Delays in using chromatic and luminance information to correct rapid reaches

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People can use feedback to make online corrections to movements but only if there is sufficient time to integrate the new information and make the correction. A key variable in this process is therefore the speed at which the new information about the target location is coded. Conduction velocities for chromatic signals are lower than for achromatic signals so it may take longer to correct reaches to chromatic stimuli. In addition to this delay, the sensorimotor system may prefer achromatic information over the chromatic information as delayed information may be less valuable when movements are made under time pressure. A down-weighting of chromatic information may result in additional latencies for chromatically directed reaches. In our study, participants made online corrections to reaches to achromatic, (L–M)-cone, and S-cone stimuli. Our chromatic stimuli were carefully adjusted to minimize stimulation of achromatic pathways, and we equated stimuli both in terms of detection thresholds and also by their estimated neural responses. Similar stimuli were used throughout the subjective adjustments and final reaching experiment. Using this paradigm, we found that responses to achromatic stimuli were only slightly faster than responses to (L–M)-cone and S-cone stimuli. We conclude that the sensorimotor system treats chromatic and achromatic information similarly and that the delayed chromatic responses primarily reflect early conduction delays.

Keywords: pointing, sensorimotor control, color vision, active vision, detection/discrimination


Introduction

The visual control of reaching

An important use of human vision is to control interactions with the environment such as reaches to objects. In the initial phase of reaching, the sensorimotor system uses visual information about the target’s location to develop a motor plan for delivering the hand to the desired endpoint (Jeannerod, 1988; Saunders & Knill, 2003). After the reach is initiated, proprioceptive and visual feedback about the position of the hand and the target may be used to refine the movement online if there is sufficient time (Ma-Wyatt & McKee, 2007; Saunders & Knill, 2003; van Beers, Baraduc, & Wolpert, 2002; Wolpert, Ghahramani, & Jordan, 1995). The initial quality of the visual information about the target location can significantly affect pointing precision and accuracy (Gegenfurtner & Franz, 2007; Ma-Wyatt & McKee, 2006).

While it is clear that visual information about target location is important for planning and updating movements online, it is not yet understood whether chromatic and achromatic stimuli are equally informative. Because of the different spatial resolutions and conduction delays associated with achromatic and chromatic information in early visual processing, and given the time constraints associated with movements, it is possible that chromatic information may be less effective as a source of visual feedback during online control. In this study, we investigate whether the time taken to update a movement (i.e., effectively integrate new information online) varies as a function of the chromaticity of the stimulus. In the following sections, we consider the neural pathways involved in sensorimotor control.

Visual pathways involved in guiding reaches

Visual information is transmitted from the retina to the lateral geniculate nucleus (LGN) via three distinct types of ganglion cells that form three different pathways. The achromatic pathway encodes luminance information as it
contrasts the sum of long (L) and medium (M) wavelength-sensitive photoreceptive cone activity, receiving negligible input from the S-cones (Lee, Pokorny, Smith, Martin, & Valberg, 1990). The (L–M)-cone-opponent pathway encodes differences in the L- and M-cone quantal catches to signal chromaticity along a roughly red–green axis. Finally, the S-cone-opponent pathway encodes chromaticity along a roughly blue–yellow axis by contrasting short (S)-cone activity with the sum of L- and M-cone activities. This pathway can be isolated by using stimuli that excite only the S-cones.

The majority of pathways continue from the LGN to area V1. Chromatic and achromatic signals are segregated in three separate pathways up to V1 where they have the opportunity to be combined (see Sincich & Horton, 2005 for review). There is physiological (Horwitz, Chichilnisky, & Albright, 2007; Johnson, Hawken, & Sharpley, 2001; Lennie, Krauskopf, & Sclar, 1990) and psychophysical evidence (Clifford, Spehar, Solomon, Martin, & Zaidi, 2003) that many cells in V1 are driven by combinations of achromatic, (L–M)-opponent, and S-cone-opponent information. However, there is also evidence that some segregation of chromatic and achromatic pathways is maintained in higher visual areas. For example, parts of the ventral surface of the occipital and temporal lobes show chromatic tuning (Brewer, Liu, Wade, & Wandell, 2005; Conway, Moeller, & Tsao, 2007; Wade, Brewer, Rieger, & Wandell, 2002; Zeki, 1983a, 1983b), while hMT+ has very weak chromatic responses (Barberini, Cohen, Wandell, & Newsome, 2005; Liu & Wandell, 2005; Seidemann, Poirson, Wandell, & Newsome, 1999).

To guide reaches to objects, information about their visual location is processed in the posterior parietal cortex (PPC; Desmurget et al., 1999). For example, the superior parietal lobule (SPL) may play a role in both converting sensory information into motor commands and providing feedforward signals for comparing to live sensory information for adjusting reaches online (Buneo & Andersen, 2006). Visual information may reach the PPC via the “dorsal stream” from V1 (Livingstone & Hubel, 1988; Maunsell, Nealey, & DePries, 1990; Merigan & Maunsell, 1993), but achromatic signals also travel directly to the parietal cortex via the retinotectal pathway to the superior colliculus (SC; Schiller & Malpeli, 1977; Schiller, Malpeli, & Schein, 1979). It is possible that achromatic information used to correct reaches may travel to the PPC via the SC and pulvinar.

**The three pathways have different conduction velocities**

Achromatic and chromatic signals seem to arrive in the cortex at different times. Electrophysiological measurements in the macaque have found that achromatic signals travel to the LGN around 7–10 ms faster than opponent red–green signals (Maunsell et al., 1999). This time difference increases to approximately 20 ms at V1 (Nowak, Munk, Girard, & Bullier, 1995) and potentially more for the S-cone pathway (Cottaris & De Valois, 1998). These differences might be even greater at a population level and in humans: Using EEG, Rabin, Switkes, Croganale, Schneck, and Adams (1994) found that S-cone-driven visually evoked potentials (VEPs) were around 75 ms slower than achromatic VEPs at a site that they identified as V1.

As with the ability to plan reaches, the ability to make online corrections to reaches also depends on the timing of visual information. Correcting responses to visual information begins approximately 110 ms after the visual cue (Brenner & Smeets, 1997; Prablanc & Martin, 1992) and there is a clear speed–accuracy trade-off for fast reaches (Fitts, 1954). Within this time frame, small differences in signal transduction speed may become highly significant. This could be because chromatic signals are delayed at the level of V1. However, additional delays are possible if evidence from chromatic channels is assigned a lower weight in an integrative decision mechanism. Such a down-weighting of chromatic information might occur precisely because these signals are delayed initially. Alternatively, it is possible that the visual system uses chromatic and achromatic information equally in guiding online corrections to reaches and the only delays incurred from using chromatic information are those associated with the early conduction speeds.

**Do conduction delay differences produce differences in motor responses?**

What evidence is there to suggest that the differences in conduction velocity discussed above translate to differences in motor response times? Previous studies have used several approaches to define chromatic and achromatic stimuli and these differences may, to some extent, account for differences in results. Therefore, we begin with a discussion of defining chromatic stimuli for use in experiments. The outputs of the three guns of a CRT can be controlled in a way that allows the experimenter to preferentially activate each of the achromatic, (L–M)-cone, and S-cone pathways (Estevéz & Spekreijse, 1982). In 1979, MacLeod and Boynton introduced the idea of a space of cone contrast values containing planes of isoluminance defined using Smith and Pokorny’s (1975) cone spectral sensitivities. This means that all points on the MacLeod–Boynton (MB) isoluminant plane are photometrically isoluminant. Derrington, Krauskopf, and Lennie (1984) went further and introduced the idea of the postreceptoral achromatic (L + M + S), (L–M)-cone, and S–(L + M) pathways forming three mutually orthogonal axes of a three-dimensional “DKL” color space. The combined MB–DKL is convenient in that it is defined by a combination of physiological...
properties: cone spectral sensitivities and postreceptoral opponent mechanisms and it contains a natural representation of both achromatic and isoluminant chromatic contrasts. Here, we use this MB–DKL space with each axis scaled from $-1$ to $1$ as shown in Figure 1b.

Brenner and Smeets (2004) use stimuli of photometric isoluminance, while White, Kerzel, and Gegenfurtner (2006) measured the response times to the generic axes of MB–DKL space while also varying the amount of luminance contrast from photometric isoluminance. While the latter is effective in determining that additional luminance does reduce response times to chromatic stimuli, it does not allow a direct comparison between chromatic and achromatic stimuli that are equally detectable.

To make these comparisons between chromatic and achromatic stimuli as precise as possible, it is important to use stimuli that aim to isolate single pathways. Activation of the achromatic pathway by nominally chromatic stimuli would, potentially, reduce the measured response times. As there are individual variations in perceptual isoluminance caused by variations in macular pigment density (Chui, Song, & Burns, 2008; Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987; Sharpe et al., 1998) or variations in the (L–M)-cone ratio, isoluminance must be adjusted on a subject-by-subject basis at the actual target location used in the experiment to reduce crosstalk. In addition, because response times are inversely related to contrast of the stimulus (McKeefry, Parry, & Murray, 2003; Plainis & Murray, 2000), it is important to equate the physical contrasts of the different stimuli and therefore their visibility in some principled manner. As the responses of each pathway vary with the spatial and temporal characteristics of the stimulus, these luminance and contrast adjustments should be made with stimuli that are as similar as possible to those presented as reaching targets. For example, if the final stimuli are static, then isoluminance should be adjusted using a static method such as minimum flicker. Minimum motion isoluminance (Anstis & Cavanagh, 1983) may activate neural substrates that have different spectral sensitivities (Webster & Mollon, 1993).

Figure 1. Adjusting the stimuli in the MB–DKL color space. (a) Experimental setup. (b) The 3 axes of the MB–DKL color space. (c) Angles of chromatic axes were determined in relation to the isoluminance plane as four independent axes. (d) Threshold detection contrast was adjusted along the new chromatic axes and the generic achromatic axis.
Bearing in mind the potential effects of having non-subjectively adjusted stimuli, we now discuss the previous findings of the effects of chromaticity on reaching corrections and reaction time (RT).

Reaching corrections

White et al. (2006) measured endpoint accuracy and reach times to Gaussian blobs at eccentricities of 3, 6, and 12°. The stimuli were from the generic axes of the MB–DKL color space presented at the maximum saturation possible on their equipment. The root-mean-squared (RMS) cone contrasts of the achromatic, (L–M)-cone, and S-cone stimuli were 100%, 10%, and 86%, respectively. They found that the MB–DKL axis of the stimulus had little effect on reaching accuracy and movement times were only 8 ms faster for the achromatic targets. This suggests that smaller conduction delays for achromatic targets did not translate into any great advantage for reaching corrections, even when the achromatic contrast was highest.

In Brenner and Smeets’ (2004) study, participants were required to reach to a red square on a yellow background. On some trials, participants had to correct the reach to an adjacent location as the target either moved to the location or swapped locations with a green square of identical photometric luminance that was already there. There could also be irrelevant luminance change with either of the location changes. Brenner and Smeets found that participants could begin to correct reaches to changes in as little as 120 ms. Participants were approximately 10 ms slower to make the correction when there was an irrelevant luminance change with the location change. This small reduction in correction speed may have been due to the luminance transient masking the apparent contrast (either chromatic or achromatic) of the stimuli—perhaps removing informative luminance artifacts and rendering the stimuli more isoluminant. Alternatively, it may simply reflect interference caused by the distracting, irrelevant stimulus modulation.

Reaction time

McKeefry et al. (2003) asked participants to raise a finger in response to the appearance of a colored Gaussian blob presented at a variety of contrasts from detection threshold up to 8× threshold. In general, they demonstrated an inverse relationship between RT and stimulus contrast. Importantly, however, they showed that equating stimuli in multiples of detection threshold gave a consistent increase in RT across the range of chromaticities tested. Conversely, when stimuli were equated for RMS cone contrast, they found that the increase in RT was different for the different chromaticities. Equating contrast in terms of cone contrast exaggerated the difference in response times between the pathways. At all contrast levels, they found that RT was longest for S-opponent stimuli. While they did not directly compare RTs for chromatic and achromatic stimuli equated for strength as RMS cone contrast or detection thresholds, they found that adding luminance to the chromatic stimuli decreased RTs. RTs were reduced by approximately 80 ms for (L–M)-cone-opponent stimuli and 130 ms for S-cone isolating stimuli when they added the maximum luminance contrast possible.

Smithson and Mollon (2004) made direct comparisons of RTs to achromatic, (L–M)-cone, and S-cone isolating stimuli presented in a format that reduced or eliminated the effects of small errors in isoluminance. Initially, participants subjectively adjusted the isoluminance with a minimum motion adjustment using a similar stimulus to that used for the RT measurements. They also adjusted the angle of the tritan line (S-cone axis) for each participant so that the presentation of the S-cone stimulus had a minimal effect on the (L–M)-cone pathway. RT measurements were then collected for conditions in which the stimuli were presented within ±0.02 log units of detection threshold. When the stimuli were masked with luminance noise, they found that achromatic and chromatic RTs varied for only one of their three participants. When the stimuli were not masked, the (L–M)-cone RT was consistently 5–20 ms slower, and the S-cone isolating RTs were 25–50 ms slower than the achromatic RTs, respectively. To explain these results, Smithson and Mollon suggested that the luminance flicker adapted or saturated responses in the three pathways differently.

White et al. (2006) compared RTs to stimuli presented at the maximum possible contrast at 12° eccentricity. They found mean RTs of approximately 250, 340, and 310 ms for the achromatic, (L–M)-cone, and S-cone pathways, respectively. Remembering that the (L–M)-opponent contrast was lowest in this comparison, the finding that RT is slower to (L–M)-cone stimuli than to S-cone stimuli is the opposite to the findings of McKeefry et al. (2003) and Smithson and Mollon (2004) and possibly suggests that the reduced levels of RMS cone contrast for the (L–M)-cone stimulus was responsible for increasing the RT. This inconsistency between relative RTs for different chromatic pathways and methods of determining contrasts shows the importance of equating contrast on response time across a range of chromaticities. While White et al. did not adjust isoluminance subjectively, they measured RT in response to chromatic stimuli with added ±1, 2, 5, and 10% luminance contrast. If any of these additions of luminance contrast was close to producing an isoluminant stimulus, it should have shown up as an increased RT. This increase was not shown for these luminance contrast increments. They found that RT was reduced by 15–20 ms when they presented the (L–M)-cone stimulus with an additional 10% luminance contrast. However, they found that this difference between two conditions was insignificant when the pure (L–M)-cone stimulus was compared to the achromatic stimulus equated at 10% cone contrast.

Finally, Bompas and Sumner (2008) compared RTs to achromatic and S-cone stimuli. They made subjective
adjustments to the isoluminance and tritan line of their stimuli in a method similar to that of Smithson and Mollon (2004). They presented their stimuli at 80% detection threshold but with less luminance noise than that of Smithson and Mollon in order to reduce the potential for adaptation. The mean RTs for all participants was 23 ms faster for achromatic stimuli than for S-cone isolating stimuli. Bompas and Sumner’s low luminance noise results therefore fell in between the high luminance noise and no-noise results of Smithson and Mollon, suggesting that luminance noise reduces the apparent differences between S-opponent and achromatic conduction delays.

The psychophysical evidence reviewed above suggests that chromatic information can be used both to initiate responses and to guide rapid reaching responses. While there appears to be a speed advantage for achromatic information in these studies, it is not clear if the same advantage is found for reaching correction. In addition, these studies collectively show that the method of equating the contrast of stimuli is critical for determining the differences between chromatic and achromatic delays. The current study used stimuli that minimized contamination across the pathways and were carefully equated for both contrast and estimated neural responses.

Aim

The current study aimed to determine the respective delays for using chromatic and achromatic location information to make online corrections to reaches. This was done by comparing reaching correction delays to achromatic, (L–M)-cone, and S-cone isolating stimuli. Importantly, this study minimized luminance artifacts by matching the spatial parameters of the stimuli used in the isoluminance adjustment (minimum flicker) and the actual reaching experiments. We hypothesized that if the conduction delays associated with the chromaticity of the stimulus were retained throughout the integration of information necessary for sensorimotor control, we would observe differences in reaching corrections that are commensurate with known differences in conduction latencies.

Methods

Participants

Six participants aged between 23 and 38 years (M = 30) participated in the study. Two participants were authors (P1 and P2), while all others were naive to the aims of the experiment. All were right-handed except P2 and P4 who comfortably used their right hands. The study was approved by the Human Research Ethics Committee of the University of Adelaide.

Stimuli

The stimuli were Gaussian blobs (SD = 0.5°) presented at an eccentricity of 10° from a dark gray fixation cross (0.57° in diameter). Their spatial and temporal characteristics were constant throughout all experiments. The stimuli were always presented for 47 ms or four refreshes of the screen in all experiments. In order to smooth the temporal onset and offset of the stimuli, their contrast on the first and last refreshes was always half of what it was on the second and third refreshes. The background was always the gray at the center of the MB–DKL color space with a luminance of 32.9 cd/m².

Six different chromaticities for the stimuli were taken from along the three axes of the MB–DKL color space. Initially, the isoluminance of the four chromatic stimuli was adjusted subjectively by each observer. The order of the chromaticities was randomized for each observer. Observers viewed a display alternating between the stimulus and a mean gray background at 10.6 Hz (cycle time = 94 ms). The stimulus was presented simultaneously at eight locations at 10° around a central fixation cross. Observers were instructed to adjust the luminance of the stimulus by moving a mouse along a left–right axis until the perceived luminance flicker was minimized. The initial stimulus luminance was randomized on each trial. We took the mean luminance adjustment from 15 trials. This process effectively rotated the two chromatic axes of MB–DKL space to improve isoluminance as measured by the response of a fast flicker-sensitive pathway. The isoluminance adjustment is depicted in Figure 1c.

Equipment

Stimulus presentation and data collection were conducted using software written in MatLab (MathWorks, version 2007a) and routines from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were generated on a PC with an NVIDIA 8600 graphics card and a 17”, 1024 × 768 pixel ELO touch screen refreshing at 85 Hz. The touch screen was a standard CRT overlaid with a touch-sensitive layer that returned a participant’s touch in x and y coordinates. The error associated with this response has previously been shown to be less than 0.1° in both the x and y directions at a viewing distance of 40 cm (Ma-Wyatt & McKee, 2006).

A Bits++ (Cambridge Research Systems) video attenuator was used to obtain 14 bit control over each of the CRT’s three primaries. The output of the monitor was gamma corrected 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 center of the CRT in a fronto-parallel orientation. All viewing was binocular and the fixation point was always a fixation cross. The experimental setup is depicted in Figure 1a.
In addition, detection threshold contrasts of all six stimuli along their respective MB–DKL axes were adjusted using a two-interval forced choice procedure with staircasing controlled by the QUEST algorithm (Watson & Pelli, 1983). The contrast of only one of the chromatic or achromatic blobs was adjusted at one time and the order of the blobs was randomized across participants. During each trial, participants fixated on a cross 5° to the right of the screen’s center and initiated the trial by a key press. The stimulus appeared 10° to the left of the cross. Its appearance was coincident with one of two beeps occurring at 500 and 1000 ms after the key press. Participants indicated whether the stimulus presentation was coincident with the first or second beep without feedback. Final thresholds were determined as the mean of four separate staircases of 35 trials. This process is depicted in Figure 1d. These adjustments determined the final settings of the stimuli used in the reaching experiment.

Figure 2a shows the mean luminance angle (±SEM) from the chromatic plane in MB–DKL space for each chromatic stimulus and participant. These results show that subjective isoluminance is typically different from the generic chromatic axes of the MB–DKL space as indicated by their offset from 0°. The blue stimulus typically required the addition of luminance and the green stimulus typically needed a luminance reduction to achieve subjective minimum flicker. There is considerable variation in the mean values between participants for each color demonstrating individual differences in observers. There is also considerable variation between observer sensitivities to luminance changes as indicated by the relative sizes of the SEM. These results suggest that subjective adjustment of chromatic axes of the MB–DKL color space is an important step in minimizing achromatic–chromatic contamination and therefore minimizing the potential reduction of apparent chromatic conduction delays.

Equating stimulus contrast and estimated neural responses

Figure 2b shows the contrast detection thresholds for all stimulus conditions and all participants. Stimulus contrasts are expressed in terms of their root-mean-squared (RMS) cone contrast. This was calculated as

\[
\text{RMS cone contrast} = \left( \frac{\Delta L}{L} \right)^2 + \left( \frac{\Delta M}{M} \right)^2 + \left( \frac{\Delta S}{S} \right)^2
\]

where \(\Delta L/L, \Delta M/M,\) and \(\Delta S/S\) are the maximum modulations of each of the respective cone catches relative to the background.

The achromatic, (L–M)-cone, and S-cone pathways vary in their sensitivity to the RMS cone contrast, so equating cone contrast does not make stimuli perceptually or behaviorally equivalent (McKeefry et al., 2003). We therefore equated the contrast of the stimuli in two other ways. First, we had participants make mid-reach corrections to blobs that appeared at twice the contrast of the detection threshold in the “2× threshold” condition. Presenting stimuli at small multiples of detection threshold is a way of attempting to equate neural responses or neural signal-to-noise ratios. This attempt may be compromised if the shape of the neural response-vs.-contrast (RVC) function differs at low contrasts for different pathways. To examine this issue further, we mapped out the entire threshold-vs.-contrast (TVC) curve for each chromatic stimulus direction and used these curves to estimate neural RVC functions. We then used these estimated neural response functions (ERFs) to equate the strength of the stimuli in a second way. Participants also made mid-reach corrections to blobs that were set at a contrast equivalent to exactly 30% of the maximum estimated neural response or saturation level in the “0.3R_{max}” condition. Our method of

Figure 2. (a) Mean (±SEM) angle from the chromatic plane at isoluminance for the chromatic stimuli for each participant. Positive values indicate increased luminance. (b) Detection threshold (±SEM) for each stimulus and participant.
calculating ERFs from psychophysical measures is described in more detail below.

**Calculating TVC functions and ERFs:** After measuring detection thresholds for the six blobs as described above, we then used a similar paradigm to determine the just noticeable difference (JND) thresholds for P1 and P2. In this case, a blob was presented in both the first and second temporal windows. The contrast of one of the blobs was a “baseline” or “pedestal” contrast, and the contrast of the other blob was the addition of the pedestal and the signal contrast. The participants had to indicate which of the two blobs had the additional signal contrast or appeared to be more salient. This was done in a single QUEST staircase of 45 trials for a range of 14 pedestal contrasts ranging from zero up to the higher end of what could be produced on our equipment, including some sub-detection threshold values. The top half of Figure 3 shows these JNDs as a function of pedestal contrast and the TVC functions fitted to these values. All conditions show the characteristic “dipper” shape of the TVC function (Chen, Foley, & Brainard, 2000a, 2000b; Foley, 1994; Legge & Foley, 1980; Nachmias & Sansbury, 1974).

To convert this TVC function into an estimated neural RVC function, we assume that detection of a contrast change requires the underlying neural signal to alter by a constant amount so as to be distinguished from noise. Mathematically, if \( R(c) \) is the neural response to an input of contrast \( c \), then we assume that some constant noise \( N \) exists so that the threshold difference of \( \Delta c \) can be detected only if \( (R(c + \Delta c) - R(c)) \geq N \). Sensitivity (the inverse of detection threshold) is therefore proportional to the slope of the underlying neural response function and so by measuring detection thresholds at several pedestal contrast levels, the parameters of this neural response function can be recovered by a simple fitting procedure. The assumption of stimulus-independent noise is common in the literature (Boynton, Demb, Glover, & Heeger, 1999; Itti, Koch, & Braun, 1999; Legge & Foley, 1980; Nachmias & Sansbury, 1974), even though it is well understood that noise is Poisson at the level of single units (Britten, Shadlen, Newsome, & Movshon, 1992; Dean, 1981; Skottun, Bradley, Ohzawa, & Freeman, 1987). One plausible explanation for this is that detection is limited not by the local neural noise at a single stage but by some more central noise source that is contrast-independent (Shadlen, Britten, Newsome, & Movshon, 1996).

The bottom plots in Figure 3 show the ERFs for the individual stimuli calculated from these TVC functions. Marked on each ERF is the 0.3\( R_{\text{max}} \) value used to determine the contrast for the final reaching experiment. The value of 0.3 (30% of saturation) was chosen as the associated contrasts were approximately 2\( \times \) detection threshold allowing a comparison of the 2\( \times \) threshold and 0.3\( R_{\text{max}} \) methods.

In Figure 4, we plot multiples of threshold from detection threshold up to 4\( \times \) detection threshold on an expanded version of the RVC curve. The top plots show the values for the individual stimuli. The bottom plots show the values for each axis calculated by averaging the JNDs for the two colors forming the axis. The dotted line

![Figure 3](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932789/)  
**Figure 3.** (Top) JND for a range of pedestal contrasts and TVC curve for each stimulus. (Bottom) Estimated neural response function for each stimulus. Markers show the contrast at 0.3 of the response’s saturation value.
starts at the point of the detection threshold and continues on through a point that is double the contrast and the neural response at detection threshold. If the RVC functions were perfectly linear over this range, the markers for 2\( \times \), 3\( \times \), and 4\( \times \) threshold would fall onto the dotted lines. These plots show that the RVC functions are approximately linear over the early part of the curve up to 2\( \times \) threshold. However, at 4\( \times \) detection threshold, it can be seen that the marker is often below the dotted line. This is more so the case for the blue stimuli for both participants. This suggests that setting contrasts at 2\( \times \) detection threshold is a reasonable method for equating stimuli in this task, as proposed earlier by McKeefry et al. (2003) for chromatic stimuli. However, caution would have to be used when presenting the stimuli at increments greater than 2\( \times \) threshold.

### Reaching experiments

Participants fixated on a cross 5° right of the screen’s center and initiated each trial in their own time. The reach began with their index finger on a button. They initiated a trial by releasing the button and reaching toward the cross with the same finger. In a third of trials, chosen at random, one of the six stimuli would appear 10° to the left of the cross. The blob would appear at a randomized time up to 157 ms after the beginning of the reach. Participants were instructed to correct their reach as far toward the blob as possible while still hitting the screen in under the maximum time. If they touched the screen in under 340 ms or over 410 ms, a “Too slow” or “Too fast” message was presented and the trial was repeated at the end of the block. If there was a blob and they made a correction of less than half of the distance, they were informed with an auditory cue (a beep). A block consisted of 144 trials with each of the stimuli appearing eight times in a random order. Participants completed between 24 and 42 blocks. Participants were permitted to saccade after the target appeared, but the short stimulus duration means that they would not be able to foveate the target if they did. It was observed that they often did not saccade, as found by White et al. (2006). The final reaching paradigm is shown in Figure 5a.

Ideally, we would have adjusted the conditions such that participants made corrections ranging from 0 up to 1 as the exposure time of the target reached its maximum. In data presented here, participants typically only achieved a mean correction of approximately 0.75 on the longest exposures. If the maximum reaching time had been longer, a greater proportion of trials in which participants made full corrections would have been expected. However, pilot experiments showed that participants given more time to integrate the new target position typically decreased their movement speed to increase the accuracy of their endpoint and correctly hit the cross or the target. Once collated across the time intervals tested, fits to these data resembled step functions rather than psychometric curves. Forcing participants to touch the screen under a time pressure gave
a more constant spread of correction values resembling a psychometric function.

Analysis

Correction magnitude and time

We measured the time and the location of the final finger position for each reach. Using trials where a stimulus appeared, we calculated the measures of “correction magnitude” and “correction time.” The correction magnitude was the relative amount that the reach endpoint had moved left of the fixation cross along the horizontal axis toward the blob’s center. If the finger hit the fixation cross, its correction magnitude was zero. If the finger hit the center of the blob, its correction magnitude was one. A diagram of this calculation is shown in Figure 5b. The correction time was the time between when the stimulus appeared and when the reach landed and is therefore the total time available to the sensorimotor system to make the correction after exposure to the stimulus (see Figure 5c).

Initially, we examined the relationship between correction magnitude and correction time in individual subjects. The raw data were sorted into ten bins based on correction time, and the mean correction magnitude for each time bin was determined. If the mean correction was $G$, it was converted to 0.01 to avoid having negative values for the probability-style analysis. Data points that were more than 2 $SD$ from the mean were removed from the earlier time bins as anticipations (high correction magnitude values) and the later time bins as lapses of concentration (low values). Weibull functions were fitted and bootstrapped for each of the stimuli and for each of the axes using Psigfit (Wichmann & Hill, 2001). The “50% correction time” ($CT_{50}$) was defined as the time taken to correct the reach halfway, the point where the magnitude vs. time functions crossed the 0.5 correction magnitude line. The means for various conditions were compared using bootstrapped confidence intervals. While limiting the reach time increased the spread of correction values, P6 struggled to correct halfway in the easiest time window, making their data unsuited for the final analysis. Even with the compromise to correction values from the restricted reach times, Weibull functions provided good fits for all other participants. An example of these fits and the calculation of $CT_{50}$ are shown in Figure 6.

Anticipation

Participants were instructed to reach toward the cross and try to correct as far toward the target as possible if it
appeared. Adherence to this instruction produced continuous correction values. Deviation from this instruction promoted bimodal correction values unsuited for fitting psychometric functions. Some participants deviated from this instruction as the time pressure for hitting the target encouraged participants to anticipate the target’s appearance. People learn probability distributions of target locations and can adjust their movements accordingly when pointing under time pressure (e.g., Ma-Wyatt & McKee, 2007; Ma-Wyatt & Navarro, 2009; Trommershäuser, Maloney, & Landy, 2002). The reach endpoint on no-target trials provided an indication of participants’ anticipation of a target’s appearance in the same scale as corrections. This anticipation could be a small systemic leftward bias in reaching endpoints. Participants would also occasionally make large corrections on trials where no target appeared (false hits). Presumably, each participant trades off the relative importance of hitting targets that appear versus hitting the cross when no target appeared. Increased number of false hits suggested that hitting the targets was valued higher. Systemic bias increased the mean anticipation, whereas false hits increased the mean and standard deviation. The mean and standard deviation of anticipation was examined periodically and participants were given feedback if anticipation was excessive to avoid biased or bimodal data. Interestingly, there was much variation between the participants’ anticipation. These trials yielded mean (SD) anticipation scores of 0.05 (0.103), 0.18 (0.206), 0.01 (0.129), 0.06 (0.171), 0.15 (0.223), and 0.03 (0.119) for participants 1 to 6. This suggests that although there is a great deal of variation in how individuals balanced the importance of hitting the cross versus hitting the target, the proportion of trials affected by anticipation remained very low.

Figure 6. Determining “0.5 correction time.” Markers indicate mean correction for time bins of correction time. Weibull functions were fitted to weighted means and bootstrapped, giving confidence intervals around the time taken to correct halfway (CT50).

Results

Reaching times and correction times

Before examining whether there are delays in correcting reaches to certain targets, we determined whether the speed of the reaches was similar to all target types. Movement time was calculated from the time the button was released until the time the screen was touched. The results of a one-way repeated measures ANOVA for each participant showed that there was no significant difference in movement time between the axis conditions, P1, F(2, 1341) = 0.70, p = 0.497; P2, F(2, 1677) = 1.91, p = 0.148; P3, F(2, 1341) = 0.14, p = 0.869; P4, F(2, 1341) = 1.28, p = 0.277; P5, F(2, 1149) = 1.49, p = 0.227; and P6, F(2, 2013) = 0.44, p = 0.644. The mean movement times across all participants were 386.5, 386.7, and 386.5 ms for the (L–M)-cone, S-cone, and achromatic axes, respectively.

If signals from one stimulus type were delayed or treated as less reliable, participants may have adjusted their reaching speed in response to the stimulus to maintain accuracy in a speed–accuracy trade-off. This speed adjustment would be apparent in the correction times between when the target appeared and when the screen was touched. The results of a one-way repeated measures ANOVA for each participant showed that the correction times were different between the axis conditions for P3, F(2, 1341) = 0.18, but not for the other participants, P1, F(2, 1341) = 0.23, p = 0.793; P2, F(2, 1677) = 7.51, p < 0.001, p = 0.832; P4, F(2, 1341) = 0.96, p = 0.384; P5, F(2, 1149) = 0.83, p = 0.438; and P6, F(2, 2013) = 0.12, p = 0.885. The mean correction times across all participants were 277.5, 277.2, and 278.6 ms for the (L–M)-cone, S-cone, and achromatic pathways, respectively. We conclude that the participants typically did not change their reach speeds significantly to chromatic targets to maintain accuracy.

Comparing CT50 at 2x threshold and 0.3Rmax

2x Threshold by stimulus: In this condition, all stimuli chromaticities were equated perceptually and CT50 values were computed for different stimulus chromaticities. While our primary interest was comparing the results for each axis, we initially compared the results for each of the two blobs that formed an axis to determine whether both stimuli of the axis-opponent pair (i.e., red and green) produced similar CT50. Figure 7 shows CT50 (+1 SEM) for each of the stimuli. The pairs were compared by constructing a 95% confidence interval around the difference between the two CT50 values. Only one of the 18 axis-opponent comparisons found a significant difference (p > 0.05, 2-tailed). An additional and more reliable indicator of similarity for the axis-opponent pairs came from pooling the data from all participants. This mean
comparison for all participants is shown on the right of Figure 7. The mean axis-opponent pairs were compared as for individual axis-opponent pairs, except that the 95% CIs were constructed using the variance around CT50 for each pair of blobs pooled from all participants. Here, it can be seen that the CT50 values for axis-opponent pairs were still similar when averaged over all participants. This suggests that equating stimuli by setting them at 2/C2 perceptual threshold was effective in making axis-opponent pairs equivalent for this reaching task. This similarity of the axis-opponent pairs also indicates that these stimuli were representative of their intended axes. There were only half as many trials used to produce these individual blob values, compared to the number of trials used to calculate the final axis values. Achieving this level of reliability with the smaller sample size for each blob suggests that the axes of CT50 values will be a reliable indicator of the times taken to incorporate reaches.

2× Threshold by axis: For each participant, data for each axis-opponent pair were pooled before curves were fitted to determine CT50 for each axis as outlined for individual stimuli. Figure 8 shows the CT50 (±SEM) for the achromatic, (L–M)-cone, and S-cone axes for each participant. Brackets and asterisks over a pair of bars indicate that

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Figure 7. CT50 (±1 SEM) by stimuli and participant with contrast at 2× threshold. Bracket and asterisks above axis-opponent pairs indicate a significant difference (p > 0.05, 2-tailed).

Figure 8. CT50 (±1 SEM) by axis and participant when stimulus intensity is 2× threshold. Bracket and asterisks above pairs indicate significant difference (p > 0.05, 1-tailed).
they differ significantly (when \( p = 0.05 \), 1-tailed, Bonferroni corrected for the 3-way comparison). \( CT_{50} \) was significantly shorter for the achromatic stimuli than for the chromatic stimuli for three out of the five participants. While the achromatic and chromatic differences were not always significant, the achromatic \( CT_{50} \) was always smallest. The plot on the right shows the mean \( CT_{50} \) for all participants. The error bars indicate one \( SEM \) from the mean derived by pooling the variance for that axes for all participants. The mean \( CT_{50} \) values for the three conditions were compared as for individual participants, again using pooled variance from all participants. The \( CT_{50} \) in the achromatic condition was 18.6 ms and 13.8 ms shorter than in the S-cone and (L–M)-cone conditions, respectively, at an alpha value of \( p = 0.05 \), 1-tailed. The two chromatic \( CT_{50} \) values were not significantly different from each other.

\[ 0.3R_{\text{max}} \text{ by stimulus and axis:} \] The same analyses applied to the 2\( \times \) threshold data were applied to the data recorded when stimuli were presented at a contrast calculated to elicit 0.3\( \times \) the maximum neural response. Figure 9a shows a comparison of \( CT_{50} \) for each of the stimuli for P1 and P2. The \( CT_{50} \) values were typically similar for axis-opponent pairs with no differences approaching statistical significance. The plot on the right of Figure 9a shows that the mean \( CT_{50} \) for axis-opponent pairs was similar when averaged for both participants. The similarity of \( CT_{50} \) for the two axis-opponent stimuli suggests the validity for this method of equating contrast.

Figure 9b shows \( CT_{50} \) to be significantly shorter for the achromatic than the chromatic pathways for both participants (\( p = 0.05 \), 1-tailed, Bonferroni corrected for the 3-way comparison). The mean differences between the achromatic and chromatic pathways were 17.4 ms and 42.9 ms for the (L–M)-cone and S-cone pathways, respectively. The difference between the two chromatic \( CT_{50} \) values was 25.5 ms.

Discussion

We have developed a series of procedures to compare the delays for mid-flight correction of reaches to achromatic, (L–M)-cone, and S-cone targets that are equated for perceptual and neural strength. We used chromatic stimuli carefully calibrated to minimize activation of the achromatic pathway. We also estimated the full neural response vs. contrast functions as well as detection thresholds for each stimulus type and subject. In this way, we were able to compare responses using stimuli scaled to a small multiple of their detection threshold contrasts as well as stimuli scaled to produce equal fractions of their estimated saturating neural response.

For stimuli scaled to 2\( \times \) detection threshold, we found that it took approximately 15–20 ms longer to correct reaches to (L–M)-cone targets than to luminance targets and approximately 20–25 ms longer to correct reaches to S-cone targets than to luminance targets. When we used stimuli that generated an equal fraction of the saturating neural response, we had relatively less S-cone contrast and this is reflected in the fact that while (L–M)-cone latencies
were similar to the scaled threshold condition, we measured a slightly longer (40 ms) relative delay for S-cone targets. We begin this discussion with a comparison of our two methods of equating stimulus contrast before discussing our results in light of the literature.

Comparing methods of equating stimuli for contrast

What stimulus contrasts should we use when we compare reaction times in different chromatic pathways? Pure cone contrast is not an appropriate scale as it equates neither perceptual salience nor neural response amplitude (McKeefry et al., 2003). Equating stimuli using multiples of detection threshold is a more principled approach. As well as creating a perceptual match, detection thresholds are assumed to correspond to similar neural signal-to-noise ratios in the areas involved in detecting the existence of the stimulus (Green & Swets, 1966). Contrast increment thresholds appear to correlate with activity in early visual cortex and may be based on the amplitude of neuronal responses in V1 (Boynton et al., 1999). Many studies therefore choose to present their stimuli at detection threshold (e.g., Bompas & Sumner, 2008; Smithson & Mollon, 2004) or at multiples of that threshold (McKeefry et al., 2003). However, one issue with using multiples of detection threshold is that neural response functions could exhibit different response nonlinearities in different pathways. These potential nonlinearities would confound attempts to match superthreshold stimuli. This led us to measure the estimated contrast vs. response function for each channel to ensure that we could equate superthreshold neural response amplitudes. We found (Figure 4) that for the stimuli used in this experiment the ERFs are approximately linear over the early part of their range. This suggests that the effects of increasing contrast in increments of threshold may be similar for all pathways up to twice the detection threshold. However, beyond this point, the ERFs are not simply predictable from linear multiples of detection thresholds. For example, stimuli at 4× detection threshold appear to generate approximately linear multiples of detection threshold responses in (L–M)-cone channels but significantly less in the S-cone channel, which has already started to saturate by this point.

Correcting reaches and reaction time to achromatic and chromatic stimuli

Figures 8 and 9 show that it takes approximately 15–20 ms less time to incorporate achromatic location information into a reach compared to (L–M)-cone information. This achromatic versus (L–M)-cone time difference is similar to the electrophysiological differences found in (L–M)-cone and achromatic information traveling to V1 in the macaque (Nowak et al., 1995). Therefore, our findings are consistent with the proposition that chromatic and luminance location information used in correction reaches travel via V1. However, this proposition would need to be reconciled with the findings that there is still some guidance for reaches when V1 is inactivated (Ro, 2008). It is possible that there is some redundancy in the processing. V1 may play a role in processing location information used in guiding reaches, while other routes may continue to function when V1 is inactivated.

Here, we are interested in comparing our response times to those found previously. While we compare our results to previous reaching correction results, we also compare our chromatic–achromatic delay differences for reaching corrections to those found in RT studies for two reasons. First, there are several studies that directly compare RT to chromatic and achromatic stimuli as we have compared CT50. These studies provide an example of how conduction delays can translate into response delays. Second, there is some chance that reaching correction and RT tasks use shared neural substrates for conveying chromatic and achromatic information up to a point where the two information types are integrated. If this were the case, then we would expect to see similar chromatic–achromatic differences for both tasks.

White et al. (2006) measured reaching corrections, RT, and saccadic initiation to Gaussian blobs from the MB–DKL axes at the maximum intensity possible. Their stimuli vary from ours in that their achromatic stimuli were relatively strong compared to their chromatic stimuli—both in terms of detection threshold and in raw RMS cone contrast. This would make the responses to achromatic stimuli relatively fast in comparison to the responses to the chromatic stimuli. Even with this high achromatic contrast, White et al. found that the achromatic pathway offered a limited advantage for the correction of reaches. They did not test the time taken to correct the reach as we did, but they found that the movement time for the achromatic targets was 8 ms shorter while accuracy was similar for the three axes.

As well as displaying their stimuli at the maximum contrast possible, White et al. (2006) also made some comparisons between (L–M)-cone and achromatic stimuli that were equated at 10% RMS cone contrast (using a slightly different formula to us). Our Figure 3 shows that (L–M)-cone and achromatic stimuli have similar RMS cone contrasts at detection threshold—at least for the spatial frequencies and stimulus eccentricities used in our experiments and so White et al.’s data can be compared to our 2× detection threshold condition. When stimuli were equated for contrast in this way, White et al. found that achromatic RTs were insignificantly 15 ms faster than the (L–M)-cone RTs. They also compare RT for two participants to (L–M)-cone stimuli with luminance contrast added to the stimuli. The addition of 10% luminance contrast reduces RT by around 15–20 ms.

As in our study, Brenner and Smeets (2004) required subjects to make online corrections to reaches based on a...
cue at a second location. They always had participants reach to a red square on a yellow background. On some trials, the target square either moved to a new location or swapped locations with a green square. They found that subjects could initiate corrections to reach trajectories in as little as 120 ms. Participants were approximately 10 ms slower to make the correction when all stimuli always changed luminance at the beginning of the reach. This small difference may be from removing the achromatic–chromatic contamination or the distraction of the luminance flicker.

Smithson and Mollon (2004) adjusted stimuli to be isoluminant and also found the tritan line for each observer. While we presented our Gaussian blobs at 10° from fixation, Smithson and Mollon presented their luminance noise masked stimuli at 3° from fixation. They found that manual RTs to (L–M)-cone stimuli were 5–20 ms slower than the achromatic RTs, using stimuli that were not masked with luminance noise. Again, this time difference is compatible with our 15–20 ms differences for correction time. However, the two studies do show some differences between the S-cone and achromatic delays. When the stimuli were masked by luminance noise, Smithson and Mollon found that luminance RTs were no more than 24 ms faster than the S-cone RTs. The presence of luminance noise, as Smithson and Mollon comment, likely led to response delay differences. When the stimuli were not masked, RTs to S-cone stimuli were delayed by an additional 25–50 ms over the achromatic stimuli. We concluded that CT<sub>50</sub> for the achromatic pathway was 20–40 ms faster than for the S-cone pathway. Bompas and Sumner (2008), who also subjectively adjusted the tritan line and used a lower level of luminance noise, found that the additional delay for S-cone RTs over achromatic RTs was 23 ms.

The speculative interpretation of these three sets of S-cone versus achromatic differences is that an early difference in conduction velocity leads to differences in response time around the order of 25–50 ms and that this difference will be reduced by luminance noise or activation of the (L–M)-cone pathways by S-cone stimuli. This is supported by the negative relationship between the luminance noise and achromatic versus S-cone delay differences seen in the three levels (high, medium, and nil) of luminance noise used by Bompas and Sumner (2008) and Smithson and Mollon (2004). In addition, since we did not set the tritan line for each observer, it is possible that our S-cone stimuli may have activated the (L–M)-cone pathway, decreasing the difference between the S-cone and achromatic responses.

### Comparing reaction times and correction times

In the interpretation of our reaching correction times and the RT studies, we suggest that RT and CT<sub>50</sub> could well show similar differences between delays to chromatic and achromatic stimuli. This is interesting as these tasks are quite different: A fast reaching correction can begin in as little as 110 ms, while a fast reaction time may be of the order of 200 ms. While the two tasks share the same visual pathways originating in the retina, it is likely that they involve very different neural substrates at higher levels. However, it is possible that there is a common point in the early visual system, such as V1, where chromatic and achromatic information could be integrated for both types of tasks.

Although the RT is typically measured as taking longer than the onset of reaching corrections, an interesting situation presents when the finger is raised as the initial part of a guided reach. The visuomotor system appears to begin to use color information to guide the reach just after the finger has been raised (Schmidt, 2002; Schmidt, Niehaus, & Nagel, 2006). In this case, the change in direction of the reach is altered much later (>230 ms) after the visual location information has been available to the visuomotor system. This implies that this ability to rapidly incorporate information into a reach depends on the reach already being in flight, showing a difference in the processing involved in online corrections and executing reaches.

These interpretations about the similarity of RT and reaching corrections are based on studies that vary greatly in terms of the stimuli used and the methods of determining isoluminance, and therefore, it would be highly speculative to draw conclusions about the similarity of these results. A direct comparison between reaching correction times and reaction times to identical stimuli would be needed to determine whether the additional achromatic delays are similar for the two tasks.

Recently, the concept of an automatic, preferred pathway for the correction for reaching (Pisella et al., 2000) has been proposed. Cressman, Franks, Enns, and Chua (2006) suggest that this preference is driven only by achromatic information. However, these two studies compared a change of location to a change of color, as opposed to having a change of location that is defined only by chromatic information. The data presented in this study suggest that the sensorimotor system is more interested in color information when it cues a change in location directly.

The ability of the sensorimotor system to effect reaches depends on the quality of its information (Gegenfurtner & Franz, 2007; Ma-Wyatt & McKee, 2006) and this includes its timing (Ma-Wyatt & McKee, 2007). Correcting responses to incorporate new information will be a trade-off between certainty about the location and how long the system takes, or has available, to make the decision (see Smith & Ratcliff, 2004, for a discussion of modeling neural decisions). Even delayed information regarding target locations may still be important in confirming previous decisions and movement plans. Our findings and those of other groups indicate that reaches to chromatic targets are almost as fast and accurate as reaches to achromatic targets.
stimuli (White et al., 2006) even when the chromatic information is delayed. In short, delayed chromatic information is still important to the sensorimotor system.

Summary and conclusion

We have estimated neural response functions for chromatic and achromatic Gaussian stimuli in the periphery. We then compared the magnitude of delays to reaching corrections cued by these stimuli when they were equated for both perceptual salience and neural response. The stimuli used in the initial adjustments are the same as those used in the final reaching experiment. The variation in mean isoluminance values between participants shows the importance of adjusting isoluminance subjectively. We found that ERFs were approximately linear from detection threshold to low multiples of this level, suggesting that chromatic and achromatic stimuli can be matched at twice the detection threshold. The similarity of the achromatic and (L–M)-cone contrasts determined by the 2× threshold conditions and 0.3Rmax conditions suggests that both methods are effective in equating contrasts with achromatic and (L–M)-cone stimuli. The consistency in the magnitude of the achromatic–chromatic delay differences across 5 participants shows that these results are reproducible. This reproducibility increases our confidence in this entire process of adjusting isoluminance, equating contrast, and measuring reaching corrections.

Our data, consistent with Brenner and Smeets (2004) and White et al. (2006), suggest that the visual areas involved in reaching guide treat chromatic and achromatic information in a very similar manner. This is consistent with the idea that color and luminance signals are combined at an early stage in the visual hierarchy (Sincich & Horton, 2005). We find that achromatic information is not preferred for correcting reaches, it is just available for use slightly sooner.

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