 1983) such as visually guiding a hand to a target. For example, some of the processing for the guidance of reaching is thought to occur in the posterior parietal cortex (PPC; Desmurget *et al*., 1999; Culham *et al*., 2003). The superior parietal lobule may play a role in both converting sensory

information into motor commands and providing feedforward signals for comparing to sensory information for the ongoing control of reaches (Buneo & Andersen, 2006). Visual information may reach the PPC via the dorsal stream from V1 (Livingstone & Hubel, 1988; Maunsell, Nealey, & DePriest, 1990; Merigan & Maunsell, 1993). But this does not confirm that the information from the pathways has been integrated, as many of the cells in higher cortical areas are still selective for either luminance or chromatic contrast. Also, achromatic signals may travel directly to the parietal cortex via the retinotectal pathway to the superior colliculus (Schiller & Malpeli, 1977; Schiller, Malpeli, & Schein, 1979; Rodman, Gross, & Albright, 1990).

Alternatively, the balance of chromatic and luminance information involved in the processing that gives rise to the percepts of stimuli, is presumably constrained to facilitate our ability to detect subtle differences in the colours of stimuli in perceptual tasks. When perceiving the stimuli, either when making decision without time pressure in perceptual experiments, or when selecting ripe fruit, there is no apparent benefit for the percepts occurring a few tens of milliseconds earlier.

So, there is a theoretical reason why we may find a difference in the processing of chromatic and luminance information for creating our percepts of stimuli, and for reacting to targets. However, it is also possible that humans have evolved to combine chromatic and achromatic information at a point before it reaches the decision making processes tested in this thesis. In this thesis, I report results of experiments in which I investigate which of two potential evolutionary paths the brain has taken; is there a single neural decision maker for the RT, perceptual masking and reaching guidance tasks, or do different tasks rely on independent decision making processes as indicated by differences in the relative latencies in responding to stimuli activating the three different pathways.

2.3. Physiological comparisons of response latencies between the pathways

To infer differences in the use of chromatic and luminance information on the basis of differences in relative response latencies, it is useful to first consider how much of a difference in response latency may be due to differences in neural conduction velocities alone. The electrophysiological study by Maunsell *et al*. (1999) found achromatic responses in the macaque LGN were 7-10 ms faster than opponent L-M signals. Nowak *et al*. (1995) found that the advantage for the achromatic pathway over the L-M pathway in V1 was approximately 20 ms. However, Schmolesky *et al.* (1998) however found a 17 ms discrepancy for the same comparison in both the LGN and V1. Cottaris and De Valois (1998) suggested that the responses of the S-cone pathway may have a response latency of another 20-30 ms more than the L-M pathway in V1. In a study examining VEP responses to sinusoidal gratings covering 18° of the visual field, Rabin *et al*. (1994) found that responses to S-cone stimuli were between 55 and 20 ms slower than the L-M response as the contrasts ranged from about 12% to 90% of the maximum possible scaled in proportion to the maximum possible excursion along the MB-DKL (MacLeod & Boynton, 1979; Derrington, Krauskopf & Lennie, 1984) axis allowed by their monitor. However, I consider these latency differences to be a rough guide as the recorded latencies to stimulation varies significantly (see pg. 6172 of Reid & Shapley, 2002).

Some of these findings may give an indication of expected relative behavioural response latencies if the information used in the decision making process of the task of interest was integrated at V1. However, the relative behavioural response delays to chromatic and luminance stimuli could be considerably different to this if the decisions

are based on information being combined somewhere other than V1. The absolute differences in response latencies would be expected to be in proportion to the length of the pathways from the retina up until the point where the information was integrated. This means that the relative differences in response latencies, based purely on differences in conduction velocities alone, cannot be determined without first determining where the information from the different pathways is combined for each task. Therefore, when trying to infer the differences in relative contributions from the different pathways to a task on the basis of different response latencies, it is not possible to simply remove the differences in transmission times from the equation.

2.4. Three tasks to investigate how visual information is used across different tasks

I used three types of tasks to investigate whether the brain combines information from the chromatic and luminance pathways to be used for different tasks, or whether different tasks rely more on the pathway that has the most suitable characteristics. These three tasks types asses relatively simple components of human behaviour that may rely on different spatial and temporal characteristics of information.

The simple RT task involves releasing a button when a stimulus is detected. It was chosen as the simplicity of this task should limit the random variance in the response latencies. Each trial only took a few seconds, allowing each participant to do many trials, in turn allowing the collection of RTs over a range of contrasts. This was important to determine that the calibration of the stimuli was effective and it allowed the issue of how to scale the contrast of the stimuli to be addressed. The details on how this was done is provided in the RT publication in Chapter 4.

The perceptual study was chosen as a direct comparison between reacting to stimuli in the RT task, and perceiving stimuli to appear. Perceptual latencies are often assessed with a temporal order judgement (TOJ) task. In the TOJ task, a stimulus pair is presented, and the participant indicates which of the two stimuli appeared first. Over a number of trials the stimulus pairs are presented with a range of asynchronies between the stimuli. The asynchrony where both stimuli have a 50% chance of being indicated as having appeared first is taken as the difference in the latencies with which the stimuli appeared to the participant. Relative perceptual latencies can also be assessed with the simultaneity judgement (SJ) task. In the SJ task stimuli are presented as they are in the TOJ task, but participants indicate whether the stimuli pairs appeared simultaneously or not. The asynchrony where two stimuli are most likely to be indicated are appearing simultaneously is taken as the difference in when the stimuli are perceived to appear. I also developed a novel 2AFC task, the mask-onset asynchrony (MOA) task that determined when the perceptions of the chromatic and luminance stimuli are affected by masking.

The reaching correction study was chosen to examine whether there was a processing advantage for the luminance pathway in a motor task that was qualitatively different to the RT task in that it involved using spatial information and ongoing feedback. The guidance of rapid reaching is known to involve a feedback loop (Crawford, Medendorp, & Marotta, 2004) that seems to need as little a 120 ms to begin to affect the reach trajectory (Brenner & Smeets, 2004), which is shorter than a fast RT. Therefore, it seemed that the advantage for the luminance pathway could be proportionately the largest in relation to the response latency in this task.

In the following sections, I review previous work that has compared performance in these tasks to chromatic and luminance stimuli.

2.5. Comparing RTs between the pathways

The simple RT task has been used extensively to investigate the processing underlying simple motor responses to different stimuli. White *et al*. (2006) measured responses to luminance, L-M and S-cone stimuli using a series of tasks including simple RT, RT in releasing a button when initiating a reach to targets at unknown locations, the reaching accuracy and reaching durations to these targets as well as saccadic latencies. Their stimuli were six (roughly red, green, yellow, blue, dark and light) Gaussian blobs (0.5° *SD*). The chromaticity of these blobs were from the ends of the three axes of MB-DKL colour space as depicted in Figure 2.

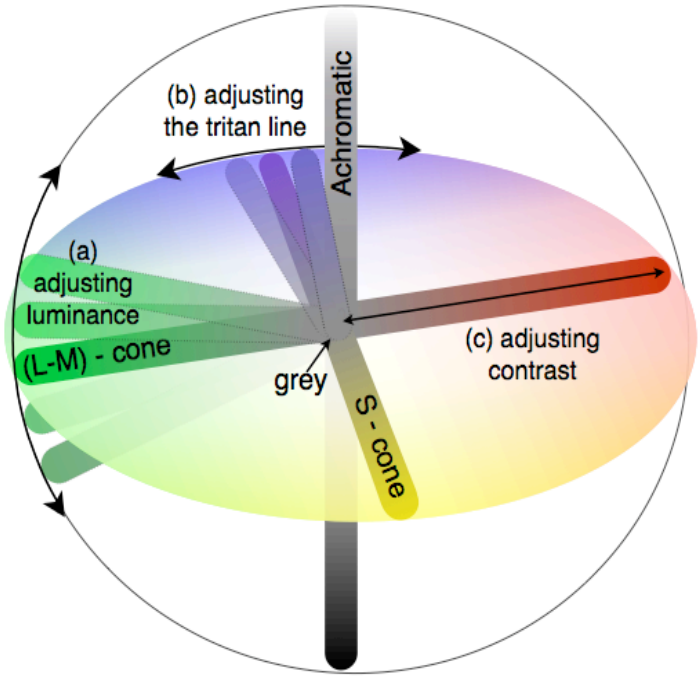

Figure 2. MB-DKL colour space, and how it was adjusted in this thesis. (a) Each of the four chromatic stimuli were adjusted to isoluminance by pivoting the axis away from the luminance plane. (b) The tritan line was adjusted by pivoting the blue end of the S-cone axis along the chromatic plane. (c) Contrast was adjusted along the new isoluminant chromatic axes and the original luminance axis.

MB-DKL colour space was first published as a three dimensional space by Derrington *et al*. (1984), building on the existing chromatic plane by MacLeod and Boynton (1979). It is a mathematical space that has three axes at (approximately) mutually orthogonal angles to each other and specifies a shade of grey at their common

balance point. Changing the specifications of a stimulus along any of the axes will maximally affect the responses of the intended pathway, while minimising the responses of the other two pathways. For example, changing the specification of a stimulus along the full length of the red-green axis would mean changing a stimulus from a pinkish red to grey and then on to green, whilst minimising changes in the activity of the S-cone or luminance pathways. A continuous range of colours can be defined (within the limits of the equipment used) by specifying their position along each of the three axes.

RTs to chromatic stimuli are very sensitive to departures from isoluminance (Schiller & Colby, 1983; Lee, Martin, & Valberg, 1989; McKeefry *et al*., 2003; White *et al*., 2006). There are significant differences across individuals for the ratio of cones that make up the retinal mosaic of photoreceptors (Moreland & Bhatt, 1984, cited in Smithson, Sumner, & Mollon, 2003; Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987; Hammon, Wotten, & Snodderly, 1997; Sharpe *et al*., 1998; Roorda & Williams, 1999; Chui, Song, & Burns, 2008). Given this high variability, it is unlikely that stimuli from the chromatic axes of MB-DKL space are ideally isoluminant for each participant. White *et al*. (2006) therefore determined whether the behavioural responses to their chromatic stimuli only reflected activity in their intended pathways, or whether the chromatic stimuli had also activated the faster luminance pathway. They included a condition where they added increments and decrements of luminance to their chromatic stimuli. One of those increments or decrements could have made the stimuli closer to being isoluminant to the background, than was the chromaticity of the standard axis of MB-DKL space. If this were the case, then RTs should have been longer at that increment creating the best approximation of isoluminance. However, they did not find an increment to which RTs were significantly lengthened for the two participants tested, suggesting that RTs to chromatic stimuli were not greatly affected by activity in the luminance pathway.

An alternative way of reducing luminance responses to chromatic stimuli is to determine the point of isoluminance for each chromatic stimulus for each participant. Smithson and Mollon (2004) and Bompas and Sumner (2008) also examined RTs to chromatic and luminance stimuli, but initially adjusted their chromatic stimuli to contain similar luminance levels to their background, using the minimum motion technique (Anstis & Cavanagh, 1983). With this technique, the chromatic stimuli are presented in an offset sequence, such that differences in luminance between the stimuli are constantly moving in a single direction. This generates a perception of motion where the stimuli are not isoluminant. It is then possible to determine luminance values for chromatic stimuli that minimise the apparent luminance motion for each participant. This paradigm has been used to estimate the contribution of the chromatic pathways to motion perception (Cavanagh & Anstis, 1991). However, as this process determines isoluminance in the motion pathways, it may be more appropriate for determining isoluminance for motion stimuli (Webster & Mollon, 1993) than for static stimuli.

Another method for adjusting stimuli and backgrounds to isoluminance is the minimum flicker technique, as used by McKeefry *et al*. (2003). This method uses static stimuli, such as those used in this thesis and the other RT tasks described here. It takes advantage of the low-frequency bandwidth of the chromatic pathways and the high-frequency bandwidth of the luminance pathway (Kelly & van Norren, 1977). If chromatic stimuli are presented as flickering on an off at a sufficiently high frequency, they appear to remain constantly visible. The frequency above which the stimuli appear to remain constant is known as the flicker fusion frequency. If a stimulus is presented as flickering at a level above the chromatic flicker fusion frequency, but below the luminance flicker fusion frequency, its colour appears to remain constant, while any difference between the subjective luminance of the stimulus and the background generates luminance flicker. The participant can then adjust the luminance of the stimulus to the point where

the luminance flicker is minimised. This stimulus is then considered to be isoluminant to the background for this participant.

Even when stimuli have been adjusted using a subjective isoluminance paradigm, it is still possible that there is a luminance response to a stimulus. Individual luminance ganglion cells have different points of isoluminance depending on the balances of L and M cones in the two components of the receptive fields (Gegenfurtner *et al.*, 1994). Also, the difference in when the phosphors of a CRT monitor are activated on a single screen refresh may generate luminance responses (Vingrys & King-Smith, 1986). Therefore some individual cells may still respond to well calibrated isoluminant stimuli.

The potential of luminance pathway responses to chromatic stimuli can be dealt with by presenting luminance noise with both the chromatic and luminance stimuli. Smithson and Mollon (2004) were interested in whether the responses of the S-cone pathway were slower than that of the L-M and luminance pathways. They collected RTs to luminance, and isoluminant L-M and S-cone 'Ishihara plate' like stimuli, both with and without spatio-temporal luminance noise. RTs were collected while concurrently determining the detection thresholds of the stimuli. Overall, they reported that there was approximately a 17 ms advantage for the luminance pathway over the L-M pathway, and a mean 35 ms advantage of the luminance pathway over the S-cone pathway. It is unclear whether using large stimulus that covered a quarter of an annulus from 3° to 4.55° eccentricity was a problem in the isoluminance and tritan calibration processes as there are steep changes in the sensitivity to stimuli surrounding the fovea (Mullen & Kingdom, 2002). However, when luminance noise was added to the stimuli to remove the potential unwanted activations of the luminance pathway to the chromatic stimuli, the differences between the chromatic and luminance stimuli were largely removed. Smithson and Mollon suggest that this may be because luminance noise adapted the luminance pathway, increasing its response latency.

The adaptation of the luminance pathway by luminance noise seems possible as Bompas and Sumner (2008) also collected RTs to isoluminant S-cone and luminance squares, but using luminance noise of approximately one third of the contrast of that use by Smithson and Mollon (2004). Bompas and Sumner found a slightly smaller 23 ms advantage for the luminance system over the S-cone system. This is also a relatively small difference compared to what was found in the RT study without luminance noise presented in this thesis. This suggests that it is best to avoid using luminance noise to mask luminance responses to chromatic stimuli if possible.

While it is important to avoid activating the luminance pathway when presenting chromatic stimuli, it is also important to avoid the S-cone stimuli activating the L-M pathway. As the mosaic of photoreceptors varies between individual participants (Moreland & Bhatt, 1984, cited in Smithson *et al*., 2003; Hammon *et al*., 1997; Roorda & Williams, 1999), the 'pure' shade of blue that does not activate the L-M pathway is also expected to vary from the blue-yellow axes of MB-DKL space. Smithson *et al*. (2003) devised a way of finding the shade of blue for each participant that isolates their S-cone pathway using transient tritanopia. The process involved a strong initial adaptation to yellow, with top-up yellow adaptors throughout the task to maintain adaption. In between the top-up adaptors, participants performed a threshold detection task on a range of chromaticities of blue. As the yellow stimulus would cause adaptation of the S-cone pathway, these detection thresholds are lower than they typical would be without adaptation. It is assumed that the shade of blue that is most affected by this adaptation is the one for which the L-M pathway has the least input into the detection task, and thus is on the blue axis for that participant. The blue stimuli can then be adjusted (e.g., for intensity) along this new axis. The adjustment of this axis is indicated in Figure 2b. Smithson and Mollon (2004) and Bompas and Sumner (2008) are the only two studies mentioned here that make this adjustment to the chromaticity of the blue stimulus.

Ideally, this adjustment should be included in any comparison of response latencies including blue/violet stimuli.

2.5.1. How should stimuli be scaled to get comparable RT across the pathways?

RTs reduce with increased contrast (see McKeefry *et al*., 2003; White *et al*., 2006). Therefore, when determining differences in RTs to stimuli activating the different pathways, it is necessary to equate the different stimuli appropriately. However, what exactly is the appropriate manner, is in itself a research question that has been described as an 'apples and oranges' problem (Switkes & Crognale, 1998). How can one stimulus be as dark as another is red or blue? While McKeefry *et al*.'s (2003) main aim was to "determine the stage of chromatic processing that is most influential in [the RT response's] generation" (pg. 2267), their results were informative about how stimuli contrast should be scaled in RT tasks. They examined simple RTs as a function of contrast scaled both in multiples of the contrast at detection thresholds (MDT) and in root mean square (RMS) cone contrast.

RMS cone contrast is calculated from electrophysiological responses of photoreceptors to light (Smith & Pokorny, 1975). Light of any given chromaticity and luminance is expected to generate a specific response in each of the three cone types. Where a stimulus varies from its background, there is a difference in the response of each cone type to the stimulus and to the background. The differences in the responses of the cone types is combined in a formula such as;

$$\text{RMS cone contrast} = ((\Delta L/L)^2 + (\Delta M/M)^2 + (\Delta S/S)^2))^{1/2}$$

where ΔL/L, ΔM/M and ΔS/S are the changes in activities of each of the cone types between when responding to the stimuli and to the background.

McKeefry *et al*. (2003) found that the RMS cone contrast scale exaggerated the differences in RTs between the two chromatic pathways considerably more than the MDT scale did. This was consistent with the processing involved in eliciting RT responses occurring in the cortex, rather than at an early post-receptoral stage. The MDT scale allows for differences that affect the response at the level of the cortex such as the differences in sensitivity or number of cells between the pathways. The MDT scale seems to be the more appropriate scale of the two to use in this thesis, as both the tasks used to determine the scale and the final tasks involve measuring behavioural responses.

White *et al*. (2006) circumvented the issue of equating contrasts by presenting luminance, L-M and S-cone stimuli at the highest contrast possible on their equipment. As detection thresholds to luminance stimuli are lower, it is likely that White *et al.'s* luminance stimuli would have been considered to be of higher contrast when scaled in MDT. However, this was not problematic for their study as they showed that the speed and accuracy of reaching responses to these stimuli was similar, despite the higher luminance contrast. Under these high-contrast conditions, White *et al*. (2006) found that simple RTs to luminance stimuli were between approximately 40 to 60 ms shorter than RTs to S-cone stimuli, with the magnitude of the difference growing as the eccentricity ranged from 3° to 12°. RTs to L-M stimuli were another 20 to 40 ms slower that those to the S-cone stimuli. However, they found that RTs to luminance stimuli were only slightly shorter than RTs to L-M stimuli when they were matched at 10% RMS cone contrast, as seen in their Figure 5.

A different approach to scaling different stimuli was taken by Smithson and Mollon (2004). They collected RTs to the three stimulus types presented at approximately the contrast required to elicit a response in a 4AFC threshold detection task. Similarly, Bompas and Sumner (2008) presented their stimuli at 80% detection thresholds in a simple RT task. In this sense, the different stimuli were equivalent in that they were all marginally above threshold. This was sufficient for both studies in their intentions of determining that overall, response of the S-cone pathway was slower for eliciting rapid behavioural responses.

McKeefry *et al*. (2003) offers a direct comparison of RTs to foveal L-M and S-cone stimuli matched for contrast, over a range of contrasts. The RTs were fit with their version of the Piéron (1932; cited in McKeefry *et al*., 2003) equation;

$$RT = RTo + k.1/C$$

where RTo is the absolute RT at asymptote, C is the contrast, and k is the constant the determines the relationships between RTs and contrast for a particular pathway. When comparing the RTo values of the three participants who completed the L-M and S-cone conditions, the absolute RTs were 38 ms shorter for the L-M pathway than the S-cone pathway. This L-M/S-cone difference is relatively large when compared to previous studies discussed. Unfortunately, McKeefry *et al*. (2003) did not collect RTs to luminance stimuli with contrasts determined as MDT.

One unclear aspect of McKeefry *et al*. (2003) was how RTs were affected by the ramping on of the stimuli. The contrast of the stimulus was ramped to increase from zero to the maximum for a particular presentation over a 190 ms period to decrease the luminance pathways response to the chromatic stimuli. This long ramp time may have affected the RT responses differentially at high and low contrasts (in comparison to what would have happened had the stimuli had a relatively rapid onset). It is unclear how this

affected the modeled relationship between contrast and RT, and hence the differences in RTo output from this model. Another aspect of the McKeefry *et al*. study that could have impacted the relative delays found for the S-cone and L-M stimuli was that they used a small foveal stimulus. It would be expected that the central half of this stimulus would fall within a region shown to be tritanopic (Williams, MacLeod & Hayhoe, 1981). Smithson and Mollon (2004) suggested that this, interacting with the long stimulus duration (also 190 ms) could increase RTs to the S-cone stimuli. It is possible that with exact fixation that the visibility of this stimulus was reduced, but that subsequent microsaccades could have positioned the stimulus in a position where its visibility was increased. In this way, S-cone stimuli could have still been equated for detection threshold, but required an additional small eye movement on some RT trials. This is a possible explanation for why the L-M/S-cone differences found by McKeefry was larger than what was found by the other studies (Smithson & Mollon, 2004).

While the MDT scale of contrast is more appropriate than RMS cone contrast, there is a theoretical limitation to comparing RTs to chromatic and luminance stimuli presented at higher MDT. The responses of cells (at least simple and complex cells) in V1 are best modeled with a model that includes a nonlinear component (Carandini, Heeger, & Movshon, 1997). The nonlinear processing of the responses appears to begin in the LGN (Bonin, Mante, & Carandini, 2005). The response functions, and how the responses begin saturate with contrast varies between the chromatic and luminance pathways, with the luminance response being the most nonlinear (Lee, Pokorny, Smith, & Kremers, 1994). Therefore, when presenting the stimuli at some linear multiples of the contrast required to achieve detection, the responses of the chromatic and luminance pathway may not be equal in terms of the response that the elicit.

To summarise the literature examining RTs to well-calibrated chromatic and luminance stimuli, it is clear that it is important that the chromatic stimuli do not activate

the luminance pathway. It is likely that chromatic Gaussian blobs adjusted to isoluminance using minimum flicker do not significantly activate the luminance pathway. However, the use of luminance noise may increase the luminance pathway's response latency. Ideally the blue stimuli should also be calibrated to isolate the S-cone pathway. Once these adjustments have been made, stimuli should be adjusted to be equal in strength. The MDT scale currently appears to be the most suited scale for a RT task.

The studies above have addressed issues of stimuli calibration, however their calculations of absolute differences in RTs across the pathways vary. For example, Smithson and Mollon (2004) found a mean advantage of approximately 17 and 35 ms for RTs to luminance stimuli over the L-M and S-cone stimuli respectively. Bompas and Sumner (2008) only found a 23 ms advantage for the luminance pathway over the S-cone pathway. McKeefry *et al.'s* (2003) data suggest that the L-M/S-cone difference is approximately 38 ms. Meanwhile, White *et al.'s* (2006) data suggest that RTs to luminance stimuli could be between 20 to 90 ms faster that RTs to L-M stimuli, depending on contrast scaling and stimulus eccentricity.

While knowing the absolute differences in RTs between the pathways would be informative, it is also unknown whether all of the differences in RTs between the pathways are attributable to differences in conduction delays. In particular, the question of whether some of the differences in RTs are due to differences in the use of chromatic and luminance information in the RT decision making process remains. To examine this, it would be useful to determine how response latencies change as a function of increasing contrast to see if the decision making process does appear to vary between the pathways. However, differences between the RT/contrast functions could also be attributed to differences in saturation function between the pathways. The effects of differences in the nonlinearities in the chromatic and luminance pathways on RTs have not be documented. Therefore, the first step to understanding why there are differences

in RT between the pathways is to determine how these response latencies change as a function of increasing contrast for chromatic and luminance stimuli, while allowing for differences in response saturation functions.

2.6. Perceptual measures of delays to chromatic and luminance information

As mentioned in 2.4 above, perceptual latencies are typically assessed with a TOJ task (e.g., Jaśkowski, 1992; Miller & Schwarz, 2006). As this task involves presenting two stimuli next to each other, but with a small asynchrony, it appears to offer the opportunity to simply and directly compare the latencies in when stimuli appear to the participant. In the perceptual latency publication in Chapter 5, I argue why examining perceptual latencies of chromatic and luminance stimuli offers an advantage over comparing latencies to stimuli of varying intensities (as is typically done) when comparing the results to RTs. Only Bompas & Sumner (2008) have examined the relative latencies in perceiving chromatic and luminance stimuli using this task. They compared relative RTs to a luminance and a blue stimulus, to the relative latencies in perceiving these stimuli. While they found a 23 ms advantage for the luminance pathway in the RT task, they did not find a difference in when the stimuli were perceived to appear (also known as a perceptual asynchrony; PA). However, the TOJ task is exposed to bias (Schneider & Bavelier, 2003; Shore & Spence, 2005; Zampini, Shore, & Spence, 2005; Yates & Nicholls, 2011), and in the publication I also demonstrate why the TOJ task in not suited to the chromatic/luminance comparison.

Lee *et al*. (2009) determined differences in the perceptual response delays of the S-cone and L-M pathways by examining the interference of clockwise and counter-

clockwise presentations of hues. Normally presenting the same hues in a rapid sequence in the two different directions creates two different sensations of colour. They found that participants could not discriminate between the two presentations when the presentations were out of phase by approximately 12 ms, suggesting that this was the additional delay for the S-cone pathway over the L-M pathway. This differed from the 21-25 ms additional delay determined in a earlier version of the experiment by Stromeyer, Eskew, Kronauer, and Spillmann (1991).

The conclusion from these studies is that there may be an additional perceptual latency for the S-cone pathway over the L-M pathway, but that the predicted magnitude of this in a simple task that is comparable to a RT task is unclear. Any potential for a reduced perceptual latency for the luminance pathway over the chromatic pathways is very unclear.

2.7. Reaching measures of delays to chromatic and luminance information

The RT task involves making a decision on the appearance of the stimulus (Shadlen *et al.*, 1996; Schall, 2003; Smith & Ratcliff, 2004), and then releasing a relatively simple ballistic motor plan as a response. The online correction of reaching assessed here is a more complex task. The planning and execution of rapid reaching depends on information processing the dorsal visual stream in areas such as the posterior parietal cortex (Desmurget *et al.*, 1999; Culham *et al.*, 2003). A reach involves an initial planning phase that uses visual information about the location of the target (Ma-Wyatt & McKee, 2006; Gegenfurtner & Franz, 2007), as well as visual and somatosensory information (van Beers, Baraduc, & Wolpert, 2002) about the current

location of the hand (see Crawford *et al*., 2004). Both egocentric and allocentric information is used to carry out the reach (Andersen, Snyder, Li, & Stricanne, 1993). Once the hand is in flight, there is ongoing assessment of the path of the hand relative to the planned path (Wolpert *et al*., 1995), that includes relative judgement of the hand to the location of the target. The current flight path can then be corrected on the basis of visual information (Ma-Wyatt & McKee, 2007; Saunders & Knill, 2003) as well as proprioceptive information.

The guidance of rapid reaching is a interesting task to use when comparing response latencies to chromatic and luminance information, because the reaching correction may begin in as little as 120 ms (Brenner & Smeets, 2004). Therefore the small advantage for the luminance pathway could have a relatively large effect on the response latency in this task. The luminance information could facilitate a faster correction that chromatic information just because of faster information conduction velocities. However, there could have been additional benefits above that due to the conduction delays alone if the reaching correction was increasingly reliant on luminance information, as is suggested to occur for the RT task. Also, luminance information can get to parts of the dorsal stream, such as area MT, without going via V1 (Girard, Salin, & Bullier, 1992; Zeki, 1995), possibly via the retino-tectal route (Rodman, *et al*., 1990; Lyon, Nassi, & Callaway, 2010), and the passage of information through this central route may be faster that having the information go via the primary visual cortex (Schmolesky *et al*., 1998). However, as the visual guidance of reaching requires information about the location of the target and the hand, the improved spatial resolution of the L-M pathway means that it may be more suited in some ways. Therefore, it is unclear whether there would be any temporal advantage for the luminance pathway above that occurring as a direct consequence of the faster conduction delays.

White *et al*. (2006) had participants make rapid reaches to Gaussian blobs that appeared at eccentricities of either 3, 6 or 12° at random. As the speed and accuracy of rapid reaches are linked (Fitts, 1954), they were interested in both the speed and accuracy of reaching. They found that participants were no more accurate when reaching to luminance stimuli than to chromatic stimuli and the movement time was only 8 ms faster to the luminance stimuli. Therefore they conclude that this demonstrates that chromatic information does make a strong contribution to the guidance of reaching, and that the chromatic and luminance information used in guiding reaches could possibly be combined in V1.

Brenner and Smeets (2004) were similarly interested in whether participants could use chromatic information to correct a reach. They had participants reach to tap a red square that was either brighter (2.8 cd/m^2) or darker (1.2 cd/m^2) than the yellow background (2.0 cd/m^2). Participants were instructed to reach as fast as possible. The trajectory of the tapping finger was tracked throughout each trial. On the 'location change' trials, the red square moved to an adjacent location. On the 'colour change' trials, the red square swapped locations with an adjacent green square that had the same photometric luminance. On half of all trials, the luminance of the target square changed in order to prevent participants using a luminance change as a guide to there being a new target location, as opposed to having to process the colour. Only an additional 10 ms was required to begin to correct the reaches in the colour only trials, when compared to the location change trials.

These two studies both suggest that there will be a limited temporal advantage for the luminance pathway in guiding hands to targets.

2.8. Comparing RT and perceptual latencies

Comparisons of RTs and TOJ to identical stimuli have been ongoing for a long time (e.g., Gibbon & Rutschmann, 1969) as this comparison offers the opportunity to examine the neural processing involved in perceiving and reacting to stimuli. However, the literature reviewed below shows that there has been limited success in determining whether reactions to, and percepts of, the same stimuli rely on the same or different processing.

2.8.1. RT/perceptual comparisons not manipulating chromaticity

There is a body of literature examining the differential effects of manipulating stimuli on RTs and perceptual latencies, where the manipulation is not the chromaticity of the stimuli. For example, it is common to compare the effects of increasing the salience or intensity of the stimuli (Miller & Schwarz, 2006). The general finding is that changes in intensity affect RTs by more than TOJ (Jaśkowski, 1992) by approximately twice as much (Miller & Schwarz, 2006). While this discrepancy in the magnitude of the response change with stimulus change has been consistently reported, it is not yet clear if this is due to differences in task demands or in the neural mechanisms underlying these tasks. For example, Neumann, Esselmann and Klotz (1993) found that brightening a stimulus had a stronger effect on RTs than on TOJ, and that masking affected RTs but not TOJ. They concluded that there is some separation of the processing that leads to the RT response and the generation of the perception of the stimulus. In a slightly different example, Steglich and Neumann (2000) examined the effects of masked priming on TOJ and RT tasks. When a prime was presented in such a way that it could not be detected in a detection task, they found that it typically improved RTs by around 20-25 ms. However, TOJ was affected less if at all by the same prime depending on the exact conditions. They conclude that the most likely explanation is an

early dissociation of processing for the two tasks, in line with the Goodale and Milner (1992) model of there being separate processing for action and for perception.

While Steglich and Neumann (2000) suggested that there was a difference in processing for the RT and TOJ tasks, they also discuss Sternberg and Knoll's (1973) simple and intuitive suggestion that RT responses reflect the time that a decision making system reaches its decision criterion, while TOJs are based on the differences in the latencies to the peak of the visual responses. Steglich and Neumann (2000) model the Sternberg and Knoll suggestion and conclude that it is a plausible explanation for much of the difference in the effects of masking on the two tasks.

There are limitations to the methodology used by Steglich and Neumann (2000) that are common in the TOJ tasks used in the literature. While they could have had a TOJ task with two identical targets, they instead used two different targets to make it similar to their choice RT task. This means that this TOJ results would be susceptible to a bias that I describe in the perceptual latency publication in Chapter 5. They also did not have both 'which came first' and a 'which came last' conditions, which again exposes the results to bias as discussed in Chapter 5. These limitations of the TOJ task generally reduce the reliability of much of the data used in this literature.

In contrast to the suggestion that this RT/TOJ dissociation reflects different processing for the two tasks, it has also been argued that there is a single decision making process for RT and perceptual (typically TOJ) responses, as put forward early on by Gibbon and Rutschmann (1969). For example, Cardoso-Leite, Gorea and Mamassian (2007) presented Gabor stimuli that changed in either contrast or orientation and determined that they had different effects on TOJs and RTs. Unlike most studies, they had participants make RT responses, followed by TOJs on each trial. They found that TOJ did have some predictive ability with RTs, suggesting some commonality

in the processing. They fit their RT and TOJ data with model that has only a single decision maker, but allows the decision criterion to vary between tasks. Their model suggested that the increase in variance in the RT task could be accounted for by there being a higher decision threshold criterion for the RT task. This model is referred to as the 1DM-2 decision criteria model.

Figure 3 is a reproduction of part of Figure 1 from Miller and Schwarz (2006). It shows the 1DM-2 decision maker model and how two different decision criteria can predict a dissociation in response times to high and low intensity stimuli for the TOJ and RT tasks. The cumulative sensory activation in their diagram is the level of activity in the Smith and Ratcliff (2004) model in Figure 1 above. The x axis indicates the duration of the accumulation of information. In this diagram, a decision is made that a stimulus has appeared at approximately 25 units of activity, and this leads to the perception of the stimulus. A similar decision is made at approximately 35 units of activity that leads to the RT response. The difference in the angles of the lines representing the rates of information accumulation for high and low intensity stimuli, means that the lines subtend to different relative response latencies at the different threshold criteria.

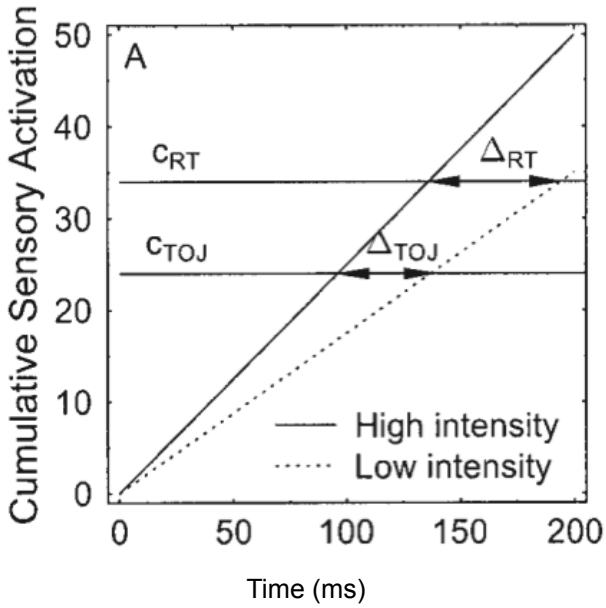

Figure 3. The potentially different effects of having different decision criterion on RT and TOJ latencies due to an increase in stimulus contrast (from Miller & Schwarz, 2006).

Cardoso-Leite, Mamassian & Gorea (2009) made a RT/perceptual latency comparison that avoided the TOJ task by comparing the effects of stimulus contrast on RT and anticipatory RT (ART). In the ART task, participants are presented with three

stimuli that were 500 ms apart. Participants had to press a button in synchrony with the third presentation. This task therefore assesses the perceived timing of the first two presentations. The RT task involved the same two early presentations, followed by a third after an unpredictable latency. Cardoso-Leite *et al*. (2009) found that the mean and variance of the RTs were affected approximately 1.5 times as much as ARTs. Again, they show that their data were well fit by a 1DM-2 decision criteria model that allowed the decision criteria to vary between tasks.

Miller and Schwarz (2006) point out that a RT/TOJ dissociation has been found for a range of stimulus manipulations including stimulus intensity, spatial frequency of visual gratings, attentional cuing and modality (i.e., auditory vs. visual). They modeled optimum decision making strategies for RT and TOJ responses and also conclude that the RT/TOJ dissociation can be accounted for by the 1DM-2 decision criteria model.

The goodness of fit of the 1DM-2 decision maker model depends on allowing the decision criterion to vary freely. In favour of the 1DM-2 decision criteria model, the three studies examined here (Miller & Schwarz, 2006; Cardoso-Leite *et al*., 2007; Cardoso-Leite *et al*., 2009), all found that the decision criterion for the RT task is higher than the perceptual task. Conversely, Tappe, Niepel and Neumann (1994; cited in Miller & Schwarz, 2006) argued that the criterion should be lower in the the RT task as it requires participants to respond as fast as possible. However, Miller and Schwarz determined the decision criteria using the optimum strategies for the TOJ and RT tasks, and found that the RT criterion should be higher. This also supports the model, but not as much as if Miller and Schwarz had constrained their criteria to match those determined to be optimal. As discussed in the perceptual latency publication in Chapter 5, a weakness in the use of this model is that if the two decision criterion are free to vary, it can fit almost any dissociation where RTs are most effected by a change in stimulus intensity. The perceptual latency publication also includes a discussion of why

a RT/TOJ dissociation based on stimulus intensity is not strictly decisive in choosing between a 1DM or 2DM model. The only reason that the 1DM model is suggested to be preferred over a 2DM model is its relative parsimony, and accordingly its relatively good fit to the data when allowing for the 1DM-2 decision criteria model having less degrees of freedom. In the perceptual latency publication, I explain why a RT/perceptual latency dissociation between chromatic and luminance stimuli is potentially more informative.

In summary, it is not yet understood whether RT responses and perceptual judgments both use the same, or different decision making processes. A limitation of this literature is the reliance on the TOJ task, and on using the 1DM-2 decision criteria model to fit dissociation created by manipulating stimulus intensity.

2.8.2. RT/perceptual comparisons manipulating chromaticity

The comparison of relative response delays to chromatic and achromatic stimuli is a different approach to investigating the similarity of processing in RT and perceptual latency tasks. There is an *a priori* expectation of why there may be a difference in the processing for chromatic and achromatic information in RT and perceptual tasks, based on luminance information being theoretically better suited to the RT task. Here, a dissociation between the tasks that is attributable to the chromatic/achromatic manipulation, would be harder to account for it with the 1DM-2 decision criteria model. In theory, if the stimuli are matched for contrast in MDT, then the stimulus intensity should be the same for chromatic and luminance stimuli. Therefore, both stimuli should be following a single intensity function in the Schwarz and Miller (2006) model presented in Figure 3. This would predict a similar difference between chromatic and luminance latencies in both tasks.

Previously, only Bompas and Sumner (2008) compared perceptual latencies and RTs to chromatic and luminance stimuli. As discussed in 2.5 above, Bompas and Sumner did not find a difference in the latency in when S-cone and achromatic stimuli were perceived to appear, but this may have been due to the limited statistical power of the study. Therefore, the differences in RTs and perceptual latencies to chromatic and achromatic stimuli still requires further investigation.

2.9. Critical points from literature review

The review above provides evidence that response latencies are expected to vary between the pathways for RTs and reaching corrections. The exact magnitude of the differences in response latencies between the pathway is unclear due to differences in the calibration routines used to selectively activate the pathways and equate the different stimuli. The response latencies are expected to reduce with increased stimulus intensity. However, where the same stimuli have been used in both reaching and simple RT tasks in White *et al.* (2006), they found a dissociation between reaching and RT responses in that the temporal advantage of the luminance pathway over the chromatic pathways was larger in the simple RT task. This is some evidence that visual tasks may vary in how they process chromatic and luminance information. However, it does not suggest that the reaching response relies heavily on the luminance information, as was suggested above.

While MDT have been used to equate the intensity of stimuli across pathways, it is not understood how differences in the response saturation functions of each pathway affects RT/contrast functions scaled in MDT. It has not been documented how the RT/contrast functions vary between the chromatic and luminance pathways when the differences in response saturations have been allowed for. Understanding these RT/

contrast functions will provide valuable insight into the decision making processes used in the RT task. The construction of accurate RT/contrast functions will require particular attention to detail in calibrating the stimuli.

It is expected that there will only be a small temporal advantage for the luminance pathway in the rapid correction of reaching, but this has not been tested for stimuli matched for contrast. The difference in perceptual response latencies to chromatic and luminance is unknown, and they are typically assessed in a way that introduces task differences in a RT/perceptual latency comparison. This needs to be investigated in order to investigate the similarities or differences in processing information for perceiving stimuli and for controlling motor responses to them.

3. Details on the experiments in this thesis

The questions addressed in this thesis required measurement of response latencies to chromatic and achromatic stimuli in motor and perceptual tasks. As the differences in response latencies are expected to be very small, it is important to calibrate stimuli to ensure that the latencies recorded reflect equivalent activations across the different pathways. As the literature review demonstrates, the way that the stimuli are calibrated can significantly affect measured latencies. In the following sections, I outline details of the experiments that are not included in the publications that follow, to demonstrate how I ensured that differences in the recorded latencies reflected differences in how the pathways process information.

3.1. The Stimuli

The contrast of the stimuli used in these experiments went from being zero at its edges to being at its maximum in the centre in a Gaussian function. This meant that the contrast of the stimuli did not change rapidly over any spatial region. Rapid spatial changes in contrast could be a problem as individual achromatic ganglion cells have different points of isoluminance depending on the balances of L and M cones in the two components of the receptive fields (Gegenfurtner *et al*., 1994). Therefore, even it the chromatic stimuli were adjusted to the ideal luminance to be isoluminant with their background, it was still possible that some individual achromatic ganglion cells would have responded.

In most tasks, the stimuli were presented with their centres at 2^{o} from fixation. If stimuli themselves were large, 2^{o} for example, then their inner and outer extremities would have been at quite different eccentricities such as 1^{o} and 3^{o}. As there are steep

changes in the sensitivity to stimuli surrounding the fovea (Mullen & Kingdom, 2002), large stimuli that were ideally calibrated in the inner most eccentricity that they covered, may not have been ideally calibrated at the outer most eccentricity that they covered. Therefore, I used small Gaussian blobs with a standard deviation of approximately 0.5°.

The initial chromaticities of these six blobs were taken from the ends of the three axes of MB-DKL space (MacLeod & Boynton, 1979; Derrington *et al*., 1984) depicted in Figure 2 above. The cones that comprise the retinal mosaic varies between participants (Hammon *et al*., 1997; Roorda & Williams, 1999). Therefore, MB-DKL space needs to be adjusted for each individual participant. The details of these adjustments are listed in the sections below. Additional details of the stimuli, including the equipment used to generate them, are provided in the methods section of the RT publication in Chapter 4.

3.2. Calibrating the stimuli for individual participants

3.2.1. Isolating the chromatic pathways

The contrast of the chromatic stimuli need to be high enough to activate the target pathway, while the potential activation of the achromatic pathway needs to be minimised. It became apparent that this was particularly important when I initially determined detection thresholds to these stimuli. When scaled in MB-DKL space, as these stimuli effectively are when the axes are rotated during the isoluminance calibration, the achromatic pathway was approaching an order of magnitude more sensitive to these stimuli than the chromatic pathways. Therefore, a small amount of achromatic information in poorly calibrated chromatic stimuli had a strong potential to decrease the response latencies to these stimuli.

In these experiments, chromatic stimuli were adjusted to be isoluminant to the background using the minimum flicker technique described in 2.5 above. The rotation of the chromatic axes during this adjustment is demonstrated in Figure 2a. When adjusting the chromatic stimuli to isoluminance for the RT and PA tasks, there was one stimulus at 2° either side of the fixation cross. When adjusting them for the reaching correction task, there were eight stimuli around the fixation cross as shown in Figure 1 of the publication in Chapter 6. More details of how I used the minimum flicker technique to determine isoluminance are provided in the methods section of the reaching publication.

3.2.2. Isolating the tritan line

When measuring response latencies to the blue stimulus, it is possible that the latencies recorded could in part reflect unwanted activation of the L-M pathway. I rotated the S-cone axis along the chromatic plane of MB-DKL space to isolate the S-cone pathway for each participant. This was done using a modified version of Sumner *et al.*'s (2003) transient tritanopia task described in section 2.5, when calibrating stimuli in the RT and perceptual asynchronies (PA) studies. Participants initially adapted to a yellow screen for 40 seconds while fixating on the fixation cross. After 38 seconds, participants heard two beeps to warn them that the first stimulus presentation was about to occur. On each stimulus presentation, the screen abruptly changed to background grey for 350 ms. Two hundred milliseconds after this change, a blue blob appeared either left or right of the fixation cross. After the grey exposure, the screen returned to yellow for a 4.65 second top-up adaptation, making a cycle of 5 seconds for each stimulus presentation. During the top-up adaptation, participants indicated whether the blue stimulus had appeared on the left or the right of the fixation cross. The contrast of the blobs were adjusted to 82% detection threshold in a staircase controlled by the QUEST algorithm

(Watson & Pelli, 1983). The staircases for a range of tritan angles were interleaved in a single block.

The blue stimuli used in this adjustment were similar to those used in the rest of the study, but with a few differences to make it more suited in the yellow-adapted setting. While the intensity of the blob was still being ramped on and off on the first and last screens of it presentation, it was presented at full intensity for three refreshes of the screen, giving it a total duration of 59 ms (presented on a monitor with a refresh rate of 85Hz). Rather than having a Gaussian spatial profile, the top of the Gaussian was removed, giving it a flat top in order to make it higher in contrast over a larger area. These modifications of the stimulus were required to make it increasingly visible during this task. The stimulus was also overlaid with luminance noise in the form of a 3.4° grid of 81 by 81 squares with linear random noise from 0 to 11.6% RMS cone contrast. Piloting of this task showed these modifications of the stimuli, and these particular timings were required for participants to reliably show a peak in a function of contrast thresholds across the tested range of tritan angles.

Even with these modifications, there was great variety in the ability of individuals to generate reproducible detection thresholds, and this ability did not improve greatly with practice. For each participant, I collected data until there was a stable angle versus threshold function. Therefore, responses were collected from each participant differently in that some functions are made from a single block with limited practice while others were generated by averaging data from a series of blocks. The detection threshold contrast versus tritan angle functions were fitted with a cubic function. The peak of the function was determined and rounded to the nearest degree. This process resulted in choosing individual tritan axes turned 1, 6, 8, and 1° towards the red axis for P1 to P4 respectively in the RT publication.

3.2.3. Equating chromatic and achromatic contrast

Each participant adjusted the six stimuli to 82% detection threshold in a 2-interval-forced-choice task. The details of this task as they were performed for the reaching correction task are given in the reaching publication in Chapter 6 (pg. 148). The task varied from this description for the RT and PA publication in that the fixation cross was central, and the stimuli were presented at 2° either side of it, as they were in the RT and PA tasks. Also, the mean detection thresholds were determined from three repeats of blocks of 50 trials.

3.3. Aim and overview of thesis

The main aim of this thesis is to investigate the commonality of the neural mechanisms that facilitate the perception of stimuli and motor responses to stimuli. This is done by examining the relative response latencies to chromatic and achromatic stimuli in perceptual and motor tasks.

The literature review shows that both chromatic and achromatic information are used in facilitating both motor responses and percepts of stimuli, and that the commonality of the neural mechanisms that facilitate the perception of stimuli and motor responses to stimuli is an area of contemporary interest. However, when inferring relative contributions on the basis of relative response latencies it is important to ensure that the measured responses do genuinely reflect equivalent activation of the intended pathways. Therefore, this thesis began by working through the methodological issues in calibrating stimuli that face the area. When this was addressed, I was in a position to begin studying the relative response latencies.

In Publication 1, I demonstrate that the stimuli have been successfully calibrated in a manner that allows a meaningful comparison of response latencies across pathways. I examined the issue of equating the contrast of the stimuli by allowing for differences in the neural response saturation functions between the pathways. Finally I discuss how the relatively rapid decrease in the luminance RT/contrast function (when compared to the chromatic RT/contrast functions) suggests that the RT decision making process may be more reliant on luminance information.

In Publication 2, I examined the different latencies with which chromatic and luminance stimuli appear to participants. I measured perceptual latencies with three different tasks. The comparison of the three sets of results is informative about the effects of the experimental tasks themselves on the outcomes, and highlights the limitations of some of these paradigms for examining perceptual latencies between different stimuli.

In Publication 3, I compare the delays in incorporating chromatic and luminance information into on-line or mid-flight corrections of reaching to a target. This was done to test the visuomotor system that uses current internal estimates and online feedback about the relative locations of the hand and target to make rapid corrections.

In the exegesis, I discuss the main conclusions from each study and what conclusions about the processing of visual information across perceptual and motor tasks can be drawn from the overall comparison of the results.

4. Publication 1; Reaction time to chromatic and luminance stimuli

Kane, A., Wade, A. R., & Ma-Wyatt, A. (text in manuscript): Reaction time to chromatic and luminance stimuli.

4.1. Statement on contribution to publication

Adam Kane (candidate)

I was responsible for the initial concept and the first authorship for this publication. I programmed and piloted the study, collected and analysed the data and wrote the manuscript. All phases from conception to publication were done with regular consultation, suggestion and guidance from Assoc. Prof. Ma-Wyatt. Prof. Wade was also involved in discussing the study plan and in revisions of the manuscript.

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Anna Ma-Wyatt (co-author)

I hereby agree that the above statement truly reflects my contribution to this study. I give my permission for this publication to form a part of a submission by Mr Adam Kane for a PhD in the University of Adelaide.

Alex Wade (co-author)

I hereby agree that the above statement truly reflects my contribution to this study. I give my permission for this publication to form a part of a submission by Mr Adam Kane for a PhD in the University of Adelaide.

4.2. Preface

When examining the relative contributions of chromatic and achromatic information to different tasks, simple RT is a useful tool to begin with because it has long been used as a model task to understand the accumulation of information for a simple decision (e.g., Piéron, 1932, cited in McKeefry *et al*., 2003). In particular, it is a useful paradigm with which to investigate any differences between the accumulation or use of chromatic and achromatic information. In my experiments, participants released a button in response to the presentation of stimuli of a range of contrasts. This simple task generated a lot of reliable data. This allowed me to meet one of my primary aims of this thesis; to determine and demonstrate how to calibrate a single set of chromatic and achromatic stimuli that could be used to make a meaningful comparison of the response latencies between different visual tasks. With that established, the next aim was to determine whether it was possible to scale the stimuli in a way that was superior to the previous best, the MDT scale. I demonstrate that the estimated neural response (ENR) of a pathway is a more linear predictor of RT, but that the MDT scale was still a reasonable scale to use, in that it typically understated the temporal advantage of the luminance pathway by less than 10 ms. I was then able to address an older, but still unclear, question of the absolute differences in RTs between the pathways. This was also informative about the relative contributions of each pathway to the RT response.

4.3. Manuscript

Reaction times to chromatic and luminance stimuli

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Key words; Reaction time, response latency, chromatic versus achromatic, perception and action

Abstract

Reaction times (RTs) to achromatic luminance stimuli are thought to be faster than RTs to chromatic stimuli due partly to faster conduction velocities. However, the absolute differences between the pathways found by previous research has varied along with the methods of isolating the pathways and equating the stimuli for contrast or salience. This study shows that RTs can be predicted on the basis of multiples of detection threshold. However, the estimated neural response (ENR) to the stimuli was a more linear predictor. When stimuli were equated for ENR, RTs to luminance stimuli were approximately 35 ms shorter than RTs to L-M stimuli and approximately 65-70 ms shorter than RTs to S-cone isolating stimuli, depending on the stimuli contrast. RTs to luminance stimuli showed a stronger dependence on contrast than RTs for the chromatic stimuli, and eventually asymptote at around five to six times detection threshold, whereas chromatic RTs do not. We discuss why this may be.

Introduction

When subjects are asked to respond as quickly as possible to the appearance of a stimulus, the response latency or 'reaction time' (RT) depends both on the time taken for the signal to reach cortex, and the duration of a cortical decision making process that determines that the stimulus has appeared. In other words, the latency of visual decision making depends both on front-end delays (essentially differences in retinocortical transduction speeds) and also on the quality and magnitude of the input.

The human visual system has three distinct pathways for photopic vision that can be defined by the way that they contrast information from the three cone types. These pathways evolved at different times and have different characteristics, such as their chromatic sensitivity and their retinocortical transduction speeds. Because of this difference in conduction velocities, RTs are expected to vary when responding to stimuli that activate the different pathways.

To infer differences in RTs between the pathways, it is important to ensure that the stimuli are calibrated to effectively isolate the intended pathways. It is also important that different stimuli are equated for strength or salience in an appropriate manner as response latencies are inversely related to stimulus contrast. Currently, there is little consensus in how these challenges are addressed, resulting in a variety of measured differences between the pathways. Resolving these issues would help identify absolute differences in latency for these pathways and also to infer something about the degree to which these pathways contribute to visual functions such as RT responses. This would in turn allow inferences about the degree to which different visually controlled tasks share common visual pathways and decision making machinery. In the current study, we address these issues by comparing RTs to stimuli carefully calibrated to activate the different pathways equally.

The heavily myelinated magnocellular pathway has the fastest conduction velocity. It carries signals generated from the sum of L and M cone inputs (Wiesel & Hubel, 1966; Schiller & Malpeli, 1978; Lee, Kremers, & Yeh, 1998; Reid & Shapley, 2002) and the sensitivity of this pathway matches that of the human V-lambda function which is the definition of photometric luminance. Stimuli comprising only L and M cone modulations also appear to carry a blue/yellow tint because they co-activate the opponent S-(L+M) cone pathway. However, because S-cones have very little contribution to luminance (Chatterjee & Callaway, 2002; Lee, Pokorny, Smith, Martin, & Valberg, 1990), it is possible to add nulling S-cone contrast to an L+M stimulus to generate an L+M+S stimulus that contains pure luminance with no chromaticity. Such a stimulus is termed 'achromatic'.

Of the two chromatic pathways, the opponent S-cone pathway has the slowest conduction velocity (Irvin, Norton, Sesma, & Casagrande, 1986; Cottaris & De Valois, 1998; Reid & Shapely, 2002). It contrasts the activity of S cones with the sum of L and M cone activity (S-(L+M)) and is driven most strongly by stimuli varying along a blue/yellow axis of color space (for a review see Hendry & Reid, 2000). The parvocellular or opponent red/green pathway signals differences in the relative activity of the L and M cones (L-M). Conduction delays in the L-M pathway are generally measured to be between those of the S-cone and luminance pathway (Nowak, *et al*., 1995; Maunsell *et al*., 1999).

The experimental challenges

To infer differences in RTs between the pathways, it is important to ensure that responses are confined to a single pre-cortical channel. 'Pure' chromatic response times are highly sensitive to departures from isoluminance (Schiller & Colby, 1983; Lee,

Martin, & Valberg, 1989; McKeefry, Parry, & Murray, 2003; White, Kurtzel, & Gegenfurtner, 2006) so activation of the luminance pathways by chromatic stimuli should be minimised. Ideally, chromatic stimuli should be adjusted to isoluminance for each participant and each retinal eccentricity. Even when stimuli are adjusted to optimize perceptual isoluminance, the possibility for cross-channel activation is still present due to differences in the ratio of L and M cones that comprise individual receptive fields (Gegenfurtner *et al*., 1994). It is also possible that differences in when the different phosphors are illuminated in a single screen refresh could generate luminance responses to isoluminant stimuli (Vingrys & King-Smith, 1986). Therefore, when trying to infer small differences in RTs between the pathways, it is important to be alert for signs of luminance contamination by chromatic stimuli. Similarly, when trying to measure responses of the S-cone pathway, it is also ideal to adjust blue stimuli for each observer to avoid unwanted activation of the L-M pathway. This involves finding the hue of blue with the detection threshold is least affected by adaptation to yellow (see Smithson, Sumner, & Mollon, 2003)

Stimuli must be compared at equivalent contrasts but unfortunately, it is not clear how to achieve this. Stimuli can be equated for raw amplitude as defined by RMS cone contrast (cone activities are, broadly, equal under this definition). However, the contrast sensitivities of the postreceptoral retinal pathways differ considerably so this does not equate the stimuli in terms of the neural response evoked in the cortex, or their subsequent visibility. However, determining absolute detection threshold does equate the stimuli for detectability. McKeefry, *et al.* (2003) have shown that multiples of detection threshold (MDT) was superior to RMS cone contrast as it did not exaggerate the differences in RTs between the pathways as much.

These issues of pathway isolation and equating contrast mean that multiple adjustments of the stimuli need to be made before the final RT task. To avoid

introducing unwanted variance, these calibrations need to be made with stimuli that have similar spatial and temporal characteristics throughout the range of tasks.

Do RTs simply reflect conduction delays?

RTs to luminance stimuli are expected to be shorter than RTs to chromatic stimuli due to the differences in conduction velocities alone. For example, Nowak, *et al*. (1995) found a 20 ms difference between the response times in the 4Cα and 4Cβ layers of V1, suggesting that parvocellular signals may take up to 20 ms longer to reach V1 than luminance signals. However, apart from the differences in RTs due to differences in conduction delays, it is possible there may be differences in RTs to chromatic and luminance stimuli because of differences in the quality or volume of the information input from each of the pathways into the process of detecting a target. To find differences in RTs between the pathways due to differences in how much each pathway contributes to the decision making process, ideally one would simply remove the differences in conduction velocity as measured physiologically. However, this involves having to take the physiological measurements from areas with know temporal relations to the desired behavioural responses. Also, the experimental calibration issues outlined above also apply to physiological measurements.

How have the calibration challenges been addressed and what were the outcomes?

McKeefry *et al*. (2003) examined RTs to small chromatic Gaussian blobs, adjusted to subjective isoluminance. They test a range of contrasts, scaled in both RMS cone contrast and MDT, to explore whether the decisions involved in the detection of stimulus were extracted at a lower cone-opponent level or at a higher level. While the MDT scale

clearly did less to exaggerate the differences between pathways, suggesting that the decisions were based on information at the cortical level, there was no direct comparison of the slope of the RT/MDT relationships. If these relationships had different slopes, as did the VEP responses found by Rabin, Switkes, Crognale, Schenck, & Adams (1994) for example, then any differences in RTs between pathways compared at a specific contrast, would in part be a function of the contrast chosen. This confounds any estimates of absolute differences in response latencies between the pathways. McKeefry *et al.'s* (2003) data from two participants shows that RTs to L-M stimuli was on average approximately 50 ms faster and 35 ms faster than RTs to blue and yellow stimuli at twice detection threshold respectively. Responses to stimuli that also had luminance contrast were faster still, but luminance contrast was not scaled in MDT.

Later, White *et al*. (2006) examined RTs and the saccadic latency to activations of the three pathways. Their stimuli were Gaussian blobs at 3, 6 and 12° eccentricity, mostly shown at the maximum contrast possible. RTs to their chromatic stimuli from the generic axes of MB-DKL space was between 50 to 80 ms longer than RTs to their luminance stimuli, depending on eccentricity. In contrast to most other studies, they found that S-cone RTs were typically shorter that the L-M RTs.

Smithson and Mollon (2004) measured RTs to their Ishihara plate-like stimuli presented at around detection threshold at 3° eccentricity. They adjusted the stimuli to be isoluminant and adjusted the tritan line for each participant. RTs were measured both with luminance noise, to reduce the effects of transient luminance information when presenting the chromatic stimuli, and without as a control. They suggested that the luminance noise may have delayed the luminance response, thereby compressing the difference between chromatic and luminance RTs. Overall, they suggest that the mean luminance RTs were around 20 ms faster than mean L-M RTs and the S-cone RTs were approximately an additional 20 ms slower again.

Bompas & Sumner (2008) measured RT, saccade initiation and temporal order judgements (TOJ) to luminance and S-cone squares. The tritan lines and luminance were adjusted for the blue stimuli, and the stimuli were presented at 80% detection threshold, making the study comparable to that of Smithson and Mollon (2004), with the exception of Bompas and Sumner's stimuli being at 8° eccentricity. They also used approximately one third of the luminance noise used by Smithson and Mollon (2004). The data of White *et al*.(2006) suggests that there may be a greater difference between chromatic and luminance RTs with increasing eccentricity. Bompas and Sumner found median luminance RTs were 23 ms faster than S-cone RTs, and median saccadic initiation to luminance stimuli to be 44 ms faster than S-cone saccadic initiation. This luminance/S-cone RT difference was less than that found by Smithson and Mollon without noise, possibly suggesting that this lower level of luminance noise still delayed the luminance response. Meanwhile, Bompas and Sumner found no difference between the pathways in the TOJ task.

Do different tasks use input from the pathways differently?

The response in the RT task is modeled as involving a neural decision on the appearance of the stimulus. For example, Figure 1 shows the Smith and Ratcliff (2004) model of decision making. In this type of model, information is accumulated in the form of an increased rate of neuronal activity. This activity rises until it reaches a threshold level at which a decision is made. A feature of this model is that the decision time (and subsequent RT) therefore depends on the rate on information accumulation. Higher contrast stimuli effectively carry more information, and this reduces response latencies. However, it is also possible that some forms of information have more input into the decision making process as they offer more efficiency in this task. For example, the

delay in when information is received is theoretically important in a RT task. If chromatic information is relatively delayed, then it may not be as valuable as luminance information in this task. Therefore any decision may be reached faster if the decision making system depends relatively heavily on luminance rather than chromatic information (when compared to the relative balance of information involved in determining how we perceive a stimulus). The suggestion that some cortical processing is more dependent on luminance information has precedence. For example, area MT which processes motion information is known to have a strong preference for luminance information (see Gegenfurtner & Hawken, 1996 for review).

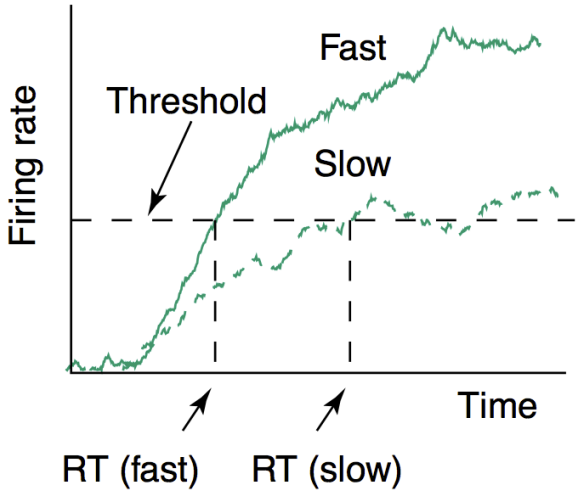

Figure 1. RT modeled as function of contrast. RT (fast) is the response to a high contrast stimulus and RT (slow) is the response to a low contrast stimulus. RT is determined by a firing rate reaching a certain threshold. This firing rate increases faster when there is more information (from Smith & Ratcliff, 2004).

Aims

We measured differences in reaction times for the luminance, L-M and S-cone visual pathways, where the recorded differences do not reflect activations of unintended pathways or poorly scaled contrasts. We determined how high the contrast of a chromatic stimulus could be before it began to activate the luminance pathway. We then investigated what contrast scales equated the stimuli effectively. Then we examined the absolute differences in RTs between the pathways, and the relative contributions of the three pathways to the RT decision process.

Method

Participants

Four participants aged between 25 and 39 years (M = 32, SD = 6.2 years) participated in the study. P1 and P2 were authors while others were naïve to the aims of the experiment. All were right handed except P2 who comfortably used their right hand. The study was approved by the human research ethics committee of the University of Adelaide.

Equipment

Stimulus presentation and data collection were conducted using software written in MatLab, (MathsWorks, version 2008a) and routines from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007). Stimuli were generated on a iMac with a ATI Radeon HD 5750 1024 MB graphics card connected to a 17” ELO touchscreen refreshing at 85Hz at a resolution of 1024 x 768 pixels. A Bits++ (Cambridge Research Systems) video attenuator was used to obtain 14 bit control over each of the CRT’s three primaries. The monitor output was gamma corrected to linear using a Minolta CS-100A photometer. Participants were seated in an otherwise dark room with a dim light reflecting off of a wall behind them. A chin rest placed their eyes 400 mm from the centre of the CRT in a fronto-parallel orientation. All viewing was binocular and the fixation point was always a central fixation cross. Participants spent five minutes adapting to the lower light levels before data collection. RTs were collected on a Cedrus RB530 response box.

Stimuli

Gaussian blobs (*SD* = 0.5°) were presented with their centres either 2° left or right of the fixation cross. There was a blob from each end of the three axes of MB-DKL space depicted in Figure 2 (MacLeod & Boynton, 1979; Derrington, Krauskopf & Lennie, 1984), being roughly green (G), red (R), yellow (Y) and blue/violet (B) as well as a luminance decrement (dark; D) and increment (light; L). Their spatial and temporal characteristics were constant throughout the initial adjustments and final experiments. The stimuli were presented for four screen refreshes which was 47 ms. To reduce the effect of the temporal transients which might drive luminance responses, stimulus onset was smoothed by ramping the contrast up and down; the first and last frames of the stimulus period were 50% of the full stimulus contrast. The background was always the grey at the centre of MB-DKL colour space with a luminance of 32.9 cd/m^2.

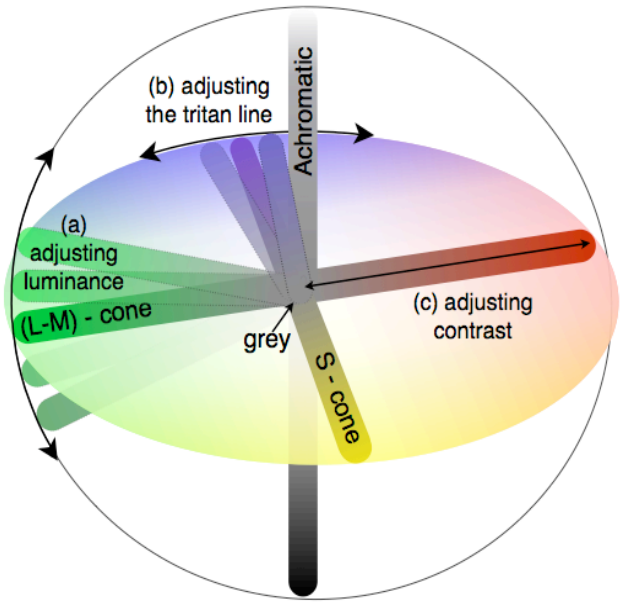

Figure 2. Adjusting the stimuli in MB-DKL colour space. (a) Each of the four chromatic stimuli were adjusted to isoluminance by pivoting the axis away from the luminance plane. (b) The tritan line was adjusted by pivoting the blue end of the S-cone axis along the chromatic plane. (c) Contrast was adjusted along the new isoluminant chromatic axes and the original luminance axis.

Initial stimuli adjustments. The four chromatic stimuli were adjusted subjectively to isoluminance using minimum flicker by each participant. This reset the chromatic

axes of MB-DKL space as four independent axes as depicted in Figure 2a. The minimum flicker task is shown in Figure 3a.

Next, we determined the blue axis that maximally activated each participant's S-cone pathway while minimising their L-M response using a modified version of the Smithson, *et al*. (2003) method. We determined the isoluminant violet/blue chromaticity that was most impaired by adaptation to a yellow screen for each participant. The angle of the chromatic plane most affected by the adaptation is assumed to elicit the least response of the L-M pathway and is therefore on the most 'pure' blue axis. This adjustment to MB-DKL space is depicted in Figure 2b, and the task is shown in Figure 3b.

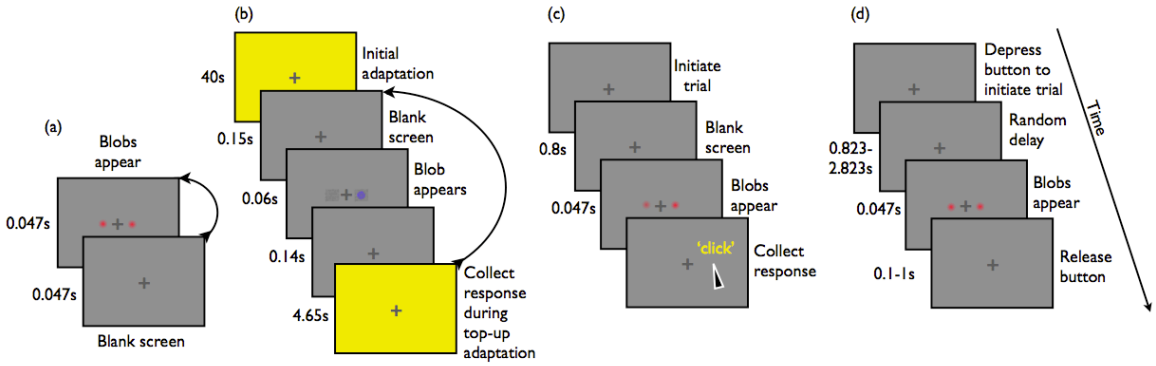

Figure 3. Paradigms for initial stimuli adjustments and collection of reaction times. (a) determining isoluminance for the chromatic stimuli by minimising flicker created by interleaved presentations of chromatic blobs and grey background. (b) finding the tritan line involved determining detection thresholds for a range of blue/violet chromaticities from along an isoluminant chromatic plane. (c) determining detection thresholds and just-noticeable-differences was done in a 2AFC task, with participants indicating which side the brighter (or only) blob was on. (d) RT was collected by depressing a button and releasing it when blobs appeared.

Then we adjusted the six stimuli to detection threshold along their new subjective MB-DKL axes, using a 2AFC procedure with staircasing controlled by QUEST (Watson & Pelli, 1983). Final detection thresholds were determined as the mean of three separate staircases of 50 trials. The stimuli in the RT experiment were presented at MDT. This adjustment is depicted in Figure 2c, and the task is shown in Figure 3c.

While McKeefry *et al*. (2003) demonstrated that MDT are useful for comparing RT, it has one theoretical challenge. The neural response is known to saturate at higher contrast, and the saturation function is thought to vary between the chromatic and luminance pathways (Lee, Pokorny, Smith, & Kremers, 1994). Therefore, equating stimuli in MDTs may not equate their evoked neuronal response. To our knowledge, RTs have not been compared when the stimuli are equated in terms of the estimated neuronal response that they generate. Therefore, we estimated the neural response function (ENR) of each stimulus over the range of contrasts that we could display on our monitor.

ENR can be calculated from just-noticeable-difference thresholds. The JND were determined in a task similar to the absolute detection thresholds, except that a control stimulus and a stimuli that also included the additional contrast were presented in the JND task, as depicted in Figure 3c. Dipper functions (Nachmias & Sansbury, 1974; Legge & Foley, 1980; Foley, 1994; Chen, Foley, & Brainard, 2000a, 2000b) are then fitted to the JND over that contrast range. These dipper functions are then used to calculate the ENR at a given contrast (Itti, Koch, & Braun, 1999). This process, and determining isoluminance and detection thresholds are described in more detail in Kane *et al*. (2011).

Measuring reaction time

Participants fixated on the cross and initiated each trial by pushing a button on a response box with a finger of their choice. Following a random delay (823 to 2823 ms) after the button was depressed, a stimulus appeared on both sides of the cross. Participants were instructed to release the button as soon as they detected the stimuli. One-in-seven trials was a catch trial where no stimulus appeared and participants were required to keep the button depressed for a minimum of 2823 ms. The stimuli were presented at 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 5.5 and 6 times detection threshold. Each stimulus was presented once at each intensity in each block, making a block 70 trials long ((6 blobs + catch trial) x 10 intensities). Stimulus intensity and chromaticity were randomised. During practice blocks, participants learnt the sound of a 'bad' beep that indicated that they had either anticipated the stimulus (RT<100 ms) or had failed to respond in time (RT> 1000 ms). These trials were discounted and repeated at the end of the block. A different beep indicated that the button had been depressed too soon after the previous trial (< ~300 after previous trial). A third beep indicated a successful trial.

Analysis

We collected data from 1.5 to 6 x MDT in order to determine how RTs behave at the highest chromatic contrast we could test on our equipment.

The median RTs for each axis and intensity condition were determined. However, of the 240 participant/contrast/stimulus conditions, there were 6 chromatic conditions where the required contrasts were beyond the range of our equipment. On these occasions, the stimuli were presented at the maximum contrast possible, and the

median RTs values used in the analysis were extrapolated from a line-of-best-fit to the median RTs from the lower contrasts.

Results

Absolute differences in RT

RTs as a function of MDT. For all participants and contrast conditions, median RTs to the S-cone stimuli was always longer than the median L-M RT. The median L-M RTs were always longer than the median luminance RT (individual data not shown). The markers in Figure 4 show the median RTs averaged across the four participants as a function of contrast scaled in MDT for each pathway. The solid lines indicate a least-squares line-of-best-fit to the RTs versus contrast functions. The broken line indicates the best fitting quadratic function. There was a negative relationship between the standard deviation of the RTs and the MDT, r = -0.164, p = .011, showing that the variance of the RTs decreased as the contrast increased.

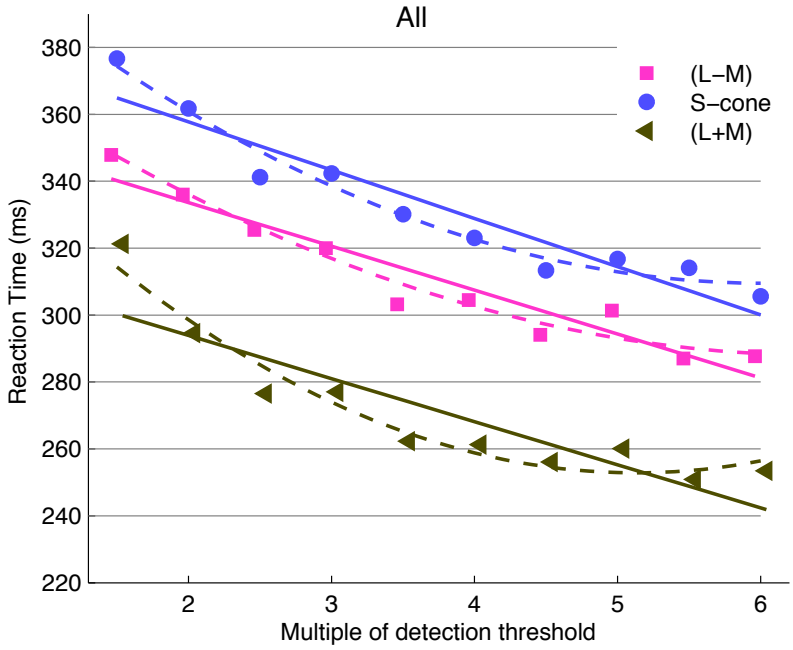

Figure 4. Mean reaction time for all participants as a function of the MDT for each axis and linear and fitted quadratic functions.

As the three RT/MDT functions are not perfectly parallel, the difference in RTs calculated between the pathways is slightly affected by the MDT at which the RTs are compared. For example, the quadratic functions show that RTs to luminance stimuli

are 34 ms and 60 ms shorter than RTs to L-M and S-cone stimuli respectively at 1.5 MDT. This luminance advantage is 43 ms and 65 ms at 3 MDT.

RTs as a function of ENR. Figure 5 shows the same mean median RTs by pathway, but as a function of contrast scaled in ENR. We determined whether ENR was a better linear predictor of RTs than MDTs by comparing R^2 values for linear fits to RTs as a function of MDT and ENR for all participant and stimulus conditions. A paired-samples *t*-test shows that ENR is a better linear predictor of RT, mean R^2 (*sd*) = 0.79(0.105), than MDT, R^2 = 0.74(0.080), $t(23) = 3.66$, $p = 0.001$.

The absolute differences in RTs between the pathways is similar when either scale is used. For example, at an ENR of .23, the advantage for the luminance pathway is 34 and 66 ms over the L-M and S-cone pathways respectively. This luminance advantage is 35 ms and 70 ms at ENR = .4. These results together suggest that the ENR scale does capture the difference in neural saturation functions between the pathways that the MDT scale misses. However, the MDT scale still allows a reasonably accurate comparison of absolute differences between the pathways.

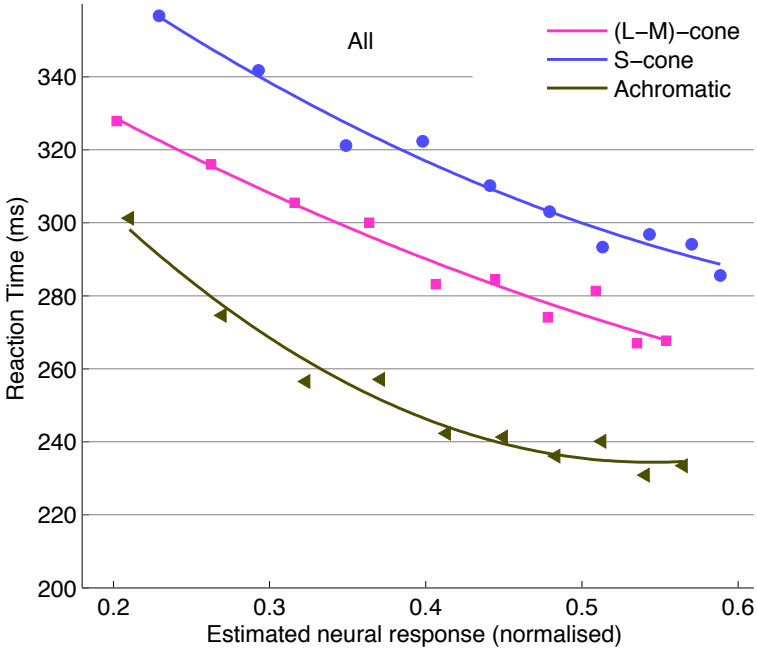

Figure 5. Mean normalised reaction time as a function of estimated neural response for each axes.

Determining linearity of RT/ENR functions

The neural decision-making time is not expected to be a linear function of contrast, even when scaled in ENR. For example, the model by Smith and Ratcliff (2004) depicted in Figure 1, suggests that RTs will reduce with contrast in a non-linear manner until it asymptotes. Therefore, Figure 5 includes quadratic functions fit to all three RT/ contrast relationships. However, the RT/ENR relationship for the L-M pathway shown in Figure 5 was best fit by a straight line. The slope, (linear coefficient) was significantly different to zero, $t(9) = 13.66$, $p < .001$. The adjusted R^2 shows that ENR predicted 95.4% of the variance in RTs. A quadratic function did not explain significantly more of the variance than the linear fit, $p = .295$.

The slope of a straight line fit to the RT/ENR relationship for the S-cone pathway was significantly different to zero, $t(9) = 13.94$. An adjusted R^2 shows that ENR predicted 95.6% of the variance in RT. Again a quadratic function was not a significantly better fit, $p = .080$.

Adjusted R^2 of a linear fit to the luminance RT/ENR relationship shows that ENR predicted only 85.9% of the variance in RT. Unlike with the chromatic functions, the slope of a quadratic function did explain significantly more of the variance than a straight line, $t(9) = 4.75$, $p = .002$. The adjusted R^2 of a quadratic fit shows that ENR predicted 96.2% of the variance in RTs.

Discussion

RTs decreased as a function of contrast scaled in MDT for all three pathways. However, ENR was a better linear predictor of RT than MDT. This suggests that some of the RT/MDT non-linearity may be from a non-linear relationship between contrast and neural response. Both scales indicate similar absolute differences in RTs between the

pathway, and the contrast at which the RTs were compared, also had a limited effect. Over the range of contrasts tested here, RTs to luminance stimuli were approximately 35 ms shorter than RTs to L-M stimuli, and approximately 65 to 70 ms shorter than RTs to S-cone stimuli when contrast was scaled in ENR. However, the luminance RT/ENR relationship, but not the chromatic RT/ENR relationships, was best fit by a non-linear function.

Why was only the luminance RT/ENR relationship significantly non-linear?

At the lower contrasts tested here, RTs initially decreased faster with increased luminance contrast than it did with increased chromatic contrast. RTs to luminance stimuli also appears to asymptote at the higher contrasts tested, whereas RTs to the chromatic stimuli does not. Here we outline two possible reasons why only the luminance RT/ENR function was significantly non-linear.

Firstly, the task used to determine the contrast scales may be different to the RT task in how chromatic and luminance information are used. The MDT and ENR scales were determined in detection threshold tasks where observers made perceptual decisions after the stimuli have been presented. As these decisions are made without time pressure, there may be limited consequences of the luminance responses being faster and more transient than the chromatic responses (Schiller & Malpeli, 1978; Schwartz & Loop, 1982). However, if the luminance response is more transient, it suggests that it is transmitting sufficient information to achieve detection in a relatively short time. This suggests that the luminance information may be accrued faster in the RT task. The RT response, as modeled in Figure 1, depends on the rate of information accrual. This rate of information accrual may affect the RT task more than the detection threshold task.

The second potential explanation is that the processing that leads to the decision making in the RT task, is different to the processing that leads to the decision making in the detection threshold task. It is possible that different tasks may use different decision making processes, and that the decision making process in the RT task may have a relatively greater input of luminance information (when compared to chromatic information) into any equivalent decision making process for the detection threshold task. For example, there could be more luminance ganglion cells carrying information to the decision maker than there are chromatic ganglion cells (when compared overall to the decision making system for the detection threshold task).

Both of these suggestions are speculative, and there is literature that fits in with both. This transient/sustained explanation is consistent with there being a single decision maker for the two tasks. This is also the view of Miller and Schwarz (2006), Cardoso-Leite, Gorea and Mamassian (2007) and Cardoso-Leite, Mamassian and Gorea (2009) who suggest that RTs and perceptual decisions may be made with a single decision maker that has different decision thresholds for different tasks. It is feasible to propose a functional model where there is a single system with a rate of activity that depends on input, but with two different decision criteria for two different outputs. However, differently to the previous studies, our task also involved the input from three different pathways. A model where the activity of a single system depends on different inputs for different tasks, would be relatively complicated and unparsimonious. This difficulty in explaining the differences in luminance and chromatic ENR/RT functions with a single decision making process, makes the 'two-decision-making-processes' explanation relatively plausible. In this respect, our conclusions support previous studies such as Klotz and Neumann (1999) and Steglich and Neumann (2000). However, more conclusive evidence to indicate one of the models above the other would come from a direct comparison of the response latencies to chromatic and

luminance stimuli in a RT and a perceptual task, but using a perceptual task that accumulates information in the same manner as the RT task.

Conclusions

Scaling chromatic and luminance stimuli in the relatively simple scale of multiples of detection threshold gives a good approximation of equating the contrast or salience of stimuli when measuring response latencies. However, they are best equated for strength by scaling their contrast in increments of the estimated maximum possible neural response. The relationship between RT and luminance contrast is nonlinear. This may reflect a difference in how the transient response of the luminance pathways is more suited to making rapid RT decisions than perceptual decisions used to determine the contrast scales. But, it is more likely to reflect a relatively greater input of luminance information than chromatic information into detecting the target in a RT task.

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4.4. Addition notes on RT study

These results show that chromatic stimuli that have been carefully adjusted to subjective isoluminance do not problematically activate the luminance pathway, reducing the measure RTs to chromatic stimuli. It is also possible to address the question of whether there was likely to be problematic activation if the chromatic stimuli were not adjusted to subjective isoluminance. For example, P4's median RT to the red stimulus presented at 5 MDT was approximately 290 ms. P4's point of subjective isoluminance for the red stimulus was almost 3° from the generic axis. If this stimulus had been presented along the generic red MB-DKL axis at this contrast, it would have had an associated luminance decrement equivalent to twice P4's luminance decrement detection threshold. P4's median RT to a luminance decrement at 2 MDT was approximately 300 ms.

Having two pathways respond to a stimulus could by itself have reduced RTs. For example McKeefry *et al*. (2003) demonstrated that RTs to a chromaticity midway between the cardinal axes of the MacLeod & Boynton (1979) chromatic plane was typically shorter than the RTs to stimulus from the two surrounding axis ends. This suggests that not having each participant adjust the chromatic stimuli to isoluminance has the potential to affect measured RTs with these stimuli over this range of contrasts. However, this case is one of the most extreme cases in my data set. Using the generic axes of MB-DKL space with Gaussian blobs, as did White *et al*. (2006), may only cause a limited reduction on RTs measured to chromatic stimuli.

These RT results differed from those of Smithson and Mollon (2004) when they collected RTs without the addition of luminance noise. Smithson and Mollon found that RTs to achromatic stimuli were approximately 17 and 35 ms faster than RTs to L-M and S-cone stimuli respectively. The difference between the two sets of results may be due to key methodological differences between the studies. Firstly, Smithson and Mollon's stimuli were presented at around detection threshold. The shape of the RT/contrast functions in Figures 4 and 5 in the RT publication suggest that we may have found a relatively smaller difference between the pathways had we collected RTs to stimuli presented close to detection thresholds. Also, Smithson and Mollon used a different method of equating the stimuli. In the RT publication, we pointed out that the perceptual 2AFC task used to determine the contrast scales may differ from the RT task in how they use transient luminance information and the relatively sustained chromatic responses. If this were the case, then it may exaggerate the advantage of the luminance pathway. However, Smithson and Mollon avoided this problem by determining detection thresholds in the RT task. This could also explain some of the greater advantage we found for the luminance pathway.

Our results varied from the comparison of simple RTs to stimuli at 3° eccentricity by White *et al*. (2006), presented in their Figure 4. Their L-M/luminance difference was similar to ours, despite the luminance contrast being considerably higher. However, in Figure 5, they show a L-M/Luminance comparison when both stimuli are equated at 10% RMS cone contrast. The contrast at 10% RMS cone contrast would have been similar to the contrasts of our stimuli presented at 6 MDT. In Figure 6 of White *et al.*, the L-M/Luminance differences appears to have dropped down to 20 ms. The major difference between our results and those of White *et al.'s* is that they found RTs to S-cone stimuli to be shorter than RTs to L-M stimuli.

5. Publication 2; Perceptual latencies for chromatic and luminance stimuli

Kane, A., Yates, M. J., & Ma-Wyatt, A. (text in manuscript). Perceptual latencies for chromatic and luminance stimuli.

5.1. Statement on contribution to this publication

Adam Kane (candidate)

I was responsible for the initial concept and the first authorship for this publication. I programmed and piloted the experiments, collected and analysed the data and wrote the manuscript. All phases from conception to publication were done with regular consultation, suggestion and guidance from Assoc. Prof. Ma-Wyatt. Dr. Yates suggested the use of the simultaneity judgement task and contributed to the revisions of the manuscript.

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Anna Ma-Wyatt (co-author)

I hereby agree that the above statement truly reflects my contribution to this study. I give my permission for this publication to form a part of a submission by Mr Adam Kane for a PhD in the University of Adelaide.

Mark Yates (co-author)

I hereby agree that the above statement truly reflects my contribution to this study. I give my permission for this publication to form a part of a submission by Mr Adam Kane for a PhD in the University of Adelaide.

5.2. Preface

This perceptual latency study follows on from a main finding of the RT study that only the luminance RT/ENR function was significantly nonlinear. This nonlinear function could be due to a difference in the use of the transient luminance responses and the relatively sustained chromatic responses (Schiller & Malpeli, 1978; Schwartz & Loop, 1982) between the RT task and the perceptual detection threshold task used to determine the ENR and MDT scales. But, it could also be that the RT responses, and the percepts of the stimuli in the detection threshold task, rely on two different decision making processes which may vary in the relative balance of chromatic and achromatic input that they use. In the discussion of the RT publication, I argued that a direct comparison of chromatic and luminance response latencies in RT and perceptual tasks, where both tasks depend on the rate of information accumulation, would provide valuable evidence to choose between these two possible explanations. In the current study, this is achieved in the final of three different experimental paradigms.

5.3. Manuscript

Perceptual latencies for chromatic and luminance stimuli

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Key words; perceptual latency, perceptual asynchrony, chromatic versus achromatic, perception and action

Abstract

It is not clear whether similar neural systems are used for perceiving, and reacting to, a simple stimulus. In this study, we present a novel approach for addressing this question which leverages well understood differences in conduction latencies between the luminance (achromatic) and chromatic pathways, and which overcomes many of the limitations of previous approaches. Previous work indicate that reaction times (RTs) to luminance stimuli are faster than RTs to chromatic stimuli. This difference has been partially attributed to differences in conduction latencies. If similar relative latencies are observed for the times at which luminance and chromatic stimuli are perceived, it would suggest a similarity in the systems for perceiving and reacting to stimuli. We used three tasks to measure the magnitude of perceptual asynchrony (PA) between luminance and chromatic stimuli. The stimuli were compared directly in a temporal order judgement (TOJ) task, and in a simultaneity judgement (SJ) task. A novel task, the mask onset asynchrony (MOA) task, was used to assess when chromatic and luminance stimuli are affected by masking. Analyses of TOJ and SJ results indicated that significant bias is possible in both paradigms. These results, and a theoretical review of the tasks suggest that the TOJ and SJ are unsuited for measuring PA between chromatic and luminance stimuli. Alternatively, the novel masking task led to very consistent results between participants. These results indicate that when information is processed to generate percepts, luminance information is processed approximately 9 ms and 14 ms faster than L-M and S-cone (chromatic) information respectively. We discuss the implications of these results for our understanding of the mechanisms underlying perception and action.

Introduction

There has been considerable debate about how visual information is used for perception and action. In a simple reaction time (RT) task, participants may release a button as soon as they see a stimulus appear. A decision that the stimulus has appeared is required to elicit this motor response. This decision has been described by drift diffusion models, such as the Smith and Ratcliff (2004) model depicted in Figure 1. The decision occurs when the neural activity level reaches a threshold, which reflects the required degree of certainty. There is evidence that the perception of a stimulus also relies on a similar neural decision making process (e.g. Palmer, Huk, & Shadlen, 2005). A central question is whether the release of the button, and the perception of the appearance of the stimulus, both rely on the same neural decision making process (the 'one-decision-maker' model; 1DM), or whether there is a different decision maker for each task (the 'two-decision-makers' model; 2DM).

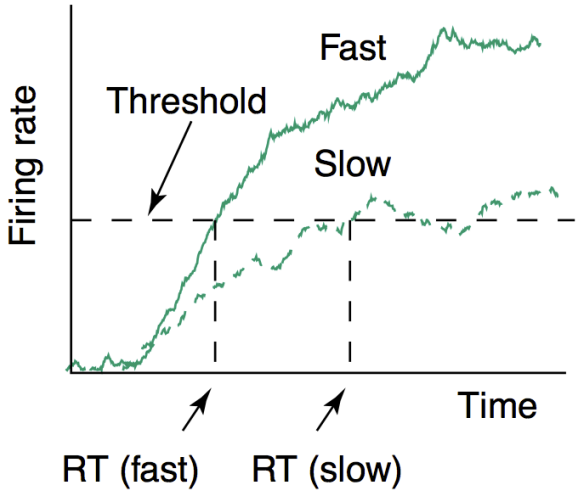

Figure 1. RT modeled as function of contrast. RT (fast) is the response to a high contrast stimulus and RT (slow) is the response to a low contrast stimulus. RT is determined by a firing rate reaching a certain threshold. This firing rate increases faster when there is more information (from Smith & Ratcliff, 2004).

Much previous research has compared RT results to temporal order judgement (TOJ) results. In the TOJ task, stimulus pairs are presented at a range of stimulus onset asynchronies (SOAs). Participants indicate which stimulus appeared *first* or *last*. The point of subjective simultaneity (PSS) is the SOA at which both stimuli have a 50% probability of being indicated as appearing first. The PSS indicates the difference in the perceptual latencies of the two stimuli

and is compared to differences in RT. Many RT/TOJ comparisons manipulate the salience of the stimulus, which typically has a greater effect on RTs than on PA (see Jaśkowski, 1996 for a review) with manipulations affecting RTs by approximately twice as much (Miller & Schwarz, 2006).

At first glance this RT/perceptual dissociation appears to suggest some difference in processing, but it is not decisive in indicating a 1DM or 2DM model. Sternberg and Knoll (1973) argue that differences in the RT and TOJ tasks could in themselves explain a dissociation. They suggest that RT responses reflect the time required to accumulate sufficient information to decide that a stimulus has appeared, while TOJs are comparisons of the latency of the peak of the visual responses. This issue may affect any perceptual task where the judgement is made without time pressure after the stimulus has been viewed for its whole duration.

Even without any differences between the two tasks, it has long been known that this dissociation can be explained with a 1DM model (e.g., Gibbon & Rutschmann, 1969). The 1DM model is often found to be the best fit to RT and perceptual data, where models allow the decision criteria to vary between the tasks (e.g., Miller & Schwarz, 2006; Cardoso-Leite, Gorea, & Mamassian, 2007; Cardoso-Leite, Mamassian, & Gorea, 2009). The three studies cited here are consistent in finding that the decision criterion is highest for the RT task. Figure 2 is a reproduction of part of Figure 1 from Miller and Schwarz (2006) showing the 1DM-2 decision criteria model. The cumulative sensory activation in their diagram equates to the firing rate in the Smith and Ratcliff (2004) model. The time on the x axis represents the time that the cells have been accumulating information. The high and low intensity functions determine the rate of information accumulation for each stimulus. In this diagram, the stimulus will be perceived if the sensory activation goes above approximately 25 units. A RT response will be made following it reaching approximately 35 units. While the 1DM-2 decision

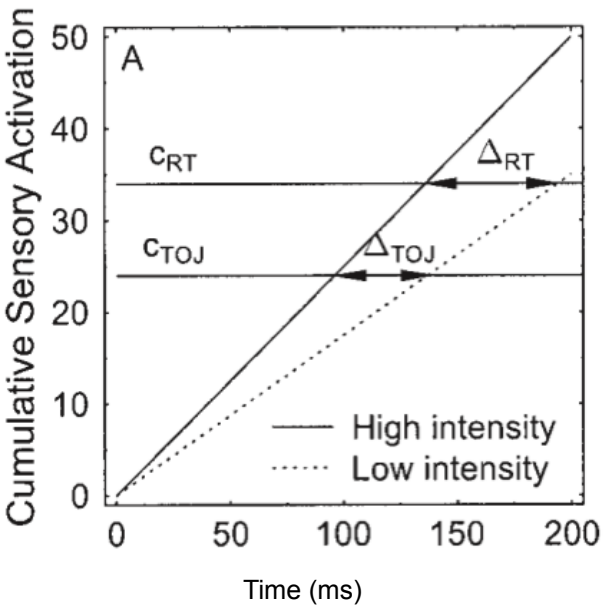

Figure 2. The potentially different effects of having different decision criterion on RT and TOJ latencies due to an increase in stimulus contrast (from Miller & Schwarz, 2006).

criteria model can provide a good and simple fit to RT/TOJ intensity dissociations, by letting the two decision criteria vary, the model can explain a large range of results, and so is hard to falsify even if it is not a good description of the underlying processing. Some evidence that it is not describing the underlying processes well comes from the confusing prediction that it makes for brief, low contrast stimuli. A brief stimulus might only elicit a response of 30 units of activity in the scale in Figure 2 for example, before the activity again declines to resting levels. The model predicts that the observer is likely to be able to perceive this stimulus, but is unlikely to produce a RT response via the normal mechanism. Therefore, the 1DM-2 decision criteria model should be tested with stimulus manipulations other than intensity. We leveraged well-known differences in conduction velocity between the chromatic and luminance visual pathways to investigate whether similar decision making systems underlie the decision that leads to the percept of a stimulus and a reaction to it.

The different visual pathway approach

To perceive or react to a stimulus, information must travel down at least one of the three pathways that lead from the retina to the lateral geniculate nucleus (LGN), and then onto V1, and/or other parts of the visual cortex. The luminance retino-geniculate

pathway conveys light-dark information. The two chromatic pathways, the L-M and the S-cone pathways, convey roughly red-green and blue-yellow information respectively. Most of the visual input relayed from the retina and on to the LGN terminates in V1 (see Henry, 1991, for review). In V1, information from the three pathways is integrated (see Sincich & Horton, 2005, for review). It is unclear whether the decision making process supporting the RT response and perception of stimuli both use chromatic and luminance information that has been integrated in an area such as V1, but this can be tested. Electrophysiological studies in the macaque show that the L-M pathway conveys information at a slower rate than the luminance pathway (Nowak, Munk, Girard, & Bullier, 1995; Schmolesky *et al.*, 1998), and that the S-cone pathway is slower again (Cottaris & De Valois, 1998). Of course, sheer cortical distance may also contribute to observed differences in processing times. The longer the paths over which chromatic and luminance remain segregated before being integrated, the greater the predicted difference in response latencies to chromatic and luminance stimuli. If both tasks use information that had been integrated at a similar distance from the retina, they should both show the same differences in response latencies to chromatic and luminance stimuli. This outcome is consistent with the 1DM model.

Alternatively, there could be a dissociation in the difference in response delays to chromatic and luminance information between the two tasks. This would be harder to explain with the 1DM-2 criteria model. In this case the differences in when the threshold criteria are reached is not a function of the differences in the rate of increase in activity, as indicated by the two 'intensity' functions in Figure 2. Chromatic and luminance stimuli matched for intensity should have an intensity function with the same slope in this model. The differences in when the thresholds are crossed would be due to differences in when information arrives and accumulation begins, as shown in Figure 3.

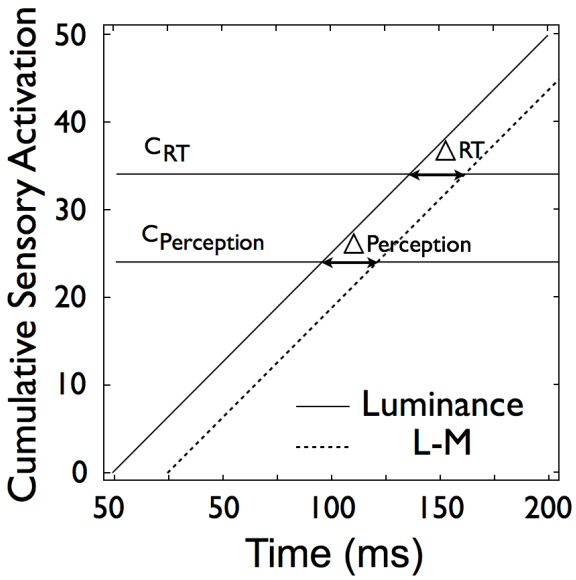

Figure 3. The predictions of the 1DM-2 decision criteria model on perceptual & RT responses to chromatic & luminance stimuli mathced for intensity. C_{RT} & $C_{Perception}$ are the criteria for the RT & perceptual tasks respectively. ΔRT & Δperception are the differences in response latencies to the high & low intensity stimul in the RT & perceptual tasks respectively.

In our previous study, RTs to luminance stimuli were approximately 40 ms and 60 ms faster than RTs to stimuli that isolated the L-M and S-cone pathways respectively (Ma-Wyatt, Kane & Wade, 2012). The intensity of the stimuli were matched by presenting the stimuli in multiples of their contrast at detection thresholds. These differences may be greater than would be predicted on the basis of conduction velocities alone. We also found that RTs initially decreased as a function of contrast more rapidly for the luminance pathway than for the chromatic pathways. We argued that this is consistent with the RT response relying more heavily on luminance information than chromatic information, at least when compared to the perceptual detection threshold task. These findings in themselves are some evidence that there is a difference in processing between the RT and perceptual tasks. A careful comparison of perceptual latencies to the same stimuli could therefore provide insight into the decision making in RT and perceptual tasks.

To our knowledge, only Bompas and Sumner, (2008) have compared chromatic/ luminance RT differences to PA to identical stimuli. They found RTs were 23 ms faster to luminance stimuli than to S-cone stimuli, but they found no PA between luminance and S-cone stimuli using a TOJ task.

To move towards understanding whether the processing for RT responses and perception differs, we determine latencies in perceiving the appearance of chromatic and luminance stimuli. We test three ways of determining perceptual latencies, using identical stimuli and similar participants throughout. Importantly, we introduce a new perceptual task that addresses the *accumulation* versus *peak comparison* concern of Sternberg and Knoll (1973). The new task determined when the percepts of chromatic and luminance stimuli are inhibited by masking. These results suggest that L-M and S-cone percepts are delayed by an additional 9 and 14 ms over percepts of luminance stimuli. Meanwhile, the TOJ task, and possibly the simultaneity judgement (SJ) task, appear unsuited for assessing differences in perceptual latencies between chromatic and luminance stimuli.

Common Methods

Participants

Five people aged between 25 and 40 years (M = 33) took part, with four in each experiment. P1 was an author. The others were naïve to the purposes of the experiment. P2 was also an experienced psychophysical observer. The study was approved by the human research ethics committee of the University of Adelaide. All participants were free to withdraw their consent without penalty.

Equipment

Stimulus presentation and data collection were conducted with MatLab 2010a, (MathsWorks) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007) on an iMac with a ATI Radeon HD 5750 1024 MB graphics card

connected to a 17” ELO touchscreen refreshing at 85Hz at a resolution of 1024 x 768 pixels.

A Bits++ (Cambridge Research Systems) video attenuator gave 14 bit control of the CRT’s red, green and blue phosphors. Monitor output was gamma corrected to linear using a Minolta CS-100A photometer. Participants sat in a dark room with only a dim light reflecting off of a wall behind them. They adapted to this light level for five minutes before data collection. A chin rest placed their eyes 400 mm from the CRT’s centre in a fronto-parallel orientation. All viewing was binocular.

Stimuli

Gaussian blobs (*SD* = 0.5°) were presented with their centres either 2° left or right of a central dark grey cross (0.57°) fixation cross. There was a blob from each end of the three axes of MB-DKL space (MacLeod & Boynton, 1979; Derrington, Krauskopf & Lennie, 1984), being green (G), red (R), yellow (Y) and blue/violet (B) as well as a luminance decrement (dark; D) and increment (light; L) as seen in Figure 4. Their spatial and temporal characteristics were constant throughout the initial adjustments and final experiments. The stimuli were presented for 47 ms. To reduce the effect of the temporal transients which might drive luminance responses, stimulus onset was smoothed by ramping the contrast up and down; the first and last frames of the stimulus period were 50% of the full stimulus contrast. The background was always the grey at the centre of MB-DKL colour space with a luminance of 32.9 cd/m^2.

Initial stimuli adjustments. The four chromatic stimuli were adjusted subjectively to isoluminance using minimum flicker by each participant. This reset the chromatic

axes of MB-DKL space as four independent axes as depicted in Figure 4a. The minimum flicker task is shown in Figure 5a.

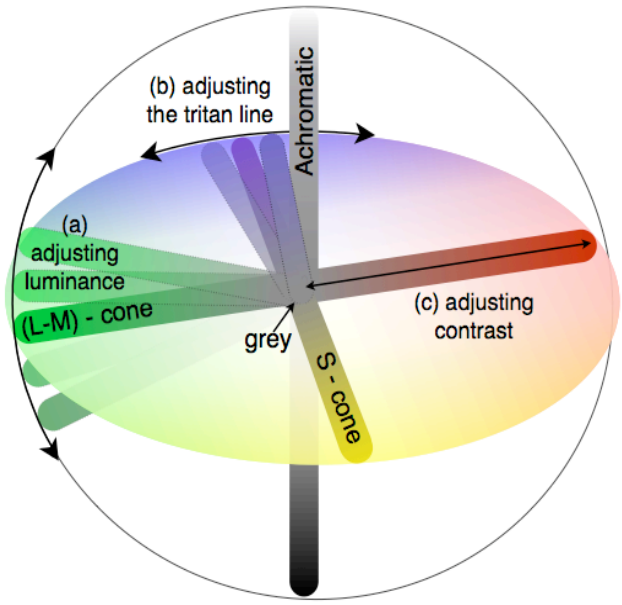

Figure 4. Adjusting the stimuli in MB-DKL colour space. (a) Each of the four chromatic stimuli were adjusted to isoluminance by pivoting the axis away from the luminance plane. (b) The tritan line was adjusted by pivoting the blue end of the S-cone axis along the chromatic plane. (c) Contrast was adjusted along the new isoluminant chromatic axes and the original luminance axis.

Next, we determined the blue axis that maximally activated each participant's S-cone pathway while minimising their L-M response using a modified version of the Smithson, *et al*. (2003) method. We found the angle of the blue axis that was most impaired by adaptation to a yellow screen for each participant. The angle most affected by the adaptation is assumed to elicit the least response of the L-M pathway and is therefore the most 'pure' blue axis. This adjustment to MB-DKL space is depicted in Figure 4b, and the task is shown in Figure 5b.

Then we adjusted the six stimuli to detection threshold along their new subjective MB-DKL axes, using a 2AFC procedure with staircasing controlled by QUEST (Watson & Pelli, 1983). Final detection thresholds were determined as the mean of three separate staircases of 50 trials. This adjustment is depicted in Figure 4c, and the task is shown in Figure 5c. The stimuli in the following PA tasks were presented at three times the contrast at their detection thresholds. We have demonstrated that this calibration procedure ensures that stimuli effectively activate their intended pathways, and elicit similar strength responses in these pathways (Kane *et al*., 2011; Ma-Wyatt *et al*., 2012).

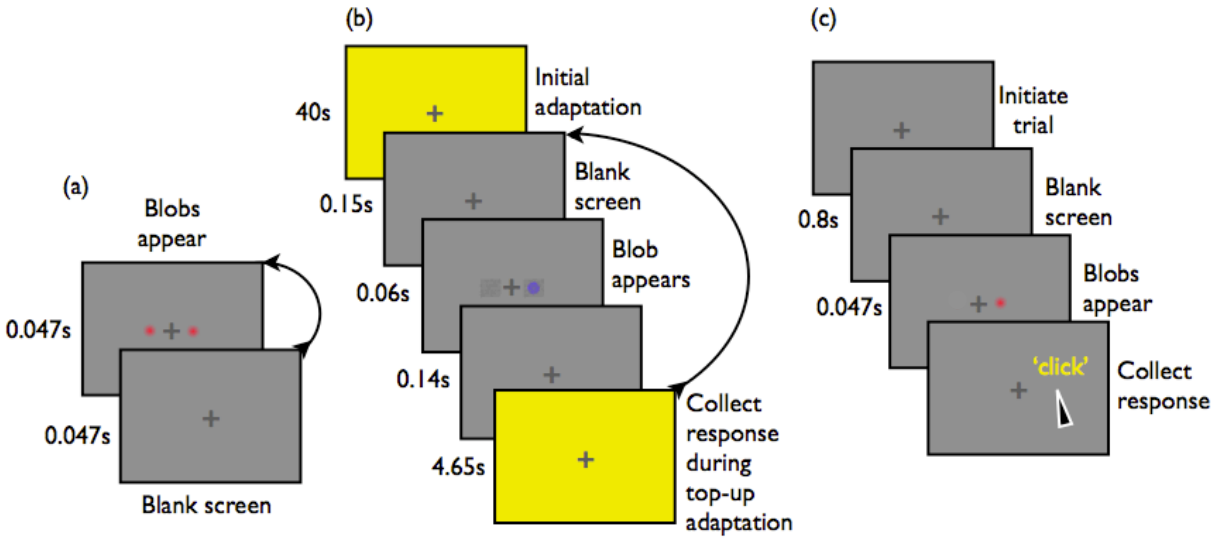

Figure 5. Paradigms for initial stimuli adjustments. (a) determining isoluminance for the chromatic stimuli by minimising flicker created by interleaved presentations of chromatic blobs and grey background. (b) finding the tritan line involved determining detection thresholds for a range of blue/violet chromaticities from along an isoluminant chromatic plane. (c) determining detection thresholds was done in a 2AFC task, with participants indicating which side the blob was on.

Temporal order judgements

Procedure

Each trial was initiated by a key press. A stimulus appeared 400 ms later. The onset of the second stimulus was pseudo-randomised at either 0, 12, 24, 35, 47, 59, 83 or 142 ms after the onset of the first stimulus. Participants clicked a mouse on the side of the screen where the stimulus had appeared *first* (or *last*). The fixation cross then disappeared and reappeared one second later, indicating that the next trial could proceed. No feedback was given.

There were 15 unique stimulus pairs that were presented in a pseudo-randomised order. Both stimuli in each pair were presented first only once at each SOA per block, giving 240 trials per block (8 SOA x 2 orders x 15 pairs). In half of the blocks participants indicated which stimulus had appeared *first,* and in the other half of the

blocks they indicated which appeared *last. First* and *last blocks* were presented in separate sessions to avoid confusion. Only P1 and P2 did the *first* blocks in the first session.

Analysis

We determined the PSS between the 15 possible stimulus combinations. The example in Figure 6 shows the proportion of trials where P1 indicated that the green stimulus was *first* when paired with the red stimulus. The y axis indicates the proportions of green *first* responses. The x axis indicates the SOA at which the pairs were presented. All data points to the right of zero indicate trials on which the green stimulus was presented before the red stimulus. The solid line is a probit function fit to these data. The PSS is the SOA where the probit predicts that both stimuli have an 50% chance of being indicated as appearing first. In this example, the PSS occurs when the green stimulus was presented 8 ms before the red stimulus.

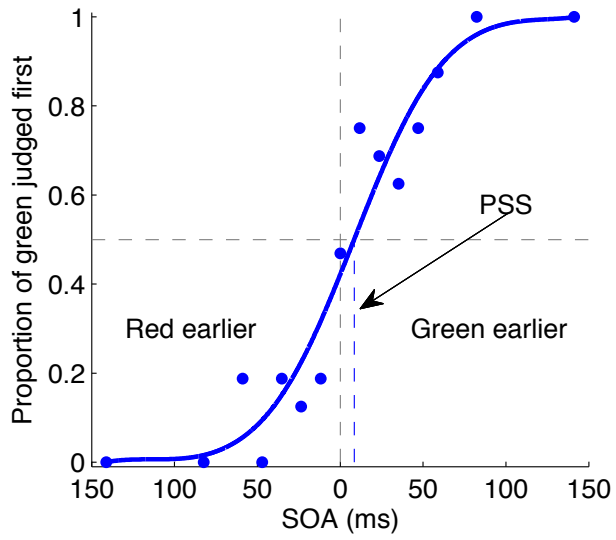

Figure 6. The relationship between SOA and proportion of green stimuli judged as appearing first, and a fitted probit function, for the red and green stimulus pair. The PSS is the probit's *x* value when both stimuli have a 50% chance of being judged as appearing first. Here, the PSS occurred when the green stimulus was presented 8 ms before the red stimulus.

Results

PSS for stimuli pairs. We initially present all of the data as if it was judged as *first.* To do this, the data from the *last* condition was converted to *'which was first'* by presenting 1 - the proportion judged *last*. Figure 7 shows the PSS for all 15 stimulus pairs. The bars extend towards the stimulus that is presented first at the PSS. The PSS from Figure 6 is the bottom left bar in Figure 7.

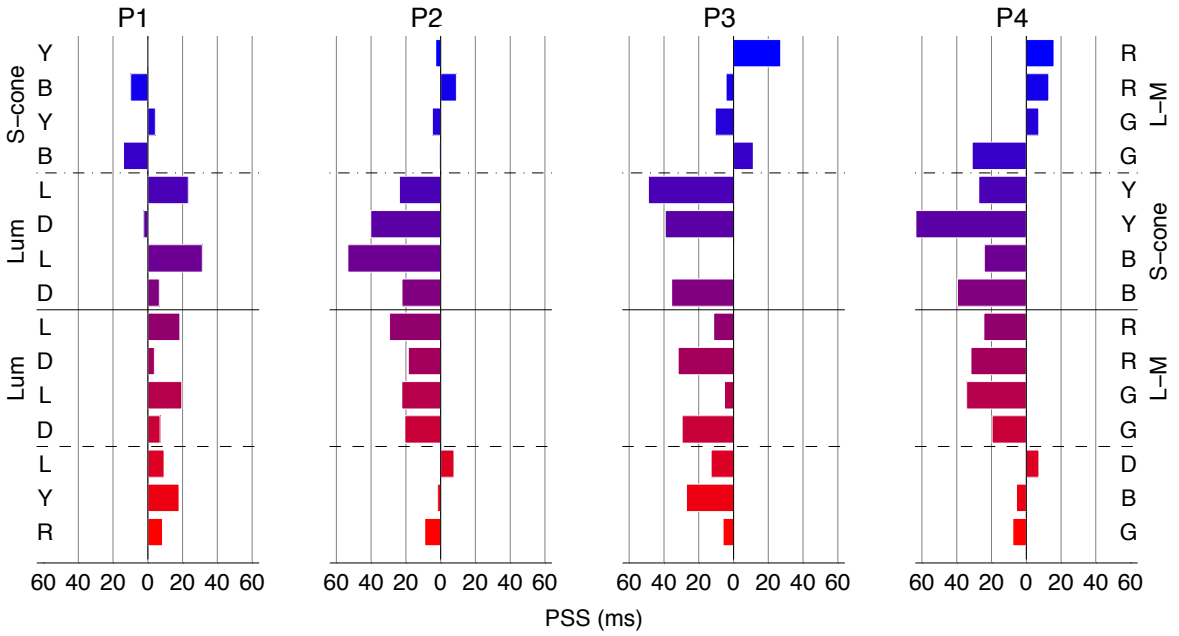

Figure 7. PSS by stimulus pair and participant. Bars extends towards the stimuli required to be presented first to achieve the PSS. G = Green, R = Red, B = Blue, Y = Yellow, D = Dark and L = Light stimuli. All S-cone vs L-M comparisons are on top, above the dot-dashed line. Below this are the luminance vs S-cone comparisons between the dot-dashed and solid horizontal lines. The L-M vs luminance comparisons are between the dashed and solid horizontal lines. The bottom section below the dashed lines show the within-axis comparisons.

It was initially determined that these PSS were not just random variance. The mean (SD) of the absolute PSS from the same-axis comparisons (the bottom 3 bars of Figure 5), for all four participants, 10.1 (2.24) ms, was smaller than the mean absolute PSS for the other 12 comparisons (the top 12 bars), 20.3 (14.87) ms, $t(58) = 2.32$, $p = .024$. The 95% CI around the mean difference is [1.42 - 19.11] ms. This suggests that axis or pathway was important in determining these PSS values.

Between axes comparisons. Participants displayed good internal consistency when comparing the four different stimulus pairs that formed any one of the between-axis comparisons. For example, 23 out of 24 of the chromatic/luminance PSS (between the dashed line and dot-dashed line in Figure 7) for P2, P3 and P4 were in the direction of the luminance stimuli.

Each stimulus pair PSS in Figure 7 was averaged to create the mean PSS (±SEM) for the three pathway comparisons in the four left panels of Figure 8. On average (SD), the L-M stimuli needed to be shown 12.2 (7.98) ms before the luminance stimuli for P1, whereas the luminance stimuli needed to be presented 22.8 (4.70), 19.5 (13.22), and 27.6 (6.75) ms earlier to achieve subjective simultaneity for P2, P3 and P4 respectively.

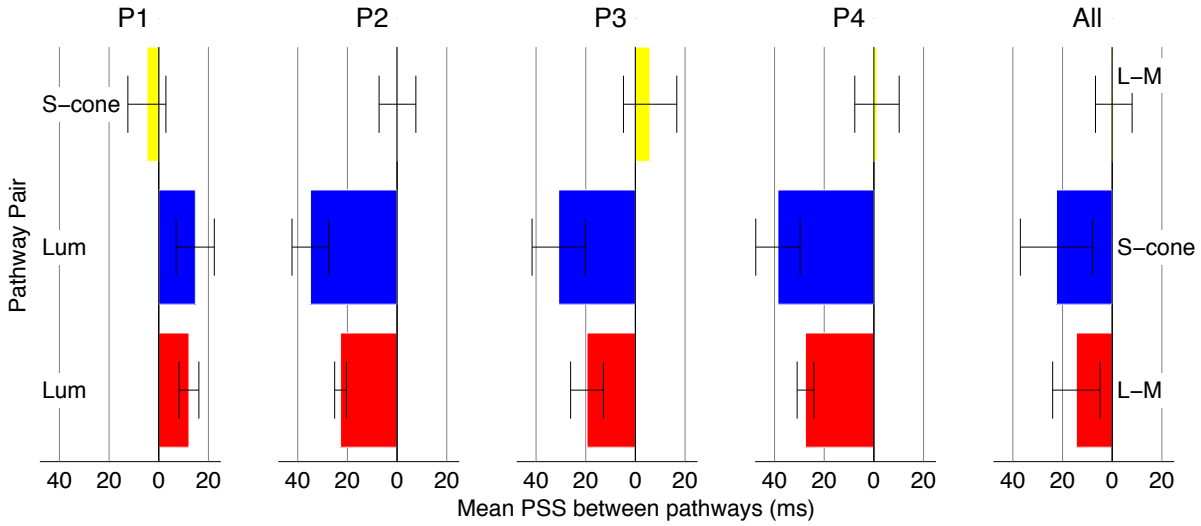

Figure 8. Mean PSS between different pathways individually for four participants (±SEM) and overall mean for all participants (±95%CI) on right. Bars extends towards the pathway of the stimulus that was required to be presented first to achieve the PSS. For example, the bottom left bar indicates that the L-M stimuli needed to be presented 12 ms before the luminance stimuli to achieve PSS.

The S-cone stimuli needed to be presented 14.7 (15.34) ms before the luminance stimuli, to achieve simultaneity for P1. Conversely, the luminance stimuli needed to be

presented 34.9 (14.80) ms, 30.9 (21.46) ms and 38.7 (17.88) ms before the S-cone stimuli to achieve simultaneity for P2, 3 and 4 respectively. Each participant's L-M/ luminance and S-cone/luminance PSS were always in the same direction. A 95% CI around the PSS between the L-M and S-cone stimuli always included zero.

Figure 8 shows all of the participants' data averaged on the right panel (±95% CI). Interestingly, these results suggest that the luminance stimuli took longer to process; the opposite of what these PSS should show if they reflected differences in conduction delays between the pathways. Only P1 (an author) gave a result consistent with the known differences in conduction delays. The literature on relative conduction velocities (Irvine, *et al*., 1986; Henry, 1991; Cottaris & De Valois, 1998) suggests that it is unlikely that these inconsistent PA are the result of great variations in individual conduction velocities. As it seems unlikely that these PSS reflect differences in conduction velocities between the pathways, we examine these data for more plausible explanations of these results.

Response bias. Making temporal judgements can be difficult for the visual system (Coltheart, 1980) and the TOJ task can be affected by biases (Schneider & Bavelier, 2003; Shore & Spence, 2005; Zampini, Shore, & Spence, 2005; Yates & Nicholls, 2011). Our TOJ task was exposed to bias as two different coloured stimuli were presented on each trial, and participants could preferentially respond to particular stimulus. Qualitatively, we observed that it could be difficult to judge which stimulus appeared first, even when they were clearly asynchronous. Under conditions of high uncertainty, there may be a greater likelihood of a response bias.

If the responses are unbiased, the responses to the questions 'which stimulus was *first*?' and 'which stimulus was *last*?' should be approximately equal but opposite.

Subtracting the PSS calculated using the *first* responses from the PSS calculated using the *last* responses should give an answer around zero. A significant non-zero value indicates a bias. As this bias would be acting in both the *first* and the *last* conditions, half of the difference in PSS between the two conditions indicates the bias towards particular stimuli, as shown in Figure 9. The mean magnitude of these biases are 24.4, 6.5, 40.1 and 15.5 ms for P1 to P4 respectively, while the mean PSS values were 11.8, 17.7, 20.1 and 23.5 ms. Therefore, this response bias was generally of a similar magnitude to the calculated PSS.

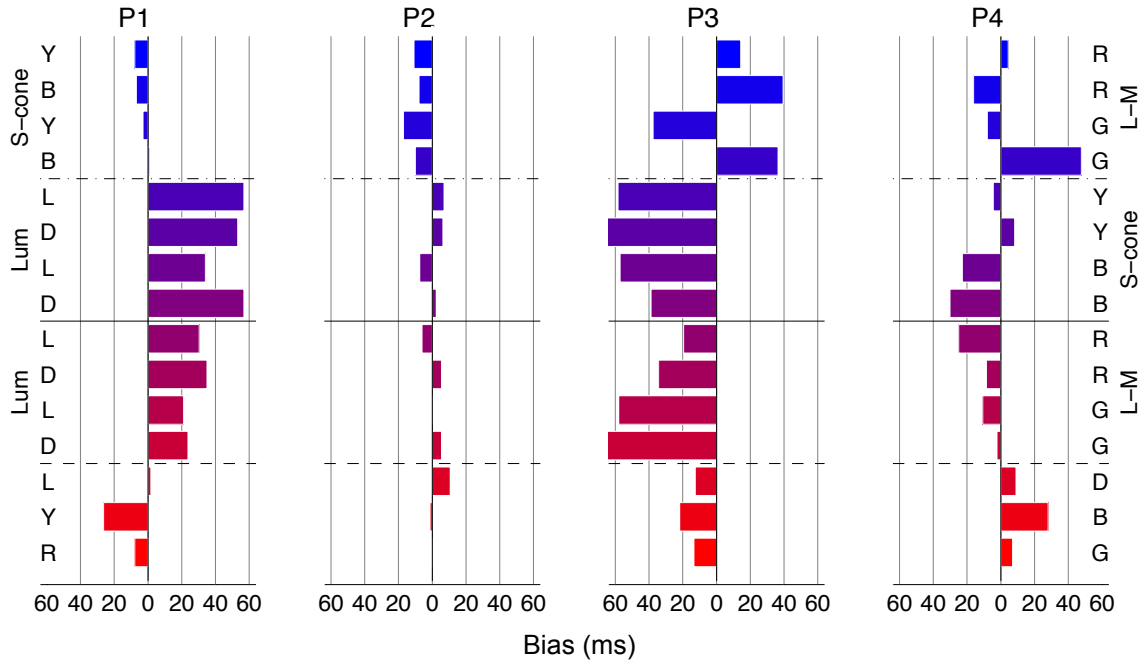

Figure 9. Response bias to particular stimuli calculated as half of the difference between PSS values calculated when participants indicated which stimulus was *first* versus which stimulus was *last*. Stimuli are indicated by the letters on the sides. The bars extend towards the stimulus that was most likely to be given as the response, regardless of whether participants indicated which stimulus was *first* or *last*. G=Green, R=Red, B=Blue, Y=Yellow, D=Dark and L=Light stimuli. The S-cone vs L-M comparisons are on top, above the dot-dashed line. Below this are the luminance vs S-cone comparisons between the dot-dashed and solid horizontal lines. The L-M vs luminance comparisons are between the dashed and solid horizontal lines. The bottom section below the dashed lines show the within-axis comparisons.

P1 and P3 show strong biases. P1 preferentially indicated the luminance stimuli over the chromatic stimuli, regardless of whether the question was worded as *first* or *last*. P3 indicated the chromatic stimuli more often, regardless of the question. No participant showed a consistent bias for the S-cone versus L-M pair comparisons.

Discussion

Because the between-axes PSS were larger than the same-axis PSS, and because individuals gave consistent pathway-dependent results, it is likely that axis is important in determining these PSS. The inconsistency between participants and the suggestion that the luminance stimuli took the longest to process suggests that these PSS measures do not reflect PA created by differences in the conduction velocities of the pathways. However, there was a bias towards indicating either the chromatic or the luminance stimuli. This bias varied between participants. While this bias was nulled by collecting both *first* and *last* responses, it demonstrates that participants do respond preferentially to stimuli. Below, we propose a related bias that could explain these results.

A 'first' bias? Some participants had a bias to indicate some stimuli more than others, as has been demonstrated above. It is equally plausible that some participants were biased in indicating which stimulus *appeared first*, either directly in the *first* condition, or indirectly by indicating the opposing stimulus in the *last* condition. We refer to this as a 'first' bias. This bias would affect the calculated PSS in a manner indistinguishable from the effect of differences in perceived latency between the two stimuli. Accordingly, it is not possible to demonstrate either its presence or absence. However, this bias appears to be a more likely explanation of the results than the

chromatic pathways having faster conduction velocities than the luminance pathways in some individuals.

Visible persistence and cues? An alternative source of variance between chromatic and luminance conditions would be the potential differences in the visible persistence of the stimuli. Visible persistence is the duration for which a stimulus appears visible (Coltheart, 1980). This duration increases with reductions in stimulus contrast. Our low contrast stimuli probably had different persistence durations. Ideally, we would have calculated these persistence durations, however, we could not separate their duration from their discriminability (as discussed in the 'Simultaneity Judgement' section below). Therefore, we calculated a combined measure of persistence durations and discriminability. Our luminance stimuli were the shortest/most discriminable while our S-cone stimuli were the longest/least discriminable.

A difference in the cues our participants used to make the TOJs may explain some of the intra-individual differences seen here. Figure 10 illustrates a trial in which a luminance and an a S-cone stimulus are presented, where the S-cone stimulus is presented one screen refresh (11.8 ms) before the luminance stimulus. It assumes the S-cone stimulus persistence duration to be twice that of the luminance stimulus. It also assumes that the luminance signal is transmitted to the relevant decision maker area 11.8 ms faster that the S-cone signal. The vertical dot-dashed line marked 'A' shows they should be judged as appearing simultaneously if they are judged by their onsets. However, arrow B shows that the S-cone stimulus should appear to be 22 ms later, if

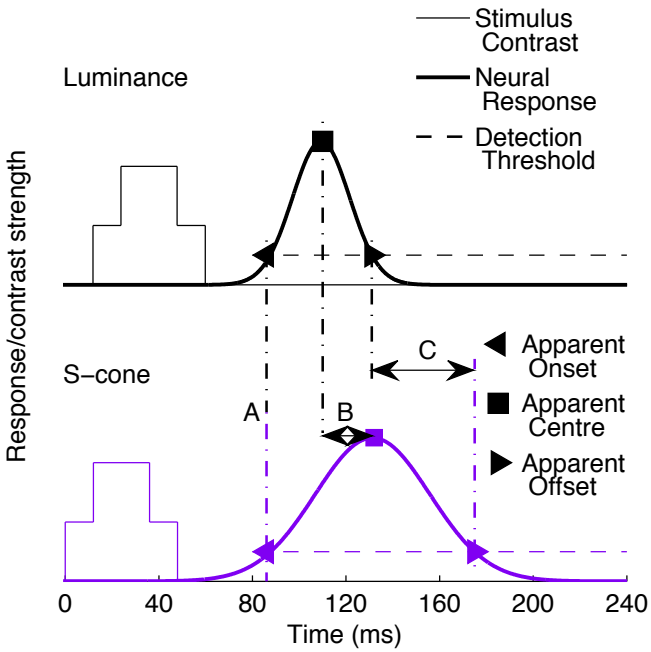

Figure 10. Illustration of the potential responses to luminance and S-cone stimuli in a TOJ trial. It shows the stepped onset of the stimuli on the left, followed by approximations of the pathway responses. Refer to text for details.

they were judged by their apparent temporal centres. Arrow C shows that the S-cone stimuli should be judged to be 44 ms later if only the stimulus offset was used. This shows that it is likely that any differences in persistence durations would have affected the PSS calculated unless stimulus onset was the only cue used. Moreover, participants could have used stimulus onset in the *first* condition, and stimulus offset in the *last* condition, meaning that correcting for a response bias by using both *first* and *last* conditions may introduce more variance.

Importantly, in the RT task, participants can start processing the stimuli from their onset until their neural decision makers have collected sufficient information to indicate the appearance of a target. While this is also true of the TOJ task, Figure 10 demonstrates that if any cue other than the onset of the stimuli is used in TOJ judgements, then differences in stimuli persistence durations introduce differences between RT and TOJ results.

Conclusion. Due to the demonstrated and theorised effects of bias, and the potential effects of differences in persistence durations and judgement cues, the TOJ task appears to have limited sensitivity to measure a chromatic/luminance PA.

Simultaneity judgements

In the SJ task, stimulus pairs are presented at a range of SOAs. Participants indicate whether the two stimuli appeared simultaneously or not. The PSS is the SOA at which the stimuli are most likely to be judged as appearing simultaneously. PSS determined using a SJ task are less prone to bias than PSS derived from TOJs (Schneider & Bavelier, 2003). Importantly, if participants have a tendency for responding simultaneous (or not simultaneous) in the presence of certain stimuli, or if they have an overall tendency to respond simultaneous or not, the PSS should not be affected.

Procedure

Stimuli were presented exactly as in the TOJ task. In the SJ task, participants typically indicate whether the stimuli appeared simultaneously. These brief stimuli were physically asynchronous on 87.5% of trials and they were rarely perceived as being simultaneous in piloting. Therefore, participants indicated whether the stimuli appeared to temporally overlap or not by mouse-clicking on the left or the right of the screen.

Analysis

Figure 11 shows the trials where P1 judged the green and blue stimuli to demonstrate the analysis. The x axis indicates the SOA at which the pairs were presented. The markers indicate the proportions of overlapping responses as a function of SOA. The markers on the right of zero are the proportions when the blue stimulus was first. The y axis indicates the proportion of overlapping responses. The solid line is

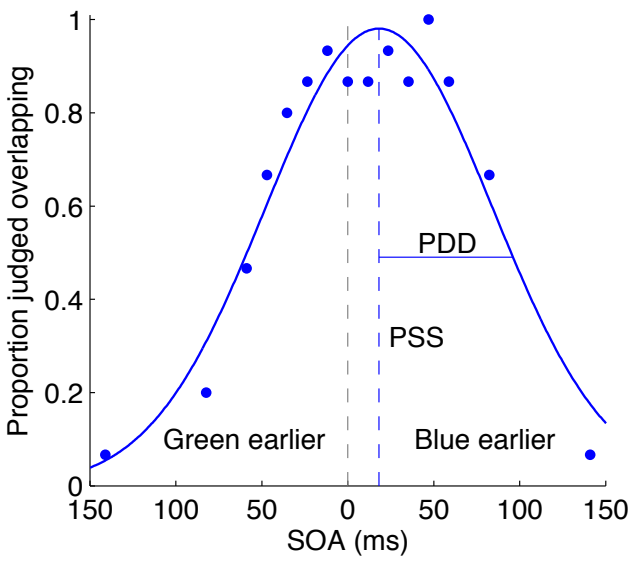

Figure 11. Example of PSS value for blue and green stimuli comparisons and the calculation of the PDD (PDD described under 'Persistence duration of stimuli').

a normal distribution with the least-squares fit to these proportions. The PSS is the mean SOA for this distribution. For example, this PSS occurred when the blue stimulus was presented 18 ms before the green stimulus. The calculation of our measure of duration and discriminability (PDD) illustrated in Figure 11 is discussed later. The blue-light SJ for P4 were excluded from analysis as they could not be fit by a Gaussian distribution.

Results

PSS for stimuli pairs. The mean (SD) absolute PSS between the within-axis pairs for all participants, 8.2 (7.74) ms (n = 12) was significantly smaller than the between-axis comparisons, 17.4 (9.66) ms (n = 47), $t(57) = 3.04$, $p = .004$. The mean [95% CI] difference between the within and between conditions is 9.2 [3.11 - 15.15] ms. This suggests that the measured PSS is dependent on the axis of the stimuli.

Between axes comparisons. The PSS between the axes are shown in Figure 12. For the L-M/luminance comparisons, P1 to P4 had PSS [95% CI] of 12.6 ms [1.9 23.3], 16.2 ms [9.0 23.3], -23.7 ms [-52.6 5.2] and 1.8 ms [-26.9 30.4], respectively, with positive PSS indicating that the L-M stimuli had to be presented first for subjective

simultaneity. For the S-cone/luminance comparisons, P1 to P4 had PSS of 30.7 ms [14.4 46.9], 19.5 ms [14.8 24.2], -16.0 [-25.4 -6.7], and -2.7 ms [-7.6 2.1] with positive PSS indicating that the S-cone stimuli had to be presented first for subjective simultaneity.

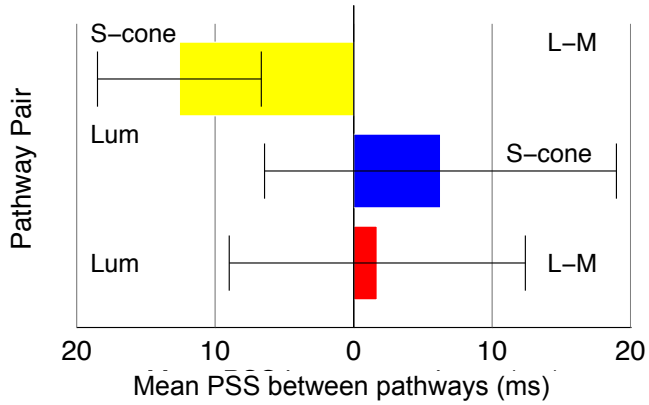

Figure 12. Mean PSS between pathways derived from simultaneity judgements (±95%CI). Bars extends towards the pathway of the stimulus that was required to be presented first to achieve the PSS.

These broad 95% CI presented above have limited statistical power, being constructed from just four data points each. However, five of the eight mean chromatic/luminance PSS values were significantly different from zero. As with the TOJ data above, this suggests that participants were consistent in the four comparisons that made up each of the between-axes comparisons. However, while individuals had internal consistency, there was again variance between individuals. P1 and P2 both had chromatic/luminance PSS with directions that were consistent with there being a PA due to differences in conduction velocities. However, P3 showed a trend in the opposite direction.

When these data were collapsed over all participants as seen in Figure 12, there were no significant mean chromatic/luminance PSS values. The small PSS relative to the 95% CIs reflects the inconsistency between participants. Interestingly, the S-cone stimuli were most likely to be indicated as overlapping when they were presented before the L-M stimuli.

Persistence duration of stimuli. The persistence duration may vary between different stimuli (see Kojima & Kawabata, 2012). Longer persistence durations should be indicated by a widening of the distribution seen in Figure 11, as they should have been judged as overlapping over a greater range of SOAs. However, these distributions will also broaden with decreased ability to discriminate which stimulus pairs are overlapping. Therefore we refer to this measure as the persistence duration and discriminability (PDD). The PDD were calculated as half of the distribution width at half of the distribution height, as demonstrated in Figure 11. The PDD were calculated for the luminance, L-M and S-cone pathways, using only the dark versus light, green versus red and blue versus yellow comparisons respectively. Mean PDD were 76.2 (6.80) ms, 89.1 (33.02) ms and 44.4 (18.57) ms for the L-M, S-cone and luminance pathways respectively. A one-way ANOVA shows that PDD varies between axes, $F(2,9) = 4.28$, $p = 0.049$. Therefore, the persistence duration of the stimuli is likely to have varied, corresponding to the relatively transient and sustained responses of the luminance and chromatic pathways respectively (Schiller & Malpeli, 1978; Schwartz & Loop, 1982).

If the chromatic stimuli persisted longer, they could still appear to overlap the luminance stimuli when they were presented increasingly earlier. This should have exaggerated the temporal advantage for the luminance stimuli.

Discussion

The within-axis PSS were smaller than the between-axes PSS, suggesting that axis is important in determining the PSS. The known differences in the conduction velocities suggests that a chromatic stimulus would need to be shown before a

luminance stimulus in order for them to both appear simultaneously. However, only the PSS of the two experienced participants were consistent with this notion.

The variance in PSS between individuals may again reflect differences in bias. It was not possible to preferentially indicate that particular stimuli were earlier or later, as could be done in the TOJ task. However, participants did respond after seeing two clearly different stimuli. It was possible to increasingly indicate simultaneity on the trials when particular stimuli were presented earlier or later.

The 'overlapping/not overlapping' decision would have been difficult on many of the early trials. Participants presumably developed their understanding of how overlapping and non-overlapping trials appear over the early trials. This could again lead to the formation of patterns that vary between participants.

While these results may reflect differences in bias between individuals, the above mechanism is speculative and there is no strong evidence that bias exists in the data of this theoretically more robust task. Therefore, it is also possible that the internal consistency of the four participants was an improbable event, and that there is no chromatic/luminance PA, or that these data indicate a chromatic/luminance PA that varies between individuals.

Mask onset asynchrony

A masking task, the mask-onset asynchrony (MOA) paradigm, was developed to prevent bias, and to avoid the complications introduced by different persistence durations. It provides a different insight into PA, in that it examines the temporal aspects of when a single stimulus can be detected, rather than a direct subjective comparison of when two stimuli appear. This point is discussed further below.

Procedure

On each trial, identical stimuli appeared on both sides of a central fixation cross; one was the target stimulus and the other was a control. They were followed by simultaneous, high-contrast, blob-shaped masks that were identical to each other. Both masks appeared on the screen refresh immediately after the fourth screen refresh of the control stimulus. The control MOA (as measured from the offset of the control stimulus) was therefore always zero. The target MOA (measured from the offset of the target stimulus) was controlled by a staircase over 26 trials. Participants indicated the target side where the stimulus had appeared earliest by clicking a mouse on that side of the screen. The target MOA decreased by 11.8 ms (a screen refresh) following two consecutive correct responses, and it increased by 11.8 ms after each incorrect response. The staircases for the six different stimuli were interleaved randomly. No feedback was given.

Rationale

When the MOA is long enough, the target signal should be processed before the mask signal, leaving the target visible. As the MOA decreases, the mask increasingly interferes with the target processing until the target cannot be detected above chance. This task therefore determined the threshold MOA at which a stimulus could be detected. This value is referred to as the MOA-D.

The masks were spatially identical to the stimuli and were presented for five screen refreshes or 59 ms. Each stimulus was followed by a mask of a similar colour in order to mask any colour aftereffects. However, to standardise the processing latencies of the different masks, they all had high luminance contrasts above where we have

previously (Ma-Wyatt *et al*., 2012) demonstrated that RTs to these stimuli had reached asymptote. The chromatic masks were set at 45° above the chromatic plane of MB-DKL space, while the dark and light masks were at the lowest and highest brightnesses possible on our equipment respectively.

While it has been demonstrated that RT latencies had reached asymptote by the contrasts used in these masks, it is only assumed that the processing latencies were also at asymptote for perceptual processing. However, the other masking options were less favourable compromises. Had all stimuli been masked with the same mask, for example a luminance increment, the change from luminance decrement to the mask would have been greatly different to the change from the luminance increment. Another option was to mask the luminance increment and decrement stimuli with luminance increment and decrement masks of the same luminance contrast as the chromatic masks. However, they then would have been different to the chromatic masks in that they lacked the additional chromatic contrast.

The target and mask could potentially have appeared as a single stimulus, and participants may have therefore simply indicated the stimulus of longer duration. However, if this were the case, it is still the onset of the targets that would have been required for the detection, and these MOA would still reflect the delays in processing the onset of the targets in exactly the same way.

Analysis

We used a two-down, one-up staircase to determine each participant's threshold. After four trials with any given stimulus, the MOA had typically reached a level at which it could stabilise. The MOA-D is the MOA at which the target stimulus location should be correctly identified approximately 67% of the time (Strasberger, 2001). The block mean

for each stimulus was its mean MOA over the last 22 of 26 trials. The MOA-D were the means of these block means.

P3 could not reliably locate targets at an MOA of > 120 ms and was therefore replaced. P1, P2, P4 and P5 performed 16, 15, 12 and 12 blocks respectively.

Results

Figure 13 shows the MOA-D by participant and stimulus. The mean (SD) difference between the MOA block means of the within-axis stimuli was 8.4 (6.85) ms, *n = 165* (3 comparisons on 55 blocks), 95% CI [7.4 - 9.5], while the mean between-axis differences were 13.5 (10.82) ms, *n* = 660 (12 comparisons on 55 blocks), 95% CI [12.7 - 14.4]. This shows that axis is important in determining these MOA-D values. Figure 14 shows the MOA-D by participant and axis. Luminance MOA-D was always the shortest and S-cone MOA-D was always the longest. The mean (SD) MOA-D for all four participants were 28.3 (7.00), 33.8 (8.21) and 19.1 (5.00) ms for the L-M, S-cone and luminance pathways respectively, as shown on the right of Figure 14.

Figure 15 shows the mean differences between the MOA-D for these four participants. The luminance MOA-D were approximately 9.0 (12.45) ms shorter than the L-M MOA-D, 95% CI [7.3 10.6], and approximately 14.3 (14.36) ms shorter that the S-cone MOA-D, 95% CI [12.4 16.2]. L-M MOA-D were approximately 5.3 (15.10) ms shorter that S-cone MOA-D, 95% CI [3.3 - 7.3].

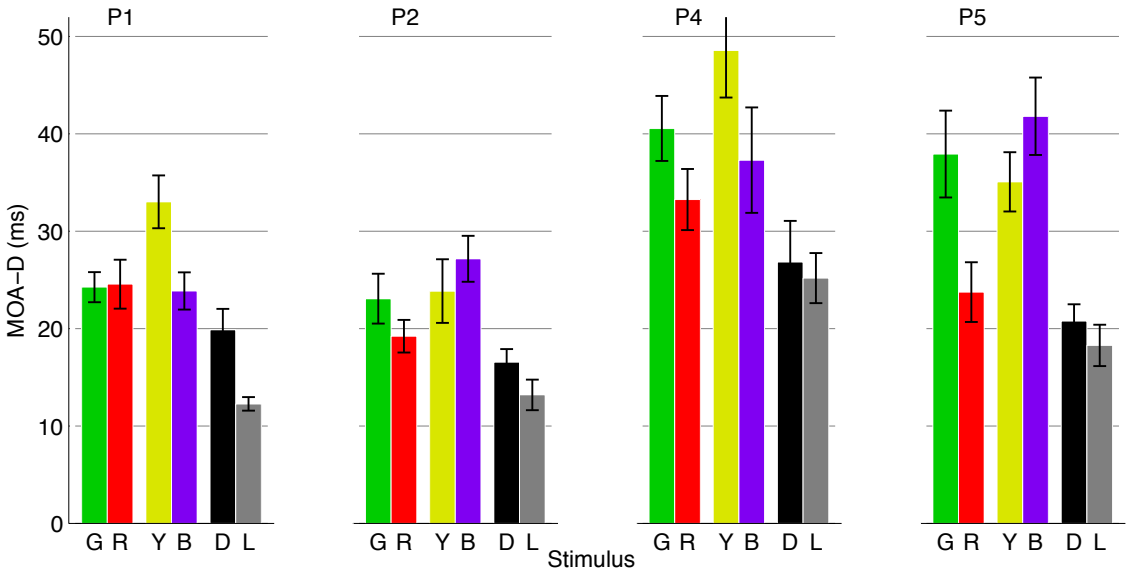

Figure 13. MOA-D. Mean MOA (±SEM) over last 22 trials by participant and stimulus. G = Green, R = Red, Y = Yellow, B = Blue, D = Dark and L = Light. Error bars are symmetrical.

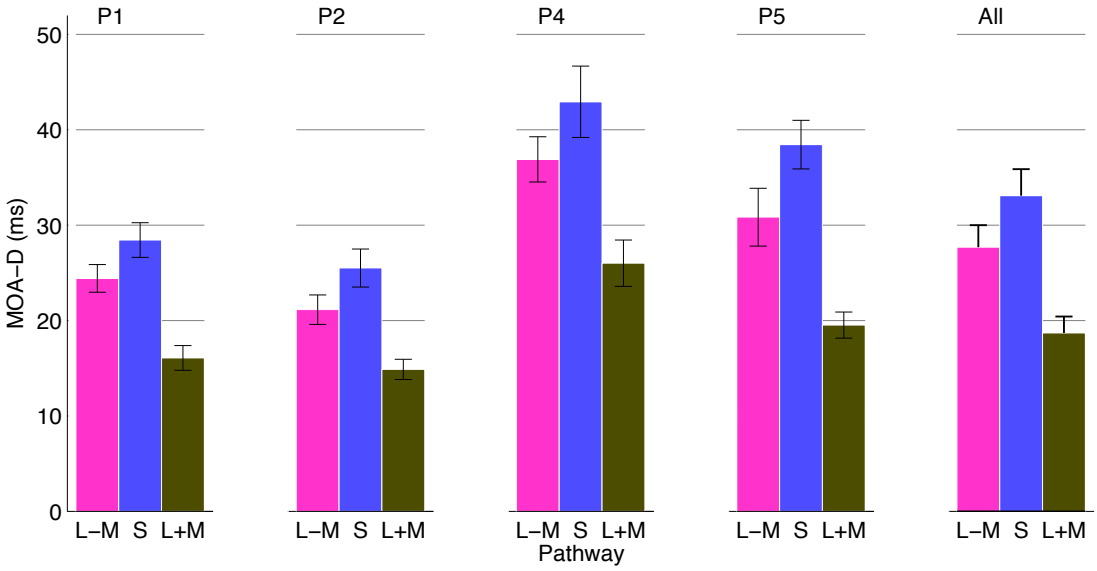

Figure 14. MOA-D (±SEM) over last 22 trials by axis and participant. Error bars are symmetrical

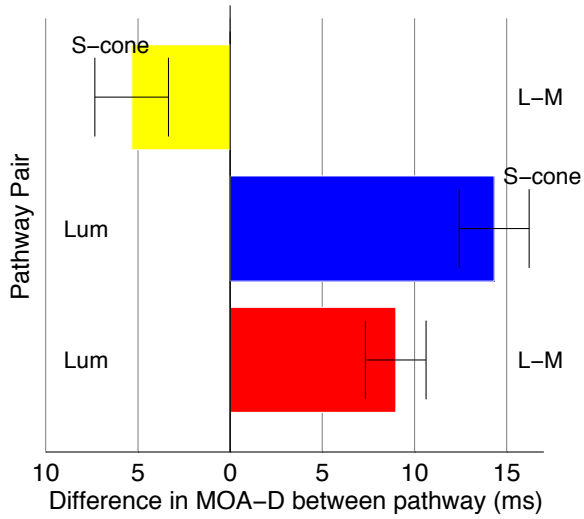

Figure 15. Mean differences between MOA (±95% CIs) for all three pathway comparisons. Bars extend towards the pathways of the stimuli that needed to be presented for longer to be accurately indicated.

Discussion

This task determined the MOA required for participants to indicate target locations with 67% accuracy. The mean MOA-D was approximately 18 ms for the luminance condition and between two to three screen refreshes for the two chromatic MOA-D. The luminance stimuli required approximately 9 ms less processing time than the L-M stimuli and approximately 14 ms less than the S-cone stimuli on average. This suggests that the luminance information was processed marginally faster than the chromatic information.

What else could explain the different results between pathways? The potential confounds in these results require examination as this task is new. It is unlikely that the differences in persistence durations have contributed to these results, as the processing of stimuli was almost always stopped by the masks before stimuli could persist beyond the physical presentation of the 47 ms. Had a stimulus persisted, it would have been of limited aid to judging which stimulus was presented earlier.

The luminance stimuli could have caused neural adaptation of the luminance pathway, delaying the subsequent processing of the luminance mask. As an example, Smithson and Mollon (2003) found that displaying up to ±3 cd of luminance noise for 280 ms immediately before target onset may have delayed RTs by up to 20 ms. If the mask's processing was delayed, targets presented relatively later would have still been

processed, shrinking the luminance MOA-D. However, the small advantage for the luminance pathway is expected because of its reduced conduction delays (see Nowak, *et al.*, 1995; Schmolesky *et al.*, 1998 for for L-M versus luminance and Cottaris & De Valois, 1998 for S-cone signals getting to V1), leaving little scope for selective neural adaptation by the luminance stimuli.

General discussion

The relative delays in perceiving the appearance of carefully calibrated L-M, S-cone and luminance stimuli were examined in three tasks. With the exception of one change of participants in the MOA task, all tasks were completed by the same participants to reduce intra-individual variation. Overall, the PSSs measured using the TOJ task were inconsistent with a chromatic/luminance PA produced by differences in conduction delays. The PSSs were inconsistent across participants, and are likely to reflect individuals' biases towards the luminance or chromatic stimuli. The chromatic/luminance PSS from the SJ task also differed between participants, and overall were not significantly different to zero. These PSS were again more likely to reflect bias than be evidence for the absence of chromatic/luminance PA, or a PA that varies between individuals. Additionally, neither the TOJ or SJ results are necessarily directly comparable to the RT results. They may involve peak to peak comparisons of the percepts of the stimuli, rather than the accumulation of information, and peak to peak comparisons are potentially affected by the differences in the persistence durations of the stimuli.

The TOJ and SJ tasks involved making difficult timing judgements about stimuli that were clearly different colours. This is problematic as participants' responses could be biased to respond based on the colour of the stimuli. This is relevant to any TOJ or

SJ study that uses stimulus pairs that are clearly different on a basis other than relative timing.

The MOA task avoids bias by presenting identical stimuli on each trial. In this task, the stimuli are processed from their onset up until there is sufficient information to indicate their presence, as occurs in the RT task. These MOA results are therefore comparable to RTs to chromatic and luminance stimuli. However, the MOA task may slightly overestimate the faster processing of the luminance stimuli due to adaptation of the luminance pathway.

Do differences in MOA reflect a chromatic/luminance PA?

The MOA results show differences in how long it takes to accumulate sufficient chromatic and luminance information to correctly identify a target. Here we speculate on how these MOA results relate to PA as it has previously been examined.

If the masking has its effect at a relatively early stage of processing, and if the cortical activity that leads to the subjective perception of the stimuli is distal to this processing, then the difference in processing latencies measured using the MOA task may not be present in the TOJ task. For example, according to Lamme and Roelfsema (2000) there is additional top-down processing required for stimuli to be subjectively perceived. Additional processing after the level assessed by the MOA task could modify the signal to facilitate contextual affects, such as the order effects found in the TOJ task by Maloney, Dal Martello, Sahm and Spillmann (2005). It could also explain some of the variance in our TOJ data. However, this is speculative, and these MOA data may match those from an unbiased TOJ task.

Are chromatic and luminance information processed differently in RT and perceptual tasks?

Previously we found that RTs to luminance stimuli were 40 and 60 ms faster than RTs to L-M and S-cone stimuli (Ma-Wyatt *et al.,* 2012), when the stimuli were identical to those used in the studies presented above. However, there was only a 9 and 14 ms advantage respectively for the luminance pathway over the L-M and S-cone pathways in the MOA task. Sternberg and Knoll (1973) had suggested that RT/TOJ dissociations can be explained by the RT responses reflecting the time that a system's activity reaches criterion threshold, while TOJs may involve the comparison of the latency of the peaks of the visual responses to the stimuli. However, the MOA task theoretically requires the accumulation of information to threshold in a similar manner to the RT task, meaning that another explanation of the dissociation is required.

Even if both RT and MOA results reflect the time taken to accumulate information, there still may be other differences in how the stimuli are processed between the tasks. For example, the RT response is made as soon as possible, while the MOA response is made after viewing the stimuli and masks without time pressure. While the RT decision duration is modelled as reflecting time that it takes for the firing rate to reach the threshold, maybe the post hoc MOA decision should be modelled as reflecting the rate of activity over the whole duration of the information accumulation. A simple interpretation of this in the 1DM-2 decision criteria model is that the chromatic and luminance MOA decisions are represented by two triangles determined as the area under the function, as depicted in Figure 16. In this case, the MOA-D would reflect the time taken for the triangle to grow to reach a threshold criterion area. However, if the slopes of the intensity functions are the same for the chromatic and luminance pathways, then the time difference calculated between the two triangles reaching the same area is unchanged. Therefore, this again predicts the same difference between

responding to chromatic and luminance stimuli for both tasks. But while this potential difference between the tasks does not explain the dissociation, it is still possible that other task differences explain some of it. However, these differences would need to be large in order to explain the large dissociation.

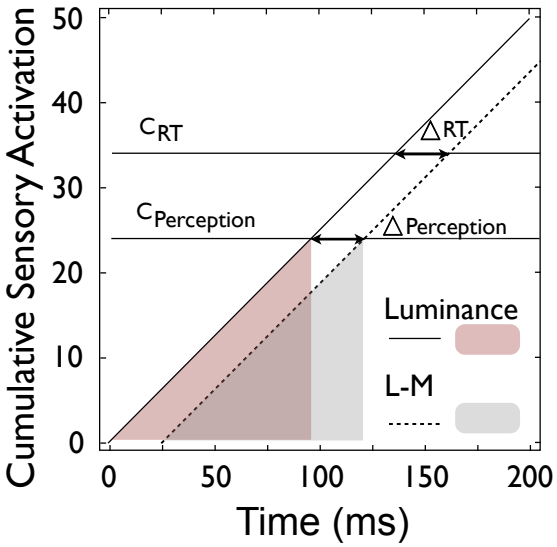

Figure 16. The differences in latencies between the RT & MOA (perception) task predicted by the 1 decision maker-2 decision criteria model, if the post hoc nature of the MOA decision is modeled as reflecting all of the information accumulated over the decision time with the shaded triangles representing the volume of information collected.

It is difficult to explain this dissociation with the 1DM-2 decision criteria model. In the model depicted in Figure 2, the slope of the intensity functions are determined by the relationship between cumulative sensory activation and time. Previously (Ma-Wyatt *et al*., 2012) we demonstrated that equating stimuli for intensity in multiples of detection threshold (MDT), on average, produced similar differences between the chromatic and luminance pathways as equating the stimuli for the the estimated neural responses (ENR) that they elicited in their intended pathways. If the chromatic and luminance stimuli were equal for intensity, then it is reasonable to suggest that they would have parallel intensity functions in the 1DM-2 decision criteria model, that are offset by the difference in their neural conduction delays, as depicted in Figure 3.

In our RT data set, we found that RTs decreased slightly faster as a function of luminance contrast than it does as a function of chromatic contrast. A possible interpretation of this result is that the RT task has a relatively larger proportion of luminance information as its input, when compared to the perceptual task used to

equate the contrasts of the stimuli (Kane, Wade & Ma-Wyatt, in preparation). This would be similar to the observation that primate area MT, known for its role in motion processing, also uses primarily luminance input (Ramachandran & Gregory, 1978; Zeki, 1978; Seidemann, Poirson, Wandell, & Newsome, 1999; Barberini, Cohen, Wandell, & Newsome, 2005; Liu & Wandell, 2005). The RT decision making process could have evolved this way to take advantage of the faster conduction velocity of the luminance pathway. This notion is also compatible with the finding that the advantage for the luminance pathway was much larger in the RT task than in the MOA task.

It also is difficult to explain the finding that RTs decrease faster to luminance contrast than to chromatic contrast with the 1DM-2 decision criteria model. The 1DM-2 decision criteria model by definition, requires that there is only a single intensity function for both tasks. But if this were the case, it would mean that the luminance intensity function was steeper than the chromatic intensity function. The predictions of the 1DM-2 decision criteria model would be consistent with our observed dissociation, but this model, as it is, would no longer be sensible. There would need to be quite different chromatic and luminance intensity functions for the chromatic and luminance stimuli equated for intensity in a perceptual task. If there were two different intensity functions for the RT and MOA tasks, it suggests that there were two different decision making process for the two tasks.

If there were two decision makers, then some of the dissociation can be explained by the two decision making processes relying on chromatic and luminance information that has remained separated for different pathway lengths from the retina. For example, the MOA decision could rely on chromatic and luminance information integrated in V1, while the RT decision could be integrated at the end of a longer pathway. Some electrophysiological studies in the macaque have found that the advantage for the achromatic pathway over the L-M pathway in V1 was approximately 17 ms (Schmolesky

et al., 1998) or 20 ms (Nowak, Munk, Girard, & Bullier, 1995), and the responses of the S-cone pathway may have a response latency of another 20-30 ms more than the L-M pathway (Cottaris & De Valois, 1998). While these latency differences are an indicative guide only (see pg. 6172 of Reid & Shapely, 2002 for a summary of a range of estimates), they are not clearly consistent with either the RT or the MOA data. However, to explain all of the dissociation with this mechanism requires assuming that the chromatic and luminance information remain separated for approximately four times as long in the RT task, than in the MOA task. Therefore, it appears more likely that this situation could only explain a small portion of the dissociation.

Another potential explanation that requires there being two distinct decision making processes is that the chromatic information going into the RT decision making process goes via a relatively indirect route, as appears to be the case for saccadic control (Bompas & Sumner, 2009; White, Boehnke, Marino, Itti, & Munoz, 2009; White & Munoz, 2011). One possible extrapolation of this is that both the decision making process in the RT task and controlling saccades could rely on the same information. However, the likelihood of this is unclear. White, Kerzel and Gegenfurtner (2006) found that there is a greater temporal advantage for luminance information in the RT task, while Bompas and Sumner (2008) found the greater luminance advantage in the saccadic condition.

The only potential explanation of our RT and MOA dissociation that is consistent with the 1DM-2 decision criteria model is that the signal is processed for perception and action after a common decision making system processes the stimuli. This has been suggested to be the case for area MT in its role for perceiving motion and using motion to guide smooth pursuit eye movements (Churchland, Gardner, Chou, Priebe, & Lisberger, 2003).

Conclusions

The results of this study contribute to the understanding of the similarity of processing of visual information for perception and for action. The results also indicate that manipulating the intensity of stimuli in a TOJ and an RT task is unlikely to lead to significant insights into this problem. The chromatic/luminance distinction provides a more theoretically sound approach. However, it seems that is is inappropriate to use the TOJ and SJ tasks to measure a chromatic/luminance PA. These two tasks may be affected by differences in stimulus persistence durations, and allow participants to give a biased response, based on information other than the apparent timing of the stimuli. These biases can be in opposing directions for different participants, and can hide any potential PA when collating data from multiple participants.

The MOA task introduced here, removes the problems of bias, persistence durations, and the *information accumulation* versus *latency between peaks of responses* task differences between the RT and perceptual tasks. It provided reliable differences in perceptual delays between the pathways, with only minor concerns about differences in mask processing times. These results show a dissociation between the relative delays in perceiving and reacting to chromatic and luminance stimuli. While this finding is not decisive in indicating either a 1DM or 2DM model as explaining the dissociation, the balance of the evidence suggests that this dissociation reflects there being separate decision making processes for the RT and MOA tasks, with the RT task having a relatively greater reliance on luminance information.

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5.4. Additional notes on perceptual latency study

While participating in the TOJ study, it became apparent that on difficult trials where I was unsure which stimulus had appeared first, that other factors were likely to influence my responses. The difference in the appearance of the stimuli (i.e., red versus dark), was obvious. The different stimuli 'appeared' differently, in that the luminance stimuli appeared with a suddenly change that grabbed my attention, while the chromatic stimuli did not (which was also the conclusion of Schwartz & Loop, 1983). I thought this unsurprising, given that the responses of the achromatic pathway are relatively rapid and transient. The problem was that I was inclined to indicate the stimulus that grabbed my attention most. These beliefs were supported by my TOJ data, which show that I was biased towards the luminance stimuli, and this was consistent with my expectation

based on the relative conduction delays. However, the potential of bias was not limited to participants with prior expectations, or to the luminance pathway. One of my naïve participants made the spontaneous comment that the blue stimuli grabbed her attention most, and her judgements show a bias towards the blue stimulus. It became obvious that there was always a potential for bias in a 2AFC trial where the two stimuli are clearly different.

In this TOJ task, the stimuli were presented at 2° either side of fixation to allow a direct comparison with our previous RT results. With a separation of 4°, it is possible that some participants may have experienced apparent motion on some trials. While the direction of apparent motion would still have been indicative of perceptual delays, the neural pathways involved in motion processing potentially differ from the pathways that facilitate the appearance of static stimuli. Therefore, I repeated 10 blocks with the stimuli readjusted for isoluminance and contrast at 5° either side of fixation where there was no apparent motion. The S-cone stimuli had to be presented 33.5 (10.13) ms before the luminance stimuli, the L-M stimuli had to be presented 17.6 (11.3) ms before the luminance and the S-cone stimuli had to be presented 19.0 (11.8) ms before the L-M stimuli to achieve the PSS. The PSS values at 5° were not significantly different to the PSS at 2° for the L-M versus luminance comparisons, $t(3) = 1.2295$, $p = .307$, the S-cone versus luminance comparisons, $t(3)$, $p = .043$, but they were nearly significantly different for the S-cone versus L-M comparisons, $t(3)$, $p = .018$, following a Bonferroni correction for the three comparisons. While this is an underpowered test that does not convincingly state that the PSS at the two locations are the same, it still does not suggest that apparent motion had an effect on the PSS. Area MT, which is considered the primary cortical area for motion processing, is an area that has mainly luminance input (Zeki, 1978; Gegenfurtner *et al.*, 1994; Seidemann *et al.*, 1999; Barberini *et al.*, 2005; Liu & Wandell, 2005) and motion responses to low contrast isoluminant stimuli

are reduced (Cavanagh, Tyler, & Favreau, 1984; Hawken, Gegenfurtner, & Tang, 1994; Mullen & Boulton, 1992). If the PSS values at 2° were affected by apparent motion, we would predict that it would overstate the processing speed advantage for the luminance stimuli, whereas here, the luminance advantage was greater when there was no apparent motion. Therefore, it is unlikely that apparent motion explains the difference between the observed TOJ PSS and what is expected based on differences in conduction delays.

A final point that is not addressing the perceptual latency publication is a question raised in the discussion of the RT publication. It was noted that the relatively rapid decline in RTs with luminance contrast could potentially result from task differences between the RT task, and the perceptual 2AFC detection threshold tasks used to determine the contrast scales, rather than to the RT/perception distinction. That is, the relatively transient response of the luminance pathway could be more suited to the RT task, while the more sustained response of the chromatic pathway may be more suited to the detection threshold task. However, as the MOA task, like the RT task, appears to depend of the rate of information accumulation, the evidence suggests that much of the non-linearity of the luminance RT/contrast response can be accounted for by the RT/perception distinction.

6. Publication 3; Delays in using chromatic and luminance information to correct rapid reaches

Kane, A., Wade, A., & Ma-Wyatt, A. (2011). Delays in using chromatic and luminance information to correct rapid reaches. *Journal of vision*, *11*(10), 3, 1-18.

6.1. Statement on contribution to this publication

Adam Kane (candidate)

I was responsible for the initial concept and the first authorship for this publication. I programmed and piloted the study, and collected and analysed the data. All phases from conception to publication were done with regular consultation, suggestion and guidance from Associate Prof. Ma-Wyatt. Prof. Wade suggested matching the stimuli contrasts for the estimated responses that they elicited, and assisted with the implementation of some of the more technical MatLab code. He was also involved in the revising the manuscript.

Anna Ma-Wyatt (co-author)

I hereby agree that the above statement truly reflects my contribution to this study. I give my permission for this publication to form a part of a submission by Mr Adam Kane for a PhD in the University of Adelaide.

Alex Wade (co-author)

I hereby agree that the above statement truly reflects my contribution to this study. I give my permission for this publication to form a part of a submission by Mr Adam Kane for a PhD in the University of Adelaide.

Kane, A.W. and Ma-Wyatt, A. (2011) Delays in using chromatic and luminance information to correct rapid reaches.
Journal of Vision, v. 11 (10), pp. 1-18, 2011

6.4. Additional notes on reaching correction study

The reaching correction study makes an important contribution to the understanding of the use of chromatic information in the visual guidance of reaching. While White *et al*. (2006) had shown that high-contrast chromatic information can be used to guide reaches with little loss of performance over the luminance information, it was possible that this finding was in part due to a ceiling effect. It was possible that White *et al.'s* chromatic stimuli provided more than enough information to guide a reach, because they were presented at the highest contrast possible on their equipment. However, the study above shows the relative latencies for using chromatic information are not any longer than would be expected on the basis of the difference in when chromatic and luminance information reach a potential stage on integration, such as V1, and that this also occurs for stimuli that were only presented at 2 MDT.

When performing fine slow, motor movements, such as threading a needle, there is an obvious benefit of having feedback with the better spatial resolution of the L-M pathway. It is possible that the processing of information (particularly in terms of the relative chromatic and luminance inputs) remains the same, regardless of the speed at which a visually controlled reach is made. However, this study also found that there was no large additional delays for the corrections to the S-cone stimuli. This is interesting since the S-cone pathway is neither known for its short response latencies (Irvin *et al*., 1986; Cottaris & De Valois, 1998; Reid & Shapely, 2002) or its spatial resolution (e.g., Mullen & Kingdom, 2002).

7. Exegesis

7.1. Summary of results and conclusions

I have presented three studies that examine the use of chromatic and achromatic information when performing a RT, a reaching correction and a perceptual latency task. The literature review shows that there has been a range of methods used to calibrate stimuli when comparing response latencies to chromatic and luminance stimuli. The measured relative response latencies have varied between these studies, probably partly due to the differences in calibrations. This suggests that an important advancement in the area was to determine and demonstrate a sound system for stimuli calibration.

The calibration of the stimuli began with Gaussian blobs that covered a small area of the retina. This limited the variance in the composition of the retinal mosaic responding to the stimulus. Differences between the mosaic responding to the inner and outer most parts of the stimuli may have decreased the degree to which a single stimulus could have been isoluminant to all of its surrounds. The chromatic stimuli were adjusted to isoluminance using a method suited for static stimuli. The tritan line was determined for the blue stimuli in the RT and perceptual latency tasks. Finally, all stimuli were adjusted to be equal in contrast as determined by detection thresholds. The planning of the system of calibration allowed for the fact that the stimuli needed to be suitable for the calibration tasks, as well as the final RT, reaching correction, TOJ, SJ and MOA tasks to enable direct comparisons between them. Then, when the stimuli were calibrated in this theoretically sound manner, it was then important to determine that this calibration was effective. The RT publication demonstrates that the chromatic stimuli do not appear to begin to activate the luminance pathway at higher contrasts. It

also demonstrates that the MDT and ENR scales of contrast produce similar absolute differences in RTs between the pathways.

RTs to luminance stimuli were approximately 40 and 60 ms faster than RTs to L-M and S-cone stimuli respectively, depending on the contrast at which the latencies are compared. The expected inverse relationship between contrast and RTs was shown for all three pathways. It is likely that the relationships between MDTs and RTs were non-linear due to differences in the response saturation functions between the pathways. This non-linearity was reduced by allowing for the strength of the responses in the ENR scale. When the contrasts were scaled in ENR, it showed that RTs initially decreased faster with contrast for the luminance stimuli, than when compared to chromatic RTs. It was discussed that, as there is no absolute scale for contrast across the pathways, that we can only state that the RT task appears to make better use of luminance information relative to the detection threshold task used to determine the MDT and ENR scales.

In trying to explain the differences in the non-linearity of the chromatic and luminance functions, there is a confound in using the detection threshold task to determine the contrast scale for a RT task. The RT response latency depends on how long it takes to accrue sufficient information to make a decision on the appearance of the stimulus. Conversely, the detection threshold task involves experiencing a stimulus for the full course of its persistence duration before responding. The relatively transient luminance response may be better for the rapid accumulation of information in the RT task, while the longer persistence durations of the chromatic stimuli may make them easier to detect in the detection threshold task.

The difference between the luminance and chromatic RT functions is a relatively weak indicator of a difference between the processing of decision making in RT and perceptual tasks. The perceptual aspect needed to be assessed using a task that could

measure relative latencies for a more direct comparison. The PA publication explored the relative latencies with which humans perceive the appearance of chromatic and achromatic stimuli. The results demonstrated that the TOJ and SJ tasks are not suited for determining PAs that can be compared to differences in RTs. I introduced the MOA task as a way to avoid bias. This new task overcomes the confound mentioned above in that the MOA task theoretically depends on the rate of information accumulation in the same way as the RT task. This allows a direct comparison between the two tasks. The MOA task suggests that achromatic information was processed approximately 9 ms and 14 ms faster than L-M and S-cone information respectively. The RT and MOA results are therefore very different in that the temporal advantage for the achromatic pathway is much larger in the RT task.

The reaching correction publication examines the use of chromatic and achromatic information in a different type of motor task. As discussed in section 6.2 above, the reaching correction response is thought to be more complex than the RT response. The two important differences between the reaching correction task and the RT task were (a) that the reaching response was ongoing continuously for a short period as opposed to being ballistic and that (b) the experiment presumably tapped into the visuomotor system that guides the hand to the target, rather than the response just being to move the hand more to the left. The key finding was that luminance information was processed approximately 15 ms and 20 ms faster than L-M and S-cone information respectively in this task. This result demonstrated that there was not a great advantage for the achromatic pathway over the chromatic pathways when compared to the RT task. This small difference may be due purely differences in the conduction velocities. For example, Nowak *et al*. (1995) and Schmolesky *et al*. (1998) found that it takes approximately 17-20 ms longer for chromatic information to reach V1 that achromatic information. However, it is not certain that the information used in the guidance of

reaching has definitely reached the parietal cortex via V1, and not via retino-tectal route (Rodman, *et al*., 1990; Lyon, *et al*., 2010). Despite this, Schmolesky *et al*. (1998) found that many regions of the dorsal stream respond to stimuli with similar delays to those found in V1, suggesting that the pathways to these areas may be of approximately similar lengths. Therefore, it is possible that the 15 - 20 ms addition delay for the chromatic stimuli still only reflects difference in processing delays between the pathways types, even if the chromatic and luminance information is not integrated in V1.

Despite the difference in relative response latencies for the different pathways, the conservation of the relative order of the delays across all three tasks suggests that the achromatic pathways has the fastest conduction velocities, and the S-cone has the slowest.

7.2. Comparing the results from the three tasks

The higher level aim of this thesis was to investigate the commonality of the neural mechanisms that facilitate the perception of stimuli and motor responses to stimuli by examining the relative response latencies to chromatic and achromatic stimuli in perceptual and motor tasks.

7.2.1. Comparing the RT and perceptual results

In a RT trial, people both perceive a stimulus appearing, and release a button in response to it appearing. However, this does not mean that participants necessarily release the button in response to their conscious perception of the stimulus. If the percept and the motor response both depended on the same neural decision, then the relative latencies in perceiving the stimuli, and reacting to them, should be similar for

the RT and MOA tasks. RTs to achromatic stimuli were approximately 40 and 60 ms shorter than RTs to L-M and S-cone stimuli respectively. This time advantage for the achromatic stimuli was only approximately 9 and 14 ms respectively in the MOA task. The achromatic advantage for the RT task was approximately four times as large as it was in the MOA task.

The general discussion of the perceptual asynchrony publication includes how Miller and Schwarz (2006), Cardoso-Leite *et al.* (2007) and Cardoso-Leite *et al.* (2009) all suggest that RT/perceptual dissociations can be explained with a model of a single decision making process that has different outputs for different tasks based on there being separate decision criteria. As this model is hard to falsify with a dissociation in the responses to manipulating stimulus intensity, I examined the potential of a dissociation where the stimuli were matched for intensity, but also known to be processed in pathways that remain separated for some distance from the retina, and known to be used differently in some parts of the visual cortex. This dissociation could not easily be explained by the 1DM-2 decision criteria model.

The examination of a dissociation based on stimuli that activated different geniculate pathways also opens up other potential explanations that require different decision making processes for each task. Firstly, the RT decision making system could use chromatic and achromatic information that is combined at a location that is 'further' (in terms of pathway length) from the retina than the perceptual decision making system. If the pathways remained in parallel for a greater length, then the faster conduction velocities would produce a relatively larger absolute difference in response latencies between the pathways. However, using Schmolesky *et al.'s*. (1998) electrophysiological responses in the macaque as a guide, response latencies in the dorsal stream are not greatly different to those recorded in V1 and V2. Therefore, it is unlikely the pathway to a RT decision making system is considerably longer that the

pathway to a perceptual decision system, and so this mechanism could only be expected to explain a limited component of the dissociation.

If there are two decision making processes, then it is also possible that there is relatively more luminance input into the RT decision making process than there is into the perceptual decision making process. As discussed in section 1.2 of the introduction, it is possible that RT is speeded by there being a relatively greater amount of luminance information going into the RT decision making system, while the balance of chromatic and luminance input into the perceptual system is determined by the sensitivity of humans to perceived changes in colour. This notion could explain some of the difference in RT that is above what it expected on the basis of conduction velocities alone. It would also explain the steeper initial RT/ENR function seen for the achromatic stimuli.

A third possible mechanism to explain the large difference in RTs between the pathways is that the chromatic information reaches the RT decision making system via a relatively indirect route. It is believed that chromatic information used to initiate saccades does not get to the superior colliculus via the retinotectal pathway (Bompas & Sumner, 2009; White *et al.*, 2009; White & Munoz, 2011).

7.2.2. Comparing the RT and reaching correction findings

The relative chromatic/luminance latencies were different in the reaching correction and the RT tasks. The luminance advantage for the achromatic stimuli was approximately 40 and 60 ms over the L-M and S-cone stimuli respectively when compared at 2 MDT (which is the contrast that the stimuli were presented at in the reaching correction task). This achromatic advantage was only approximately 15 and 20 ms respectively over the L-M and S-cone stimuli in the reaching task.

There is a confound in this comparison of reaching correction and RT. The stimuli in the RT task were presented at 2° eccentricity, while a stimulus was presented at 10° eccentricity in the reaching correction task. Therefore, it was possible that some of the dissociation between RTs and reaching corrections was due to differences in eccentricity. Therefore, I collected RTs to stimuli at 10° eccentricity from participants who had also performed the reaching correction task. The chromatic stimuli were adjusted to individual isoluminance and detection threshold was determined for this eccentricity, using the same protocols used in the reaching correction publication. The stimuli were presented at twice detection threshold only in this RT task. This RT data was not included in the publications presented above. The RT data is presented by axis and participant in Figure 4 below, with the mean RT for all participants on the far right. It shows that each participant had the longest RT to S-cone stimuli and the shortest to the luminance stimuli. Overall, RTs were approximately 50 and 60 ms slower to the L-M and S-cone stimuli respectively than to the luminance stimuli. For comparison, the reaching correction results (CT_{50}s), presented in Figure 8 of the reaching correction publication, are re-presented in Figure 5 below in the same format and time scale as used in Figure 4. This similarity in the relative RTs to stimuli at 2° and 10° eccentricity indicated that at the difference in eccentricity between the RT and reaching correction task is unlikely to explain much of the dissociation between the two tasks. Therefore, another explanation is required.

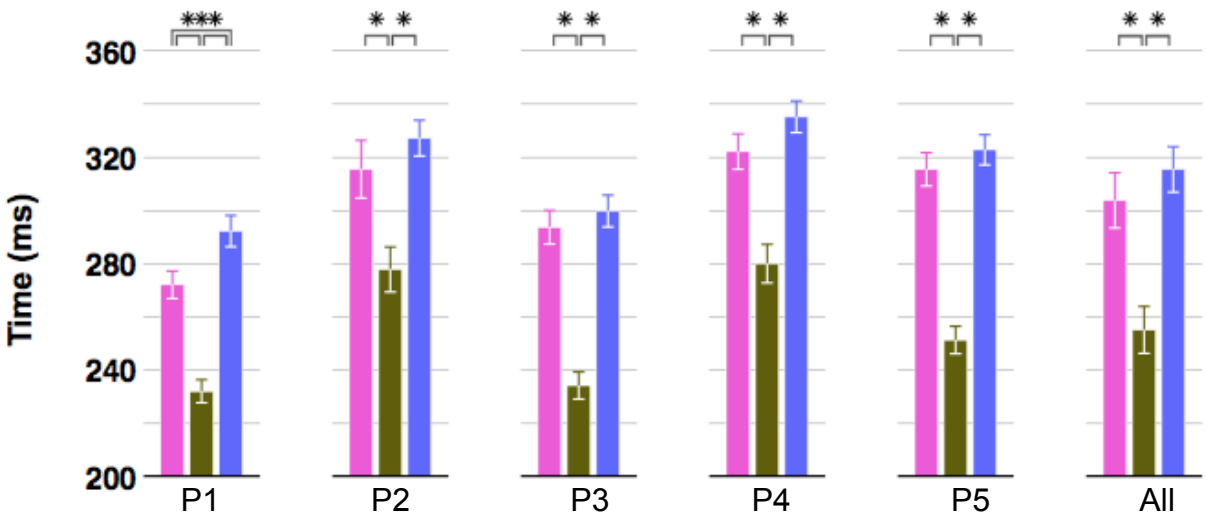

Figure 4. Mean RTs (± 95% CI) to (from left to right) L-M, luminance and S-cone stimuli by participant with means RTs for all participants on the far right. Asterisk above a pair of pathways indicates significantly different RTs ($p < .05$).

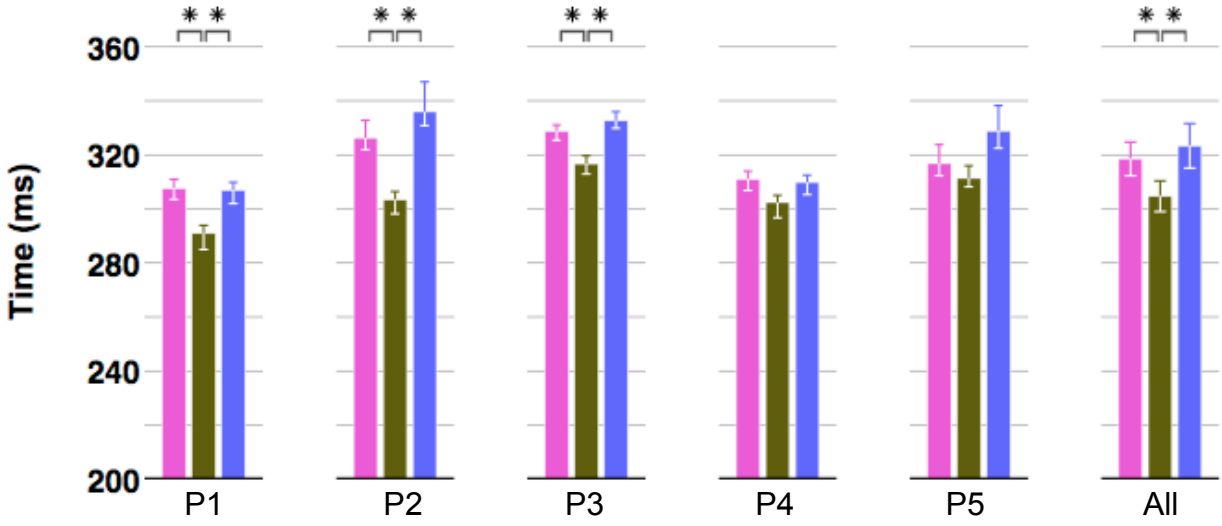

Figure 5. CT_{50} (± 95% CI) to (from left to right) L-M, luminance and S-cone stimuli by participant with means CT_{50} for all participants on the far right. Asterisk above a pair of pathways indicates significantly different CT_{50}s ($p < .05$).

It may be that there is a separate decision maker for each motor task, and the each has its own location, and relative balance of chromatic and luminance input. However, it would be speculative to assume that the reaching task necessarily relies on a decision maker in the same way as the RT task. It may be that the guidance of

reaching involves a constant representation about the location of the target that is based on both prior information (e.g., Ma-Wyatt & Navarro, 2009) and current information about the target. Goal directed reaching is modeled as involving a continuous process of comparing the location of the hand to the location of where it should have been according to the reach plan, and according to where the target is (Wolpert *et al*., 1995; van Beers *et al*., 2002; Crawford *et al*., 2004). Corrections to on-line reaching begin around 120 ms after the presentations of the stimuli (Brenner & Smeets, 2004), highlighting the difference in how information is processed in reaching and RT tasks. While it seems that reaching control has evolved to be a continual process, it is unclear how the sudden change of location of the target, as occurs in the laboratory setting, is processed in terms of whether is involves a similar decision making process to those modeled as being involved in the RT and perceptual tasks.

As with the RT/MOA dissociation described above in 7.2.1 above, it is possible that the RT/reaching correction dissociation results from a difference in the length of the pathways for which chromatic and luminance information remain separate for between the two tasks. In this case, it would suggest that the information remains separate for longer in the RT task. However, there is no additional information to support this speculation.

As discussed above, there is some evidence to suggest that the RT task could be relatively more reliant on luminance input that on chromatic input (at least when compared to the chromatic/luminance input balance for perception). A similar explanation could also explain the RT/reaching dissociation. As discussed in section 6.4 above, the process of correcting reaches may be aided by the greater spatial resolution of L-M pathway, and so the reaching correction process could rely on L-M information. However, this does not account for the relatively small temporal advantage of the luminance pathways over the S-cone pathway in the reaching correction task, as S-

cone information does not appear to be theoretically suited for controlling reaches. Here, the more plausible interpretation of the whole situation is that the reaching and perceptual tasks rely on similar balances of chromatic/luminance input, and that it is the RT task that is relatively reliant on the luminance information.

7.2.3. Comparing the reaching and perceptual results

The temporal advantage for the luminance pathway in the reaching task and the MOA task were not identical. However, they were quite similar when considering the differences in the two tasks. The larger chromatic/luminance response latency is predicted by the greater stimulus eccentricity (10° rather than 2°) for the reaching task. There could also be small differences attributed to the calculation of the MOA and CT_{50} measures. I can not say that the small difference reflects differences in neural processing for the two tasks rather than just differences in the protocols used to collect the data.

It is possible that the same neural decision making system determines the appearance of the stimuli in both the reaching correction and MOA tasks. However, it is also possible that there is a division in the processing for the two tasks, and that both tasks have similar relative input of chromatic and luminance information, and that the chromatic and luminance pathways remain parallel for a similar length before being integrated for each task.

7.3. Novel contributions from this thesis

The results reported in this thesis make a significant contribution to the understanding of the potential difference in the neural information processing that

facilitates the visual perception of stimuli, and the motor responses to stimuli. In particular, the results demonstrate a dissociation between the use of chromatic and luminance information in the RT task, when compared to both the MOA and reaching correction tasks. While it is unclear exactly what differences in chromatic and luminance latencies should be expected on the basis of conduction velocities alone, it is feasible that this difference is reflected in the latency differences found in the MOA and reaching correction tasks. Meanwhile, the chromatic/luminance response latency differences found in the RT task may be greater than are due to conduction velocities alone. Previously it has been suggested that RT/perceptual task dissociations could reflect task differences, or there being a single decision making system for both tasks, with a difference in the decision criteria for the tasks. This RT/MOA is not as easily explained by either of these theories. Therefore, this thesis offers new evidence for there being different decision making processes for RT and perceptual tasks.

This thesis makes a significant contribution to the understanding of the use of chromatic and luminance information in the RT task. In section 7.2.1 above I argue why the RT/MOA dissociation most likely reflects the decision making process in the RT task as having a relatively greater volume of luminance input over the chromatic input, as compared to the processing the MOA task. This is important as it investigates an organisational principle of neuroscience. That is, is it more efficient to combine chromatic and luminance information, and use the combined information as a basis for different tasks? Or is it better to have independent decision making systems that use the information that has the most suited characteristics for that task. The RT/MOA dissociation is consistent with the theory presented in this thesis that, in order to facilitate good performance in the RT task, it should be relatively reliant on the faster luminance information.

In contrast to the RT task, these results demonstrate that the luminance pathway does not show a temporal advantage in the reaching correction task above what might be anticipated on the basis of conduction velocities alone. It provides an estimation of the differences in the reaching correction latencies to well-calibrated, low contrast targets that are equated for salience. It also introduces a simple method of calculating reaching correction latencies using only a touchscreen.

In this thesis, I explored issues of how to calibrate stimuli to use in chromatic/ luminance response latency comparisons. It demonstrates that the use of minimum flicker on Gaussian blobs allows the adjustment of chromatic stimuli to be sufficiently isoluminant with their backgrounds that they do not effectively activate the luminance pathway to a degree that shortens the measured RTs. It therefore demonstrates a relatively simple way (i.e. less than 10 mins for each participant) of avoiding luminance responses to chromatic stimuli. This removed the need to collect additional responses to chromatic stimuli with additional luminance increments (e.g. McKeefry *et al*., 2003; White *et al*., 2006; Brenner & Smeets, 2004), and without introducing the confound of additional luminance noise masking (e.g., Smithson & Mollon, 2004; Bompas & Sumner, 2008).

I also investigated the issue of equating the stimuli to be of equal strength. The ENR scale was a better linear predictor of RT than the MDT scale, suggesting that ENR can be used to relate response latency to contrast without the confound of differences in response saturation functions. However, the absolute differences in RT calculated using the MDT scale were not typically more than 10 ms different to those calculated using the ENR scale. This has implications for all research comparing response latencies to chromatic and luminance stimuli scaled in MDT.

While the ENR scale was the best scale tested here, this thesis raised the question of whether the common 2AFC threshold detection task used to calculate this scale was suited for determining the MDT and ENR scales to use for motor control tasks, due to the information accumulation versus post hoc nature of the tasks. However, when the post hoc/accumulation difference is removed (ie., in the RT/MOA dissociation), their still appears to be a difference in chromatic and luminance information use.

The results reported here demonstrate that the TOJ task is inappropriate to use to determine differences in perceptual processing latencies between chromatic and luminance stimuli. They also provide some evidence that the SJ task may also be inappropriate for this question. The MOA task was introduced as an unbiased way of comparing perceptual latencies, that allows a direct comparison between RT and perceptual latencies where both tasks theoretically rely on the accumulation of information. The results reported in this thesis also provide the first estimates of the relative latencies in when chromatic and luminance information is processed as a part of generating the perception of the stimuli. This is important as it was this comparison that allowed the determination of the RT/MOA dissociation that challenges the 1DM-2 decision criteria model of processing visual information for motor and perceptual responses.

7.4. Possible directions for future research

The studies presented here represent a slow and cautious effort in comparing information processing across tasks. The groundwork done in calibrating the stimuli, and collecting data so far provides an excellent basis for more studies that can be compared directly back to the studies presented in this thesis. The results in this thesis

provide some evidence that there are different neural mechanisms for the processing for motor and perceptual responses. More research with these stimuli, building on the existing results, offers the opportunity to develop the understanding of the differences in processing for action and perception.

A simple example of this would be the examination of MOA as a function of contrast, as was done for the RT responses. Being able to compare the MOA/contrast functions and RT/contrast functions may allow stronger inferences about the differences or similarities in decision making for the two tasks. Should another version of the MOA task be run, it would be informative to equate the stimuli for ENR. An additional modification that could be made would be to use masks comprising of random luminance and chromatic noise (Mark Yates, personal communication). This would remove the possible confound of the luminance masks being processed faster than the chromatic mask, which had lower luminance contrast.

The use of formal models of decision making may assist this process. For example, reaction time can be considered (e.g. Smithson & Mollon, 2004), or modeled, as at reflecting two individual stages (McKeefry *et al*., 2003; Smith & Ratcliff, 2004). One stage reflects constant delays such as the transmission latencies for information reaching a decision making process, and the time for a decision to be converted into the manipulation of the button. The second stage reflects the decision making process itself. There are tools (e.g., the DMAT toolbox, Vandekerckhove & Tuerlinckx, 2008) that allow raw RT data to be broken into these two stages using the well-established drift diffusion model (Ratcliff, 1978; Smith & Ratcliff, 2004). The modeling of the RT data presented in this thesis would allow a calculation of the differences in conduction velocities between the pathways. It would also allow a comparison of just the decision making processes using chromatic and luminance information in the RT task.

MOA data taken over a range of contrasts could be modeled in a similar manner. The comparison of the difference in the model outputs of conduction latencies between pathways and tasks would be informative in exploring whether both tasks are based on chromatic and luminance information that is integrated at a similar distance from the retina. Similarly, a comparison of the model outputs of the decision making processes for both tasks would allow a better comparison of decision making in the two tasks.

As noted in the perceptual latency publication discussion, White *et al*. (2006) found that there was a greater temporal advantage for the luminance pathway in RT responses than for saccadic latencies. However Bompas and Sumner (2008) found the opposite. It would be possible to compare the current RT/ENR functions to saccadic latency/ENR functions using identical stimuli and similar participants to allow a more direct examination of a RT/saccade dissociation. This comparison would allow investigation of whether a similar decision making process underlies the two tasks.

The perception of a stimulus is presumably required in order to discriminate its colour in a forced choice task. It would be possible to run participants in a color discrimination choice RT task in red versus green, blue versus yellow and a dark versus light conditions, using identical stimuli to those used in the RT task above. It may be that the relative temporal advantage for the luminance pathway over the two chromatic pathways shows the same pattern as found in the simple RT task. This would be consistent with most of the differences in the simple RTs being due to differences in conduction delays. However, it is possible that the results could show a 10-20 ms advantage for the luminance pathway, reflecting a discrimination task that relied on a similar balance of chromatic and luminance information used in other perceptual tasks.

Building on the conclusion that luminance information reaches the superior colliculus faster than chromatic information, White & Munoz (2011) had monkeys

perform a choice chromatic discrimination task. They found that saccades were initiated faster, but with less accuracy when the stimulus contained both chromatic and luminance information, than when the stimuli were purely chromatic. This result suggests that luminance information may have a strong role in initiating saccades, but chromatic information is still required for accurate target selection. Replicating this study in humans using both a choice saccadic and a RT task would allow another way of investigating the similarity in the decision making systems underlying these tasks.

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