RESEARCH ARTICLE

Brian J. White · Dirk Kerzel · Karl R. Gegenfurtner

Visually guided movements to color targets

Abstract The pathways controlling motor behavior are believed to exhibit little selectivity for color, but there is growing evidence suggesting that color signals can be used to guide actions. We investigated this by having observers make a saccade or a rapid pointing movement to a small, peripherally flashed (100 ms) Gaussian target (SD = 0.5°) defined exclusively by luminance (maximum contrast) or color (from cardinal DKL red–green or blue–yellow axes, at maximum saturation). We found no difference in saccadic or pointing accuracy for luminance or color targets. The same was true using shutter goggles during pointing (to minimize the use of external cues), and when the luminance contrast of color targets was varied by up to ±10%. In terms of response times, both eye and hand latencies increased with target eccentricity for R–G targets only, in a manner consistent with the sensitivity of this channel across eccentricity. We found little difference in response latencies between luminance and color targets once matched in terms of cone contrast. While RTs were longer when coupled with a goal directed pointing movement (versus a simple reaction without pointing), the difference was the same for color or luminance targets, suggesting that the spatial coding for the movements was also the same. In a final experiment we compared the accuracy of pointing to color-naming performance in a 4AFC procedure. The psychometric functions relating pointing accuracy (% correct quadrant) to color-naming (% correct color-name) were identical. Taken together, the results show that human observers can efficiently use pure chromatic signals to guide actions.

B. J. White (✉) · K. R. Gegenfurtner
Justus-Liebig-Universität Giessen, Abteilung Allgemeine
Psychologie, Otto-Behaghel-Strasse 10F, 35394 Giessen, Germany
E-mail: brian.j.white@psychol.uni-giessen.de
Tel.: +49-641-9926106
Fax: +49-641-9926119

D. Kerzel
Université de Genève, Uni Mail, FaPSE, 40 bd du Pont d'Arve,
1205 Genève, Switzerland

Introduction

Primates are the only mammals with trichromatic color vision (Jacobs 1993), and it is generally believed that this system was driven by the nutritional benefit of detecting specific food sources (e.g., ripe fruit, Mollon 1989; leaf color selection, Dominy and Lucas 2001). Color is also useful for image segmentation, thereby facilitating recognition of natural scenes (Gegenfurtner and Rieger 2000; Wichmann et al. 2002), or enabling us to quickly find a target embedded in a field of distractors (D'Zmura 1991; D'Zmura et al. 1997; Olds et al. 1999). In terms of visual detection, chromatic pathways are in fact more sensitive than achromatic pathways when stimuli are equated for cone contrast (Chaparro et al. 1993). Color signals therefore ought to be used to guide motor behavior. This is supported by accumulating evidence showing effects of color on actions (e.g., Brenner and Smeets 2004; Schmidt 2002; Toth and Assad 2002), despite that the neural pathways controlling motor behavior are believed to exhibit little, if any, selectivity for color. Here we present three experiments that directly test the efficiency with which color information can be used to guide the eyes and the hand.

Visuomotor pathways

One of the most intriguing aspects of the primate visual system has been in understanding the functional nature of its pathways. Once light is absorbed by the photoreceptors (long-, middle- and short-wavelength cones, or L-, M- and S-cones), retinal ganglion cells transform the signals into three distinct channels, one luminance and two color opponent (Derrington et al. 1984; Kaplan et al. 1990). An L + M channel adds the inputs from the L- and M-cones and is mostly sensitive to luminance

information. An L − M channel computes the difference between the L- and M-cone inputs and is mostly sensitive to colors modulated along a reddish to greenish dimension. An S − (L + M) channel computes the difference between the S and L + M cone inputs and is mostly sensitive to colors modulated along a bluish to yellowish dimension. These paths remain anatomically distinct through to primary visual cortex (V1) with L + M signals passing through the magnocellular layers of the lateral geniculate nucleus (LGN) to layer 4Cα in V1, L − M signals passing through the parvocellular layers of the LGN to layer 4Cβ in V1, and S − (L + M) signals passing through the koniocellular layers of the LGN to layer 2/3 in V1 (see Sincich and Horton 2005 for review).

The segregation into distinct pathways becomes less clear as we move into the visual cortex, although there is evidence for two commonly known streams (Ungerleider and Mishkin 1982): a *ventral stream* including areas V2, V4 and inferotemporal cortex (IT), believed to be primarily involved in form and color computations for object identification, and a *dorsal stream* including areas V3, middle temporal area (MT), lateral intraparietal cortex (LIP), and parietal reach region (PRR), believed to be primarily involved in motion analysis and determining where objects are spatially.

These streams were once thought to be a direct extension of the retinogeniculate pathways (Livingstone and Hubel 1988), but there is growing evidence against it (Gegenfurtner and Hawken 1996; Merigan et al. 1991; Merigan and Maunsell 1993; Schiller et al. 1990; Sincich and Horton, 2005). The signals from the magno, parvo, and konio pathways begin to mix in V1, such that layer 2/3 receives input from all three sources (see Sincich and Horton 2005 for review). As such, analyses of color and luminance are not strictly separate in the cortex (Johnson et al. 2001), making it likely that color, form and motion are also not processed in isolation (Gegenfurtner 2003; Sincich and Horton 2005).

Color and the control of movements

The M-path has strong connections to middle-temporal area (MT) (Maunsell et al. 1990), a dorsal region particularly important for the analysis of motion. While few, if any, individual cells in MT show selectivity for color (Zeki 1983), they can respond to photometrically isoluminant stimuli (Charles and Logothetis 1989; Dobkins and Albright 1994; Gegenfurtner et al. 1994; Saito et al. 1989). This is because of the natural variation in individual cells' isoluminant point: cells in MT show a null response point at a specific luminance ratio between the two stimuli (e.g., target against the background). This null response point varies from cell to cell, which amounts to a significant response to photometrically isoluminant stimuli at the population level, even though MT contains no color-opponent cells.

There is also growing evidence that chromatic signals may be used to guide motor behavior (e.g., Anderson and Yamagishi 2000; Brenner and Smeets 2004; Schmidt 2002; Toth and Assad 2002). For example, in a non-speeded task, both M- and P-type targets (flashed for 100 ms, at 10° eccentricity) have been reported to be localized with the same efficiency using manual pointing (Anderson and Yamagishi 2000).

Chromatic signals have also been shown to affect speeded movements. For example, Schmidt (2002) reported that visually masked color primes could affect the trajectories of speeded pointing movements to subsequent targets of the same luminance, even when the color of the primes could not be reliably determined by the observer. Brenner and Smeets (2004) have also shown that observers can very rapidly adjust their pointing movement in response to chromatic information. Observers had to tap a red target, which sometimes switched locations with a green distractor of the same luminance as soon as the hand started to move. Observers could make this correction within 120 ms of the change. This however has not been exclusively the case (Cressman et al. 2005), as Cressman and colleagues recently reported a similar but somewhat weaker effect for pure chromatic stimuli.

Finally, recent evidence also suggests that cells in monkey dorsal area LIP respond selectively to color when it is relevant for the task (saccade task; Toth and Assad 2002). Given that color and luminance are no longer strictly segregated in the cortex (Gegenfurtner 2003; Johnson et al. 2001; Sincich and Horton 2005), evidence seems to suggest that motor areas should have access to both these signals as well.

Color and response latency

Visual attributes such as color, motion and form are also believed to have different neuronal latencies, which are thought to represent different levels of visual processing (Barbur et al. 1998). The conduction time from the optic chiasm to the LGN is only about 3–4 ms slower for the P-layers relative to the M-layers (Schiller and Malpeli 1978). This difference is only slightly larger in terms of visual response latency, with reports from 7 to 10 ms (Maunsell et al. 1999; Maunsell and Gibson 1992). In area V1, the difference increases to about a 20 ms between layers 4Cα and 4Cβ (Nowak et al. 1995; Schmolesky et al. 1998).

Behavioral latency differences between color and luminance stimuli are sometimes explained in terms of this slightly faster, transient response of the magnocellular channel (e.g., Schwartz 1992). However, in order to make a fair comparison, stimuli should be matched in terms of cone contrast or psychophysical detection performance. Where this was done, some find that response latencies are still slower for chromatic stimuli in terms of saccades (e.g., van Asten et al. 1988; Perron and Hallett 1995; Satgunam and Fogt 2005), and manual reaction times (Burr et al. 1998; Schwartz 1992). However the size of the effect varies, and may be attributable to differences in the target-stimulus characteristics (e.g., CIE coordinates, target duration) and methods of

matching stimuli (e.g., matched cone contrast, CIELab contrast match, contrast detection thresholds). For example, van Asten et al. (1988) reported only a small difference in saccade latency between luminance and red (CIE $xy = 0.636$, 0.339) or green (CIE $xy = 0.319$, 0.596) isoluminant squares presented at $1.5\times$ detection threshold (17–23 ms longer for color targets). Similarly, data from Perron and Hallett (1995) showed only slightly longer saccade latencies for isoluminant gaussian-targets in a sequential tracking paradigm. In contrast, saccade latencies have recently been reported at up to 50 ms longer for isoluminant targets using CIELab space to match contrasts (Satgunam and Fogt 2005). Similar results have been shown with manual reaction times to the motion onset of gratings of matched cone contrast (Burr et al. 1998).

Since differences in visual latency between the M- and P-paths are only in the range of 7–10 ms (Maunsell et al. 1999; Maunsell and Gibson 1992), behavioral latency differences larger than this suggest the contribution from cortical areas. For these reasons, we also consider the pattern of latencies during tasks requiring different motor demands (e.g., during pointing versus a simple manual reaction), and with targets of matched cone contrast.

Rationale

The main idea behind the series of experiments presented here is that if luminance and color information are treated in fundamentally different ways by the brain, we should see differences in saccadic or pointing behavior between targets defined by these two properties. For this reason, the primary experiments simply tested the efficiency with which observers could make a saccade or rapid pointing movement to targets defined exclusively by either luminance or color. We then performed the same test while varying the target's luminance contrast by small amounts and holding chromatic contrast constant to determine the degree to which variations in individual isoluminance might contribute to the results. In addition, we measured the pattern of response latencies (eye and hand) across a wide range of target eccentricities, and under conditions of equal cone contrast. We then compared RTs when coupled with a goal directed pointing movement to a simple reaction without pointing, in order to determine if the cost of programming a movement is greater for color targets. Lastly, we obtained psychometric functions relating pointing accuracy (a motor task) to color-naming (a perceptual task) while varying the saturation of color targets. While the dorsal stream might respond to the isoluminant component of a stimulus, e.g., due to natural variation in individual cells' luminance balance (Gegenfurtner et al. 1994), it may not have access to information about the color itself, which is necessary for color-naming. Similar performance between color-naming and pointing accuracy would suggest the same signals can be used in both tasks.

Methods

Observers

Ten observers took part in the primary Experiments 1A (pointing) and 2A (saccades) (same observers in each experiment, nine of whom took part in the RT-only control Experiments 1C as well). Experiments 1D and 2C (latencies to targets of matched cone contrast) had five observers each, and control Experiments 1E and 2D (varied luminance contrast of color targets) had two observers each. Finally, two observers took part in Experiment 3 (pointing vs. color-naming dual-task). All observers had normal or corrected to normal visual acuity, and normal color vision.

Each observer was informed of the task requirements and the duration of the experiment prior to their consent to participate. The experimental procedures were in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Stimuli

Targets and background

The central fixation stimulus was a small, black point with a diameter of approximately 0.2°. Targets were Gaussian dots (SD = 0.5°) derived from the DKL color space, whose cardinal color axes show a close correspondence to the color-opponent mechanisms in early vision (Derrington et al. 1984; first introduced by Krauskopf et al. 1982). This three-dimensional spherical space has an equal-energy white center point. Extending outward in one direction increases the lightness or darkness of a stimulus (i.e., luminance energy) while effectively holding color constant. Along a given cardinal color direction (L − M "red–green" axis or S − (L + M) "blue–yellow" axis), color saturation is increased while the energy from the luminance and the remaining cardinal color axis are effectively held constant.

Targets were always chosen from these cardinal axes, and unless otherwise stated were presented at the maximum contrast/saturation possible on our equipment (see Footnote 1). The background was uniform gray at 32 cd/m². Using the Judd (1951) modified luminosity function, the CIE chromaticity coordinates of our color stimuli at maximum saturation were as follows: red (0.33, 0.28), green (0.23, 0.33), blue (0.25, 0.22) and yellow (0.36, 0.52).

Dealing with individual variation in isoluminance

A common problem with trying to isolate chromatic pathways is the natural variability in individual isoluminance. Researchers deal with this in different ways. Traditional methods involve determining each observer's isoluminant point using, for example, heterochromatic flicker photometry, or the method of minimum motion (Cavanagh et al. 1987). However, different methods

might have different neural substrates and could therefore lead to different results (Webster and Mollon 1993). Another problem is that the spatial and temporal properties of the stimulus in one task (e.g., the one devised for determining isoluminance) are often quite different from that of another task (e.g., the one in which the stimuli are later assigned). One way to get around this is to use the same task in both cases, e.g., by measuring performance while varying the luminance contrast of a color stimulus. If individual variation in isoluminance is an important factor in our results, we should see deviations in performance around some "true" isoluminant point for a given observer. In this regard, we collected additional data where we measured saccadic and pointing performance (accuracy and latency) while varying the luminance contrast of the color targets by ±1, 2, 5 and 10%.

Equipment

Stimuli were displayed on a 21 in. CRT touch-screen monitor (ELO Touchsystems) driven by an ASUS V8170 GeForce 4 MX440 graphics board at a non-interlaced refresh rate of 100 Hz. The resolution of the monitor was set at $1,280 \times 1,024$ pixels, which corresponded to physical dimensions of 37 cm wide by 29.6 cm high. At a viewing distance of 47 cm, the display occupied a retinal area of 45° horizontally and 36° vertically. The relationship between the monitor's voltage and luminance was linearized.

Eye-movements were measured using EyeLink II (video-based tracker from SR Research Ltd., Mississauga, Ontario) at a sample rate of 250 Hz. The touch-screen was used to record pointing end positions.

Procedure

The observer's head was stabilized by a chin rest. Eye calibrations were made before each block of trials (approximately every 60 trials), and consisted of fixating nine consecutive bull's-eye stimuli at various locations on the screen. Average spatial accuracy for each calibration was maintained at 0.35° or lower.

Figure 1 illustrates the general procedure for Experiments 1, 2 and 3. In Experiments 1 and 2, the fixation stimulus was present awaiting initiation of the trial by the observer. On each trial, observers had to fixate this stimulus, and then start the trial by pressing a key on a game-pad. This allowed for a drift correction procedure at the start of each trial (if observers were not fixating within 1° of this stimulus, an error-tone was presented, and the trial had to be reinitiated). After the button was pressed, there was a 500 ms + 0–500 ms random interval before the fixation point was extinguished. This was followed by a 200 ms gap, and then the appearance of the target for 100 ms at one of three eccentricities (3, 6 or 12° from center) randomly around an imaginary circle. What follows is a more detailed description of the primary and control experiments.

In Experiment 1A (*pointing movements*), the start-button had to be pressed and held down until the fixation point was removed and the target appeared. Observers then had to release and touch the target location with their index finger as quickly and accurately as possible. A button release earlier than 50 ms after target onset, or movement time longer than 400 ms from the time of button release resulted in an error message. We employed 10% catch-trials in which no target appeared in order to ensure that observers were in fact responding to the target and not to the fixation offset. For the catch-trials, observers were to remain holding the button down until the fixation point reappeared for the next trial. Reaction time, movement time, pointing accuracy, and eye movements (saccade accuracy and latency) were measured.

We also ran the same test using liquid-crystal shutter-goggles (Exp. 1B), which closed 100 ms after target onset. This forced observers to rely on some internal spatial representation of the target's location, while reducing the possibility of using external information for online control of the movement (e.g., vision of the hand relative to some external object such as the edge of the monitor). Eye movements were not measured in this case.

In addition, it was in our interest to compare the pattern of latencies in Experiment 1A to a situation in which a goal-directed pointing movement was not required, only a simple reaction time response. Experiment 1C was designed for this purpose and was identical to Experiment 1A in every respect except observers simply released the button when the target appeared (eye movements were not recorded). The idea behind this control is that if the mechanisms that guide goal-directed movements do not have access to color information, we might expect a longer response delay to color targets when a goal-directed movement is required (because presumably a simple reaction time response does not necessarily require the encoding of specific spatial coordinates).

Experiment 1D was designed to compare absolute latency profiles between luminance and color (R–G only) targets over a range of contrasts by matching the targets in terms of cone contrast. Note that earlier we chose maximum contrast/saturation as a conservative means of comparing accuracies between color and luminance targets (see Footnote 1). If the mechanisms guiding goal-directed pointing can utilize color as effectively as luminance, we might expect only small differences in latency when stimuli are matched in terms of cone contrast. Slightly longer latencies for color targets (e.g., ≤10 ms) would be consistent with neuronal latencies of the somewhat slower P-path (Maunsell et al. 1999; Maunsell and Gibson 1992; Schiller and Malpeli 1978), but differences greater than this might suggest the contribution from higher cortical areas.

Finally, to deal with the problem of individual variation in isoluminance, Experiment 1E was designed to measure pointing accuracy while varying the target's luminance contrast by small amounts from -10 to 10%, and holding chromatic contrast constant at 80% of the maximum possible on our equipment. Small variations in

Fig. 1 (*Top*) The sequence of a trial for Exp. 1 and 2. In Exp.1 observers had to fixate the central dot, then *press-and-hold* a button to initiate the trial. After a random period, the fixation point was removed and a target (derived from DKL color space) was flashed (100 ms) in the periphery at 3, 6 or 12° eccentricity, randomly around an imaginary circle. Observers had to release the button and touch the target location as quickly and accurately as possible. Movement time was constrained to ≤400 ms, and 10% catch trials were employed to ensure target driven responses. The same was tested in a saccade task (Exp. 2) except observers simply fixated, pressed a button to initiate the trial, and then looked to the target location. (*Bottom*) Details of Exp. 3. Stimulus presentation was identical to Exp. 1 except observers had to point to the target, and then name its color (only color targets). Target saturation was varied. We later divided the screen into four equal sectors, and defined psychophysical pointing performance as % correct quadrant. We then obtained psychometric functions relating pointing accuracy (% correct quadrant) to color-naming (% correct color, R, G, B or Y)
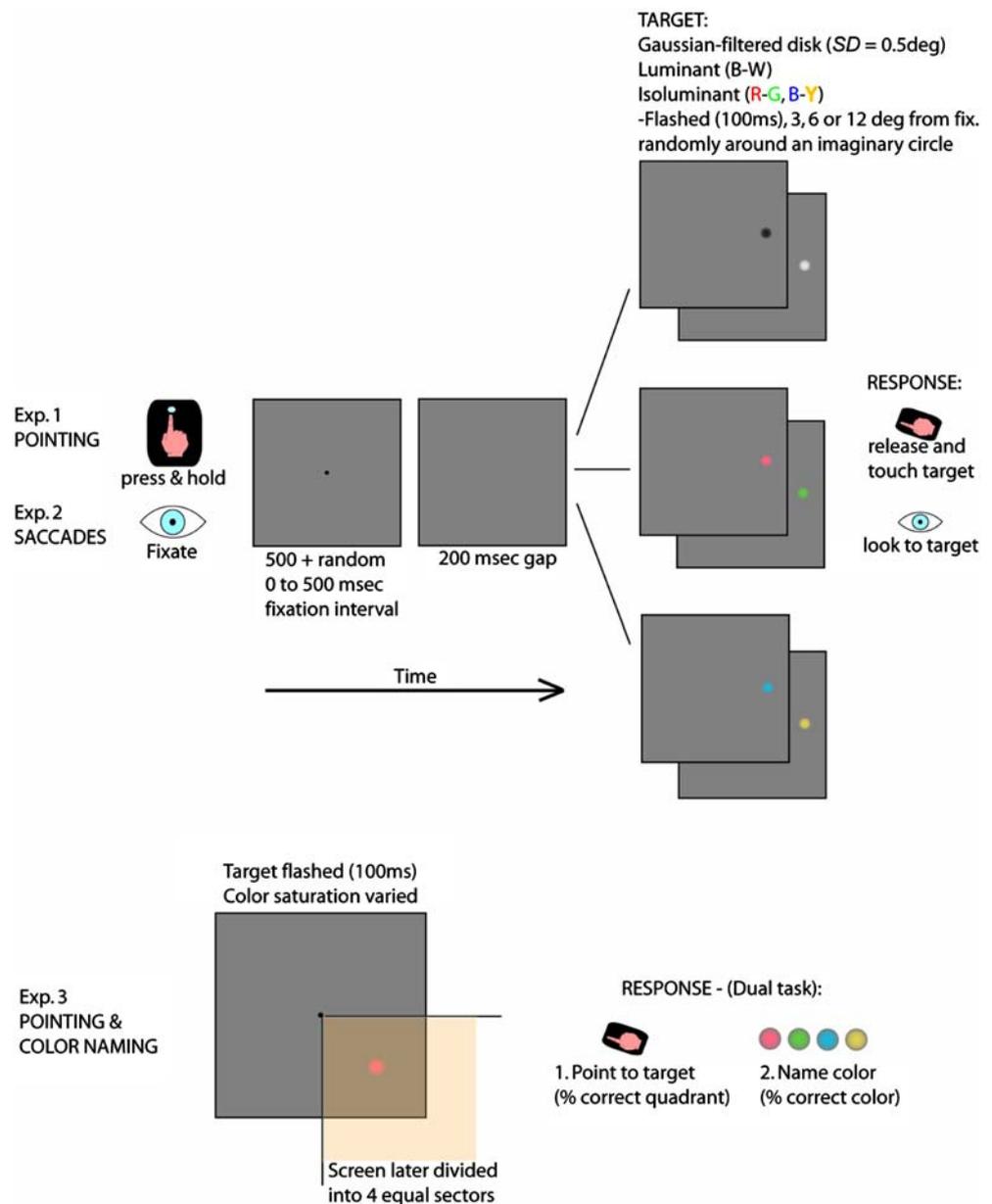
the luminance balance of color targets should allow us to determine if pointing accuracy is sensitive to the natural variation in subjective isoluminance. If this is the case, we should see an increase in position error as we approach some optimal isoluminant point for a given observer.

In Experiment 2A (*eye movements*), we employed the very same paradigm as Experiment 1A but only measured accuracy and latency of the first saccade. Observers pressed the game-pad button to start each trial (they did not hold the button as in the pointing task). For consistency, catch trials were also employed here with respect to a saccadic response, but we also included data in which catch trials were not used (Exp. 2B), and target duration was extended to 500 ms (since saccades are ballistic movements).

As with pointing, Experiment 2C was designed to compare saccade latency between luminance and color

(R–G only) targets matched in terms of cone contrast (see Footnote 1).

Finally, we also measured the effect of varying the target's luminance contrast on saccadic accuracy and latency (Exp. 2D). Again, luminance contrast was varied by small amounts from −10 to 10% while holding chromatic contrast constant at 80% of the maximum possible on our equipment.

In Experiment 3 (*pointing vs. color-naming*), we compared performance on a motor task (pointing) versus a perceptual task (color-naming) (see Fig. 1, bottom). On each trial, observers were required to first point to the target (again randomly located around an imaginary circle, but at one eccentricity, 6° from center), and then name its color by pressing the appropriate key. Only targets from the two cardinal DKL color axes were used, and chromatic contrast was varied. To compare pointing to

color-naming, we later divided the screen into four equal sectors, and defined pointing performance in terms of the percent of trials where observers pointed in the correct quadrant. We compared the psychometric functions of pointing accuracy (% correct quadrant) to color-naming (% correct color, R, G, B or Y), using psignifit toolbox for Matlab (see Wichmann and Hill 2001a, 2001b).

Due to the natural variation in individual cells' luminance balance (Gegenfurtner et al. 1994), the dorsal stream might respond to the isoluminant component of a stimulus, but not have access to information about the color itself, which is necessary for color-naming. This should result in a performance difference between these two tasks. Similar performance, however, would suggest that the same signals are used for both tasks.

For all experiments, observers were simply requested to perform the movement as quickly and accurately as possible. Each observer completed at least 24 trials per condition. All analyses were done offline.

Analyses

Pointing and saccadic error were the Euclidean distance in degrees between the target location and touch-screen pointing locations or end point of the first saccade. Reaction time was the time between target onset and the button release (or the onset of the first saccade for saccade latency) in ms. Saccades were based on a velocity criterion of 30°/s or greater. Movement time was the time between button release and contact with the touch screen in ms. No outlier procedure was used, but we considered trials with saccadic latency less than 80 ms as anticipatory (see Wenban-Smith and Findlay 1991). As previously mentioned, anticipatory manual responses were controlled by online feedback (a warning signal was presented for RTs < 50 ms) and catch trials. Misses were defined as no response on a target present trial within a 1 s period following target onset (i.e., no button release in terms of Experiment 1). However, in terms of saccades, we thought it might be difficult to maintain steady fixation for a 1 s period, so we felt it was necessary to use some additional criteria for determining whether or not the target was detected. Therefore, for the saccade experiment (Exp. 2), trials with saccadic error greater than half the target eccentricity were also considered misses. Catch trials and error trials (anticipatory responses, misses and false alarms) were removed from analyses.

We derived median values (for latency and position-error) for each observer on each of the conditions since these values are less affected by outliers than the mean. When combining subjects' data, we used the mean of these median subject values.

Experiment 1 (Pointing movements)

As previously described, the observer's task was to point to the flashed target on a touch screen as quickly and accurately as possible (eye movements were simultaneously recorded). Surprisingly, most observers made relatively few saccades during this procedure (primary Experiment 1A). These observers performed the task reasonably well with peripheral vision, though it is likely that foveal vision can help guide the hand to a desired location (Admiraal et al. 2003, see Footnote 2).

Results and discussion

Misses and false alarms

The mean proportion of misses and false alarms was low (0.03, and 0.08, respectively) suggesting that observers had little difficulty seeing the targets. It is worth noting that the majority of misses came from three observers, and only for the most eccentric (12°) red–green targets. Given the short target duration (100 ms), and that these targets had the lowest cone contrast (see Footnote 1), they may have been close to some observer's detection threshold. However a correlation between number of misses and pointing error for 12° R–G targets was not significant ($r = -0.08$, $P = 0.58$, $n = 10$), indicating that even observers who did not see these targets on some trials were just as accurate when they did see it. In short, if observers perceived a target, they could accurately point to its location as well.

Accuracy

Figure 2 shows pointing error for each of the targets as indicated by the color of the lines. The length of the lines indicates the Euclidean distance from the target. From these plots we see no obvious difference between targets defined by either luminance or color. The only difference was an increase in pointing error with eccentricity as can be seen from Fig. 3. A 3×3 (target-color × eccentricity) repeated measures ANOVA revealed a significant effect of eccentricity only, $F(2, 36) = 58$, $P < 0.001$. The effect of target-color and the color × eccentricity interaction was not significant ($F < 1$ in both cases). We obtained the same result when using shutter-goggles (Exp. 1B). That is, there was no difference between luminance and color targets.

Latency

Figure 4 shows reaction time (RT) as a function of target-color and eccentricity. The dotted lines represent a control condition where RT only was measured (Exp. 1C). RTs when pointing showed essentially the same pattern as the RT control condition except that latencies were elevated by about 30 ms. The pattern can be best described by a relatively even RT across eccentricity for luminance and B–Y targets, whereas R–G targets show a clear increase across eccentricity. In addition, isoluminant targets were elevated relative to luminance targets. This is most likely due to the fact that the maximum cone contrast physically possible for isoluminant stimuli
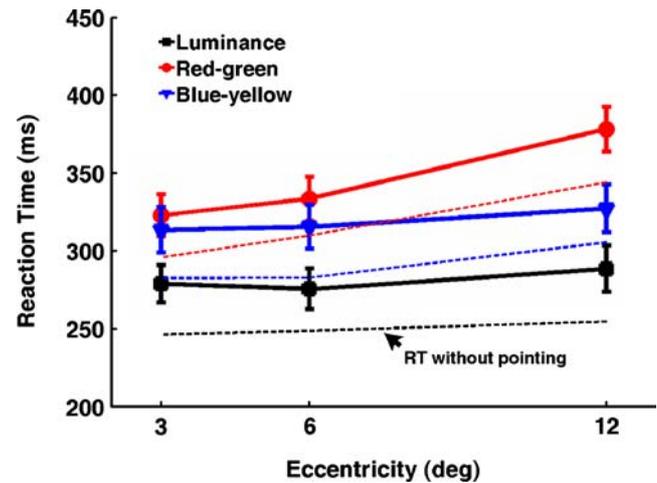
Fig. 2 Pointing error for each target color, at each eccentricity (Exp. 1A) (raw data from all observers combined): The length of the lines represents the distance of the touch point from the target location. As mentioned in the methods, this only includes trials without anticipatory responses (RTs > 50 ms), and movement time less than 400 ms. Catch trials were also removed

Pointing Error (raw data)
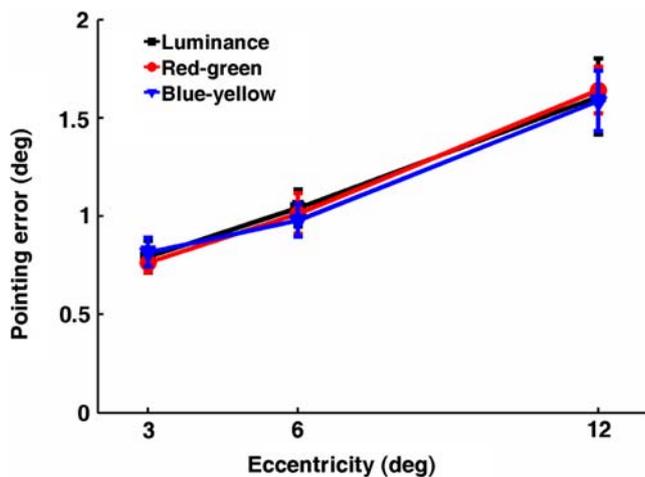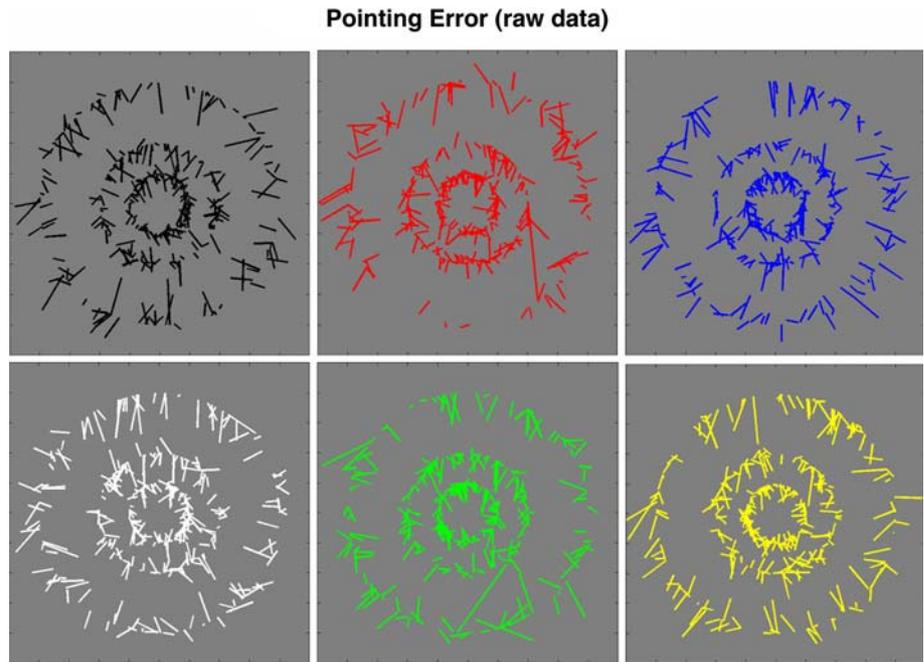
Fig. 3 Mean pointing error for color and luminance targets across eccentricity (Exp. 1A). *Error bars* represent ±1 standard error

Fig. 4 Mean reaction time for color and luminance targets across eccentricity (Exp. 1A): The dotted lines represent an RT-only control experiment (Exp. 1C) in which observers did not have to make a goal directed pointing movement. *Error bars* represent ±1 standard error

is necessarily less than luminance stimuli (Gegenfurtner 2003; Gegenfurtner and Hawken 1996; Gegenfurtner et al. 1994), and is further constrained by the limitations of CRT monitors (see Footnote 1).

We ran a $2 \times 3 \times 3$ repeated measures ANOVA with task (RT-only versus RT during pointing), color (Lum, R–G and B–Y) and eccentricity (3, 6 and 12°) as factors. The use of an RT-only control condition is based on the premise that a reaction alone should require a lesser degree of dorsal processing than reacting and pointing, because some representation of target location is required for the latter. This is presumably less of a requirement for a simple RT task (only that something occurred irrespective of where). Thus latencies should be longer in the task that requires the programming of a goal directed movement, and this should be particularly

elevated for stimuli with limited access to the dorsal stream (e.g., color targets). In this case we would predict an interaction between target-color and task (RT-only versus RT during pointing). However, the interaction was not significant, $(F(2, 16) < 1, P = 0.79)$; although, it begins to approach statistical significance when we considered the entire latency period of the pointing task (RT + movement time) versus the RT-only control task $(F(2, 16) = 3.1, P = 0.07)$. However, if this effect is real, it would in fact be consistent with our basic premise because the latency difference between luminance and color targets was, if anything, slightly smaller when programming a goal-directed movement

(R–G − Lum = 56 ms, B–Y − Lum = 31 ms) versus the RT-only condition (R–G − Lum = 67 ms, B–Y − Lum = 40 ms). In other words, the relative advantage for luminance targets was in fact smaller when programming a goal directed movement. In general, RTs were simply elevated when combined with pointing (approximately 30 ms longer) for all target-color conditions (although, the main effect of task was not statistically significant, $F(1, 8) = 2.47$, $P = 0.15$). Thus, the latency-cost of programming a goal directed movement was not largely different for luminance or color targets (at least not in the direction predicted to counter our argument), which is consistent with the idea that the dorsal stream has access to chromatic signals for guiding pointing.

There was however a significant color × eccentricity interaction, $F(4, 68) = 20.32$, $P < 0.001$, which was likely due to an increase in RT for R–G targets as a function of eccentricity relative to the other target conditions. We ran two repeated measures ANOVAs (with Bonferroni correction) to test this: one on the difference between R–G targets and B–Y across eccentricity, and another on the difference between B–Y and luminance targets across eccentricity. As predicted, RT to R–G targets becomes increasingly longer across eccentricity relative to B–Y targets, $F(2, 36) = 16.54$, $P < 0.01$. However, the difference between B–Y and luminance targets did not vary significantly across eccentricity, $F(2, 36) = 2.3$, $P > 0.05$. The RTs for B–Y targets are simply elevated relative to the luminance condition, but the R–G channel is affected in a different way. We will discuss a possible reason for this later.

Finally, movement time was fairly constant across conditions ($M = 315$ ms). A 3×3 (target color × eccentricity) repeated measures ANOVA revealed a negligible effect of color only (8 ms advantage for isoluminant targets, $F(2, 18) = 7.2$, $P < 0.05$). As previously mentioned, a longer response to isoluminant targets should not be surprising given that the maximum cone contrast physical possible for isoluminant stimuli is necessarily less than luminance stimuli (Gegenfurtner 2003; Gegenfurtner and Hawken 1996; Gegenfurtner et al. 1994). Therefore, we also compared RTs between luminance and color targets (R–G only) of matched cone contrast (Exp. 1D). This was achieved by reducing the contrast of luminance- relative to color-targets by a factor of 0.1 (see Footnote 1).

As can be seen from Fig. 5, there was little difference in reaction time between luminant and isoluminant R–G targets once stimuli were matched in terms of cone contrast. Both show nearly the same increase in reaction time as contrast was reduced from 10 to 5%. We ran a two-way (contrast × target-color) repeated measures ANOVA on the data from the 5–10% contrast points to test whether reaction times differed between luminance and color targets. The ANOVA revealed a significant effect of contrast only ($F(3, 12) = 6.41$, $P < 0.05$). The effect of target-color was not significant ($F(1, 12) = 4.69$, $P = 0.1$). This is in contrast to some previous work that has reported longer reaction times for isoluminant stim-
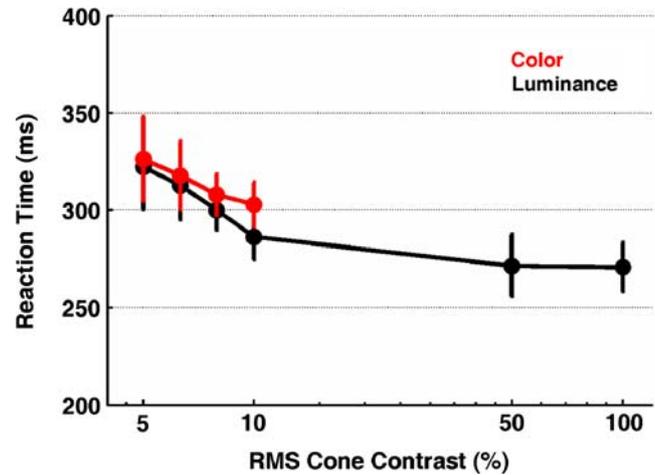

Fig. 5 Mean reaction time for color and luminance targets as a function of RMS cone contrast (Exp. 1D). *Error bars* represent ±1 standard error

uli (Burr et al. 1998; Schwartz 1992). We will return to this issue later.

Effect of individual variation in isoluminance (pointing)

To control for the possibility that the results were due to variations in individual isoluminance, we examined pointing accuracy and reaction time to color targets whose luminance contrast was varied (Exp. 1E). It was necessary to examine the results of separate observers in this case because any difference in performance due to individual variation in isoluminance would cancel out when combined. We therefore tested only two observers using a large number of trials (approximately 65) per condition.

Figure 6 shows the results from the two observers. The shaded area represents the 95% confidence interval for mean of the two highest contrast end-points (±10%). As can be seen, there was very little deviation from this in terms of pointing accuracy (Fig. 6a). An ANOVA revealed a non-significant difference across contrast for both observers ($F(8, 603) = 0.62$ for S-1 and $F(8, 584) = 0.30$ for S-2, $P > 0.05$ in both cases). Furthermore, the reaction time profiles were centered around 0 for both observers, with a fairly steady decrease as luminance contrast increased in both directions (Fig. 6b). If pointing accuracy was particularly sensitive to the natural variation in individual isoluminant points it should have resulted in elevated position error around some optimal isoluminant point for a given observer. This was not the case.

Experiment 2 (Saccades)

To ensure this experiment was comparable to the previous, the visual presentation was identical to Experiment 1A (i.e., 100 ms target duration and 10% catch trials) except that the task involved eye movements only.
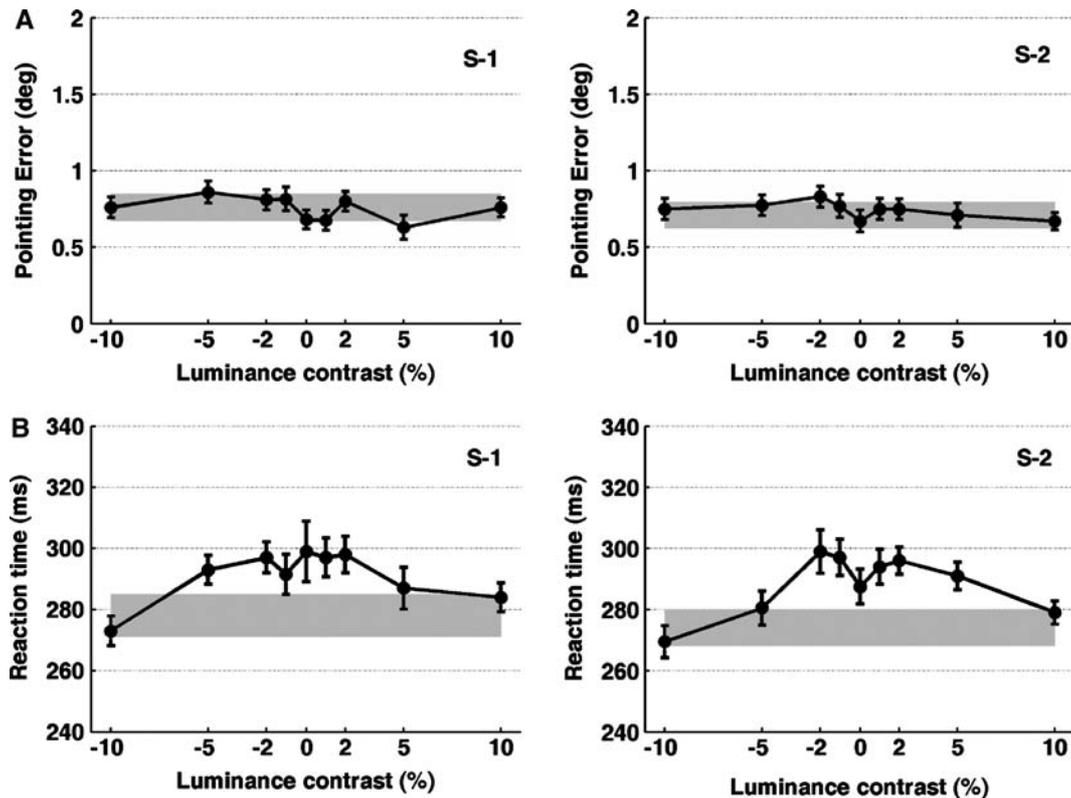
Fig. 6 Contribution of individual variation in isoluminance (pointing). The plots show pointing error (**a**), and reaction time (**b**) to color targets as a function of luminance contrast for two observers (Exp. 1E): Color saturation was held constant at 80% of the maximum possible on our equipment, while luminance contrast was varied. The *shaded area* represents the 95% confidence interval for the mean of the highest contrast end-points ($\pm 10\%$)

Observers were simply requested to look to the target when it appeared. No outlier procedure was used, but we removed trials where the saccadic landing positions were less than 50% accurate (i.e., where position error > half the target eccentricity). Since saccades are ballistic movements, we should see similar results with an extended target duration and without catch trials, so Experiment 1B was designed to test this. Target duration was 500 ms, and a target appeared on every trial.

Results and discussion

Misses and false alarms

The proportion of misses (0.057) and false alarms (0.1) was again reasonably low indicating that that targets were visible, and that observers were responding selectively to the target and not the fixation offset. As with Experiment 1, the majority of misses came from three observers, and only for the most eccentric R–G targets, which again may be due to the fact that these targets necessarily had lower cone contrast (see Footnote 1). As with pointing, the correlation between number of misses and saccadic error for the most eccentric R–G targets was also not significant ($r = -0.28$, $P = 0.4$, $n = 10$). Thus, while these targets may have been less visible for some, this result suggests that if observers could detect the tar-

get, they could also accurately shift their gaze to its location.

The use of catch trials for saccades might seem problematic: e.g., on target absent trials, once the fixation spot is removed, maintaining fixation on an empty gray field might seem difficult. If this were true, there should be a greater proportion of false alarms for saccades than pointing in Experiment 1. This was however not the case: the mean proportion of false alarms for pointing (0.08, Experiment 1A) was not significantly different from false alarms for saccades (0.1, Experiment 2A), $t(18) = -0.7$, $P > 0.05$. In a similar way, saccades might have occurred when the target was in fact undetected, but would appear as a valid response (resulting in a lower miss rate). However the proportion of misses was very low (0.02), and was not different from the previous pointing experiment (0.03), $t(18) = 0.6$, $P > 0.05$, indicating that observers only responded to the target when they saw it.

Accuracy

Figure 7 shows saccadic error for each of the targets as indicated by the color of the lines. The length of the lines reflects the Euclidean distance of the end point of the first-saccade from the target. As with pointing, there was no obvious difference between targets defined by either

Fig. 7 Saccadic error for each target color, at each eccentricity (Exp. 2A) (raw data from all observers combined): The length of the lines represents the distance of the touch point from the target location. As mentioned in the methods, this only includes trials without anticipatory responses (Saccade latencies > 80 ms excluded). Catch trials and trials where saccadic error was more than half the target eccentricity were also removed

Saccadic Error (raw data)
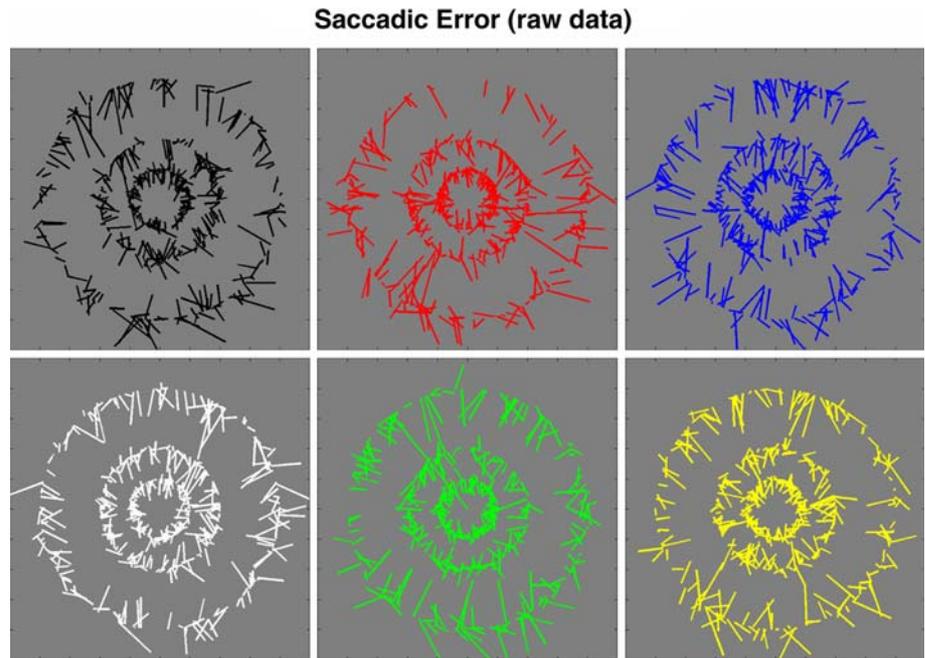
luminance or color, except for an overall increase in error with eccentricity (see Fig. 8). The solid lines in Fig. 8 show the primary task which was identical to Experiment 1A except the task involved a saccadic response (i.e., 100 ms target, 10% catch trials). The dotted lines are the results with an extended target duration of 500 ms and no catch trials (Experiment 2B; error bars not included for clarity). As can be seen, the pattern is nearly identical except for slightly better accuracy with longer duration targets (Exp. 2B). We ran a mixed ANOVA with task (Primary versus extended target duration) as a between subjects factor, and color (Lum, R–G and B–Y) and eccentricity (3, 6 and 12°) as within

subjects factors. As with pointing, saccadic error also increased with eccentricity, $F(2, 36) = 187$, $P < 0.001$. Thus while target duration may play a role in the accuracy of saccades overall, color signals are used as efficiently as luminance in guiding the eyes. The results mirror that of the pointing task. In fact, when we plot pointing error along side saccadic error (Fig. 9) the lines fall nearly on top of one another.
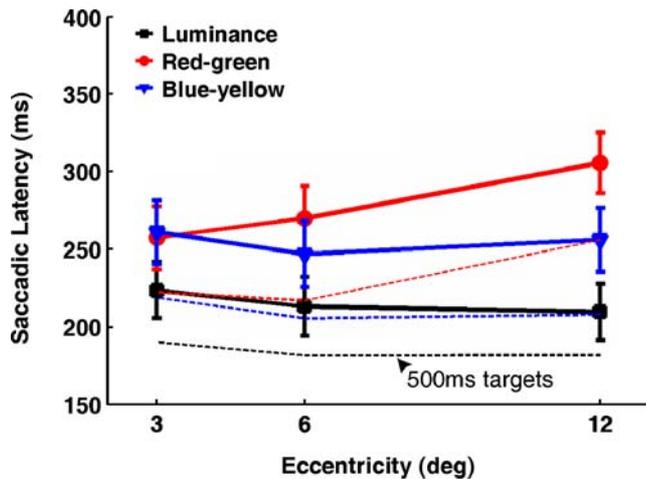
Latency

Figure 10 shows saccadic latency as a function of target condition and eccentricity. The dotted lines repre-
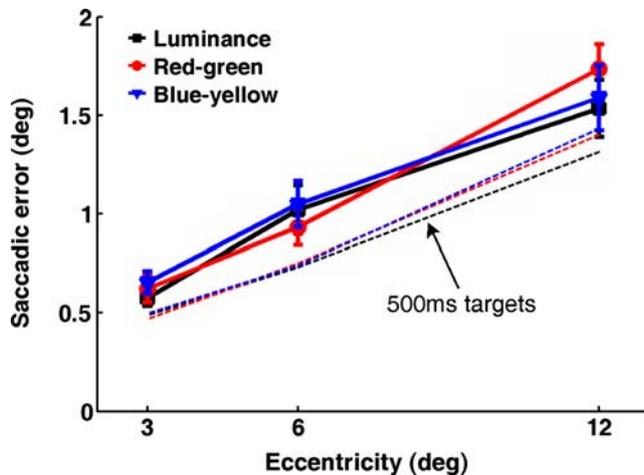
Fig. 8 Mean saccadic error for color and luminance targets across eccentricity (Exp. 2A, *solid lines*): the *dotted lines* represent saccadic error for targets with an extended duration of 500 ms, and without catch trials (Exp. 2B). *Error bars* represent ±1 standard error
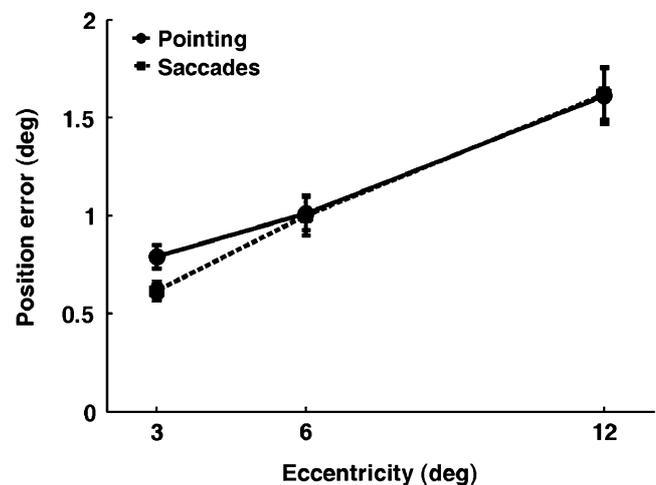

Fig. 9 Comparison between pointing error (Exp. 1A) and saccadic error (Exp. 2A), collapsed across target-color condition. *Error bars* represent ±1 standard error

Fig. 10 Mean saccadic latency for color and luminance targets across eccentricity (Exp. 2A, *solid lines*): The *dotted lines* represent saccade latencies for targets with an extended duration of 500 ms, and without catch trials (Exp. 2B). *Error bars* represent ±1 standard error

Fig. 11 Mean saccadic latency for color and luminance targets as a function of RMS cone contrast (Exp. 2C). *Error bars* represent ±1 standard error

sent the condition with the extended target duration (500 ms), and without catch trials. Note the similarity to the pattern of manual RTs in the previous experiment (Fig. 4). As with Experiment 1, we found a significant color × eccentricity interaction, $F(4, 72) = 46$, $P < 0.001$. In addition, the pattern for the longer duration targets mirrored that of the flashed targets, except that latencies were shorter overall (the effect of target-duration condition approached significance, $F(1, 18) = 3.4$, $P = 0.08$). The color × eccentricity interaction was again the result of increasing saccade latencies for R–G targets across eccentricity. The difference between R–G and B–Y targets increased with eccentricity, $F(2, 38) = 54$, $P < 0.01$, whereas the difference between B–Y and luminance targets remained even across eccentricity, $F(2, 38) = 2.8$, $P > 0.05$ (with Bonferroni correction).

We also compared saccade latency between luminance and color (R–G only) targets of equal cone contrast (Exp. 2C). As can be seen from Fig. 11, the results are very similar to manual reaction times (Fig. 5), showing virtually no difference between luminance and color targets at points of equal cone contrast. We ran a two-way (contrast × target-color) repeated measures ANOVA on the data from the 5–10% contrast points to test whether saccade latency differed between luminance and color targets. The ANOVA revealed a significant effect of contrast only ($F(3, 12) = 14.40$, $P < 0.05$). The effect of target-color was not significant ($F(1, 12) < 1$, $P > 0.05$). That is, there was no difference in saccade latency between luminant and isoluminant stimuli matched in terms of cone contrast. This result differs from some previous work that has reported longer saccade latencies for isoluminant stimuli (van Asten et al. 1988; Perron and Hallett 1995; Satgunam and Fogt 2005). We will return to this issue in the general discussion.
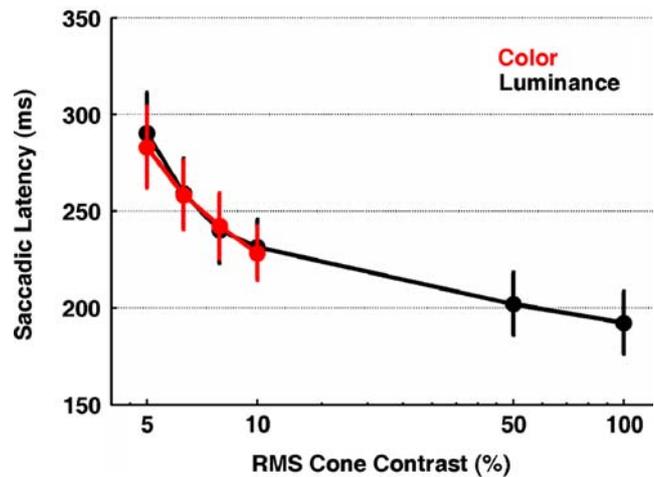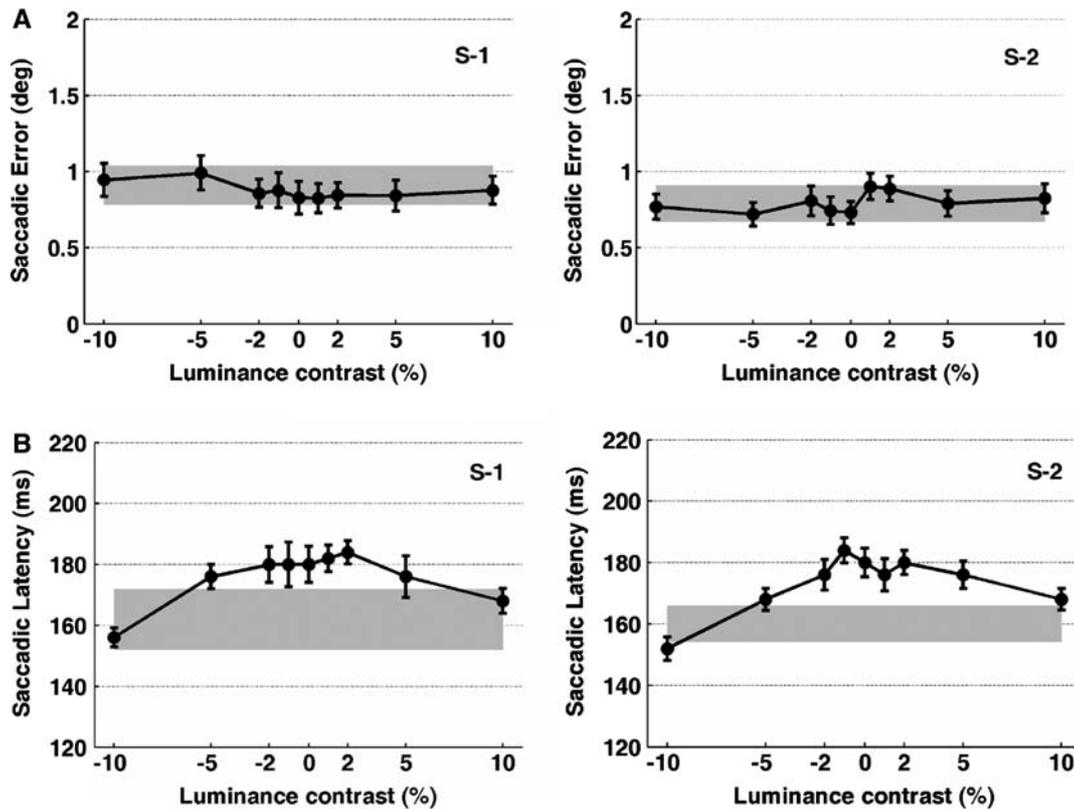
Effect of individual variation in isoluminance (saccades)

As with pointing (see Fig. 6), we also varied the luminance contrast of the color targets for the saccade task (Exp. 2D) to determine the degree to which variations in individual isoluminance might have contributed to these results. Figure 12 shows the results from the two observers. The shaded area represents the 95% confidence interval for mean of the two highest contrast end-points (±10%). As can be seen, there was very little deviation from this in terms of saccadic error (Fig. 12a). An ANOVA revealed a non-significant difference across contrast for both observers [$F(8, 577) = 0.61$ for S-1 and $F(8, 623) = 0.69$ for S-2, $P > 0.05$ in both cases]. Furthermore, the latency profiles were centered around 0 for both observers, showing a fairly steady decrease as luminance contrast increased in either direction (Fig. 12b). If saccadic error was particularly sensitive to the natural variation in individual isoluminant points it should have resulted in elevated position error around some optimal isoluminant point for a given observer. As with pointing, this was not the case.

Experiment 3 (pointing versus color-naming)

The results of the previous two experiments could be due to the ability of the dorsal stream to exploit the natural variation in individual cells' luminance balance (Gegenfurtner et al. 1994), thereby responding to the isoluminant component of a stimulus without necessarily having access to information about the color itself. If this is the case, we should see a difference between pointing accuracy and color-naming performance, because only the latter requires discrimination of the color itself. Similar performance, however, would suggest that the same signals are used in both tasks.

Fig. 12 Contribution of individual variation in isoluminance (saccades). The plots show saccadic error (**a**) and saccade latency (**b**) to color targets as a function of luminance contrast for two observers (Exp. 2D): Color saturation was held constant at 80% of the maximum possible on our equipment, while luminance contrast was varied. The *shaded area* represents the 95% confidence interval for the mean of the highest contrast end-points (±10%)

We used a dual task procedure in which observers had to first point to the target, and then immediately name its color by pressing the appropriate key (see Fig. 1, bottom). Targets were presented at a single eccentricity (6°), randomly around an imaginary circle. Target contrast was varied. As described earlier, in order to compare pointing to color-naming (% correct color), the screen was later divided into four equal sectors depicted in Fig. 1 (bottom), defining the four alternatives in terms of pointing (% correct quadrant).

Results and discussion

Figure 13 shows the psychometric functions relating pointing to color-naming for two observers. Note that the *x*-axis represents relative contrast. At 100%, R–G targets were approximately equal to 10% cone contrast, and B–Y targets were approximately equal to 86% s-cone contrast. Because the R–G channel is inherently more sensitive, all targets were of approximately equal visibility at points of equal relative contrast. This was verified by the fact that the functions for the separate target colors were the same. Therefore, we collapsed the data across target color.

As can be seen, the functions relating pointing to color-naming were essentially identical for both observers. This is remarkable given the difference between these two tasks. This result suggests the dorsal stream not only responds to the isoluminant component, but can discriminate the color itself, which is consistent with neurophysiological data from area LIP (Toth and Assad 2002).

Figure 14 shows a plot of the pointing positions relative to the targets at four different contrasts (data from both observers combined). The length of the lines represents the Euclidean distance of the finger's landing position from the target location, and the color of the line represents whether the psychophysical judgment was correct (blue) or not (red). It can be seen that when the target's color is correctly identified (blue lines), the lines are generally shorter, whereas with incorrect judgments of target-color (red lines), the lines are more often longer. The correlation between naming errors and pointing error (line length) was highly significant ($r = 0.58$, $P < 0.001$, $n = 597$; see Fig. 15). This result is essentially the same pattern reflected in the psychometric functions. Basically, if observers were able to name the color of the target, they could accurately point to its location as well. This suggests that the signals driving the perception of the target's color may be the same as those used to guide pointing.
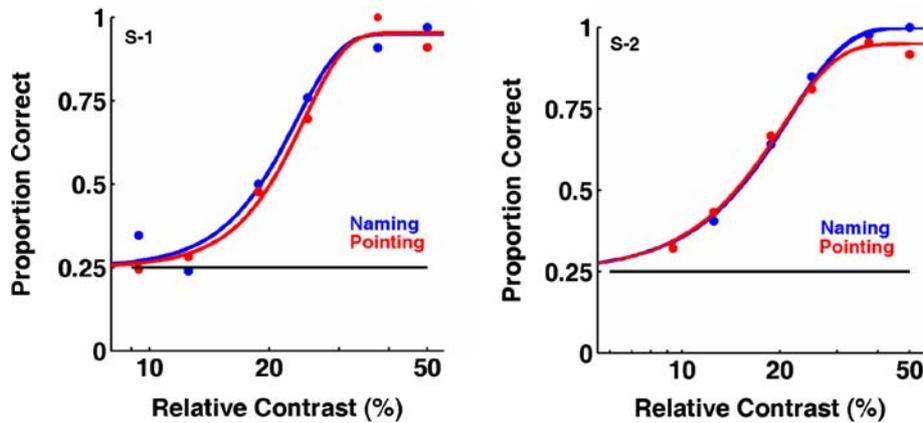
Fig. 13 Psychometric functions relating pointing accuracy (% correct quadrant) to color-naming accuracy (% correct color), as a function of relative contrast (Exp. 3). Note that at 100% relative contrast, actual cone contrast was approximately 10% for the R–G targets, and 86% S-cone contrast for the B–Y targets. At the same relative contrast, all targets were at nearly equal visibility. This was verified by the fact that the underlying functions for the separate targets colors were the same. Therefore, the data were collapsed across target colors
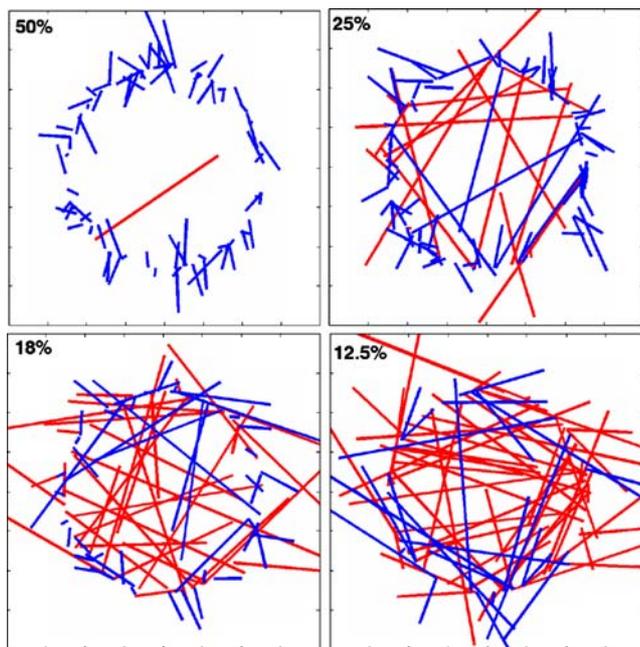
Fig. 14 Pointing error as a function of relative contrast (Exp. 3) (raw data from the two observers combined). The *length of the lines* represents the distance of the touch point from the target location, and the *color of the lines* represents the color-naming response: *blue* correct and *red* incorrect
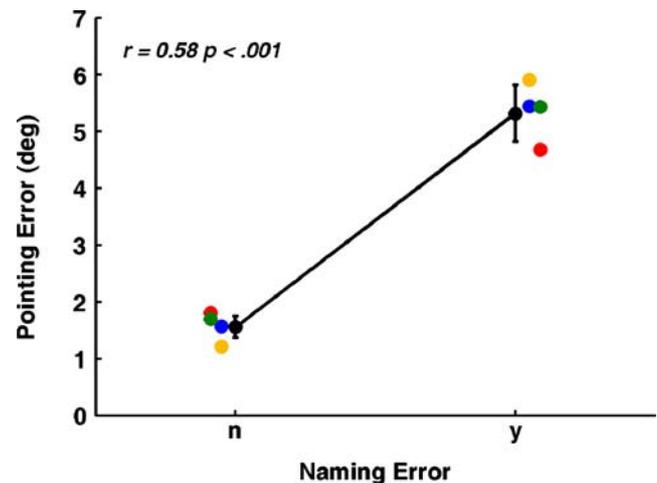
Fig. 15 Mean pointing error (±2 standard errors of the mean) as a function of color-naming errors (Exp. 3) (mean of the separate target colors plotted in color along side). As can be seen, pointing error (degree) was substantially larger when color-naming errors occurred. The correlation between pointing error (degree) and color-naming errors plotted in the upper left

General discussion

Summary of the findings

The question addressed here was to what extent human observers can successfully use pure chromatic signals to guide the eyes and the hand. Both color and luminance can be used to segment objects from backgrounds, which can facilitate recognition memory for natural scenes (Gegenfurtner and Rieger 2000; Wichmann et al. 2002), and help us find a target amongst a field of distractors (D'Zmura 1991; D'Zmura et al. 1997; Olds et al. 1999). So it may not be surprising that color information might be available to guide actions towards such objects. But if the dorsal stream does not have access to color information, we would expect at least some difference in pointing or saccadic accuracy using targets made visible by only a chromatic difference from the background. Studies have suggested that color can influence actions (e.g., Brenner and Smeets 2004; Schmidt 2002), and our results extend these findings: we have found no difference in the accuracy of saccades or rapid pointing movements to targets defined exclusively by luminance or color. The same was

true when we varied the luminance contrast of color targets by small amounts, which makes it unlikely that the results were due to individual variations in isoluminance. Furthermore, observers were able to use these signals under restricted conditions (i.e. flashed targets, restricted movement time of 400 ms, and with shutter-goggles) to guide actions with surprisingly good precision.

The results are also in good agreement with those of Anderson and Yamagishi (2000) showing that both M- and P-type targets can be localized with the same efficiency using manual pointing in a non-speeded task (e.g., they report 1.3° localization accuracy for targets at 10° eccentricity, versus approximately 1.5° accuracy for targets at 12° eccentricity with both speeded pointing and eye movements in our task).

Response latencies also showed an interesting pattern across eccentricity: latencies for both the eye and the hand increased as a function of eccentricity for targets isolating the R–G color opponent channel only. The effect of eccentricity on saccade latency is believed to form a bowl-shaped function, with a sharp increase for near foveal targets ($<0.75°$), and a gradual increase for targets greater than 12° (Kalesnykas and Hallett 1994). Between 0.75 and 12°, latencies remain fairly constant. This is consistent with our data. Our targets were within the range expected to produce a flat function across eccentricity (3–12°), which is what we saw with luminance and B–Y targets. It has also been reported that cone contrast sensitivities for the luminance and B–Y color opponent systems remain constant over a wide range of the visual field (30°), whereas the R–G system shows a steeper decline in sensitivity with eccentricity (Mullen and Kingdom 2002). We believe our data fit this quite well: both eye and hand latencies increased across eccentricity for R–G targets only.

We employed a RT-only control condition to measure the relative contribution of color versus luminance signals to latencies when the computation of target position was not required. If the dorsal stream has little access to color, we might have expected elevated latencies especially for color targets when a goal-directed movement was required. This was not the case: except for an overall increase in latencies when a goal-directed movement was required, the pattern between luminance and color targets for each task was largely the same.

When stimuli were matched in terms of cone contrast on our equipment, we found virtually no difference between luminance and color targets for both manual reaction times (Fig. 5) and saccade latency (Fig. 11). If luminance and color signals are treated in largely different ways (whether dorsal or ventral), it is quite surprising that latencies were nearly identical at points of equal cone contrast, especially given their sensitivity to small variations in contrast as suggested by Figs. 6 and 12. This was also surprising in light of previous studies that report longer latencies for isoluminant stimuli (van Asten et al. 1988; Burr et al. 1998; Perron and Hallett 1995; Satgunam and Fogt 2005; Schwartz 1992). It is important to note that the results of these studies vary a

lot, from a moderate 17–23 ms saccade latency difference for the Asten et al. (1988) study, to a large 93 ms reaction time difference for the Schwartz (1992) study. There are several possible reasons for this variation, one being the method of matching luminance and color stimuli: e.g., using CIELab space (Satgunam and Fogt 2005), presenting targets at some multiple of contrast threshold (van Asten et al. 1988), or matching cone contrast (Burr et al. 1998). This makes a direct comparison to our results difficult. While Burr et al. (1998) used stimuli of matched cone contrast, their stimuli were quite different from ours (i.e., they measured reaction time to motion onset of a drifting grating), and their method allowed a much larger range of cone contrasts.

Finally, the act of pointing versus color-naming provided a useful means of comparing perception and action (Exp. 3). If the results of Experiments 1 and 2 were due to the ability of the dorsal stream to exploit the natural variation in individual cells' luminance balance (Gegenfurtner et al. 1994), and not color selectivity per se, we might expect at least some difference between pointing accuracy and color-naming performance. This is because only the latter required discrimination of the color itself. However the functions were identical: if observers could name the target's color, they could accurately point to its location as well.

Potential routes for visuomotor color signals

We have argued here that the dorsal stream may have access to color signals as suggested by the equally high level of precision of goal-directed movements to targets defined by either luminance or color. As previously noted, dorsal area MT is not entirely blind to color signals (Dobkins and Albright 1994; Gegenfurtner et al. 1994), even though it has little or no color-opponent cells. The cells instead act like poorly calibrated photometers which do respond to photometrically isoluminant stimuli. It is possible that the motor system takes advantage of this fact, but the results of Exp. 3 (Figs. 13, 14 and 15) also suggest that the two systems might share the same signals.

In terms of saccades, visually responsive neurons in the superior colliculus (SC), frontal eye fields (FEF) and lateral intraparietal area (LIP) are not believed to be selective for visual features such as color (Bruce and Goldberg 1985; Colby and Duhamel 1996; Robinson and McClurkin 1989). There is however a rich network of direct and indirect connections between these areas and striate and extrastriate areas (e.g, see Bruce et al. 2004; Sommer and Wurtz 2004 for reviews), which provide several possible routes for access to color signals. Furthermore, selectivity for a certain visual feature in parietal cortex may sometimes depend upon whether the visual feature (e.g., color) is relevant for the task, as was the case for area LIP (Toth and Assad 2002).

It is also important to consider the nature of the task in attempting to isolate certain underlying pathways. A good example of this is by Sumner et al. (2002). They

utilized pure S-cone isolating stimuli which are apparently blind to the SC and magnocellular pathway (Sumner et al. 2002). While these stimuli failed to produce a oculomotor distractor effect (Walker et al. 1997), they were quite efficient at producing an attentional cueing effect (Posner 1980). This suggests that the colliculus may not be a candidate for the effects we have shown here (at least in terms of our S-cone isolating targets). However, it may depend on the nature of the task, since the remote distractor effect has been suggested to be related to direct retinal inputs to the SC (Walker et al. 1997). Furthermore, the presence of two completing stimuli (target and distractor) presumably involves higher level decision processes, perhaps involving more frontal cortical areas. We have tried to keep the task as simple as possible in an effort to limit interpretations to what might be considered more typical dorsal- and ventral-type processing.

One could argue however that ventral mechanisms might detect and code the coordinates of both color and luminance signals (from early retinotopic areas such as V1 or V2), and then pass these coordinates on to the dorsal stream to perform the movement. This is an intriguing possibility, which is in line with the fact that the signals from the magno, parvo, and konio pathways begin to mix in as early as V1 (see Sincich and Horton 2005 for review). This is also consistent with our results, especially Exp. 3 which suggests that the mechanisms driving the perception of the target's color may share signals with the mechanisms guiding motor behavior. However, spatial coding is believed to be a defining characteristic of the dorsal processing stream (Ungerleider and Mishkin 1982), whereas color selectivity is believed to be inherently ventral. We have simply tried to demonstrate here that while this dichotomy exists, the mechanisms controlling actions can nonetheless very efficiently make use of pure chromatic signals. It nonetheless remains to be seen whether this efficiency is strictly due to the dorsal stream processing color signals per se, or whether motor areas make use of the spatial coordinates of this attribute, which may be computed elsewhere via recurrent connections between ventral areas highly selective for color (e.g., V4) and earlier retinotopic areas.

Conclusion

While color processing from the retina to the cortex is reasonably well understood, much less is known about the nature of color in the cortex (Gegenfurtner 2003). It has been thought of as a specific attribute that is processed independently of form and motion, and used only by the ventral stream to facilitate perception (Livingstone and Hubel 1988). It is now believed that cortical color processing does not occur in an isolated area, but is in fact an attribute of neurons in several areas (Gegenfurtner 2003). The signals from the magno, parvo, and konio channels begin to combine in V1 (see Sincich and Horton 2005 for review), so it is quite possible that the dorsal stream takes advantage of these combined signals. Taken together, our results show that human observers can efficiently use chromatic signals across a wide range of the visual field to accurately guide the eyes and the hand.

Footnotes

Footnote 1

The maximum cone contrast physically possible using isoluminant R–G stimuli is necessarily constrained by the overlap in spectral sensitivities of the L- and M-cones. It amounts to approximately 15% for the L-cones and 34% for M-cones (Gegenfurtner et al. 1994). This is further constrained by the limitations of CRT monitors. On our equipment, R–G stimuli at maximum saturation resulted in cone contrasts of approximately 7% for the L-cones, and 12% for the M-cones. The root-mean-squared (RMS) cone contrast of the L- and M-cones is calculated by the following: $[((\Delta L/L)^2 + (\Delta M/M)^2)/2)]^{1/2}$, where L and M are the average cone excitations, and ΔL and ΔM are the differences between the peak and the average excitations (Gegenfurtner and Hawken 1996). At maximum saturation, RMS cone contrast was about 10% for R–G targets on our equipment. For the primary experiments comparing accuracies, we did not equate targets in terms of cone contrast, but chose the maximum contrast/saturation as a more conservative alternative. If accuracies are no better for luminance than color targets, it furthers supports our claim that the dorsal stream can efficiently use chromatic signals to guide actions. In a subsequent experiment we did match the cone contrast of luminance and color targets.

Footnote 2

While observers performed Exp. 1A reasonably well with peripheral vision (since few observers made eye movements), central vision should nonetheless better guide the hand to a desired location (Admiraal et al. 2003). When observers were explicitly asked to make a saccade during this procedure, this is what we find: average pointing error is significantly lower when observers made saccades (0.9°) versus when they did not (1.2°), $t(14) = 2.4$, $P < 0.05$.

References

Admiraal MA, Keijsers NL, Gielen CC (2003) Interaction between gaze and pointing toward remembered visual targets. J Neurophysiol 90(4):2136–2148

Anderson SJ, Yamagishi N (2000) Spatial localization of colour and luminance stimuli in human peripheral vision. Vision Res 40(7):759–771

Barbur JL, Wolf J, Lennie P (1998) Visual processing levels revealed by response latencies to changes in different visual attributes. Proc Biol Sci 265(1412):2321–2325

Brenner E, Smeets JB (2004) Colour vision can contribute to fast corrections of arm movements. Exp Brain Res 158(3):302–307

Bruce CJ, Friedman HR, Kraus MS, Stanton GB (2004) The primate frontal eye field. In: Chalupa LM, Werner JS (eds) The visual neurosciences (Vol. 2) MIT, Cambridge, MA

Bruce CJ, Goldberg ME (1985) Primate frontal eye fields I: single neurons discharging before saccades. J Neurophysiol 53:603–635

Burr DC, Fiorentini A, Morrone C (1998) Reaction time to motion onset of luminance and chromatic gratings is determined by perceived speed. Vision Res 38(23):3681–3690

Cavanagh P, MacLeod DI, Anstis SM (1987) Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. J Opt Soc Am A 4(8):1428–1438

Chaparro A, Stromeyer CF 3rd, Huang EP, Kronauer RE, Eskew RT Jr (1993) Colour is what the eye sees best. Nature 361(6410):348–350

Charles ER, Logothetis N (1989) The responses of middle temporal (MT) neurons to isoluminant stimuli. Invest Opthalmol Vis Sci 30:427

Colby CL, Duhamel JR (1996) Spatial representations for action in parietal cortex. Brain Res Cogn Brain Res 5(1–2):105–115

Cressman EK, Franks IM, Enns JT, Chua R (2005) No automatic pilot for visually guided aiming based on colour. Exp Brain Res 171(2):174–183

Derrington AM, Krauskopf J, Lennie P (1984) Chromatic mechanisms in lateral geniculate nucleus of macaque. J Physiol 357:241–265

Dobkins KR, Albright TD (1994) What happens if it changes color when it moves?: the nature of chromatic input to macaque visual area MT. J Neurosci 14(8):4854–4870

Dominy NJ, Lucas PW (2001) Ecological importance of trichromatic vision to primates. Nature 410(6826):363–366

D'Zmura M (1991) Color in visual search. Vision Res 31(6):951–966

D'Zmura M, Lennie P, Tiana C (1997) Color search and visual field segregation. Percept Psychophys 59(3):381–388

Gegenfurtner KR (2003) Cortical mechanisms of colour vision. Nat Rev Neurosci 4(7):563–572

Gegenfurtner KR, Hawken MJ (1996) Interaction of motion and color in the visual pathways. Trends Neurosci 19(9):394–401

Gegenfurtner KR, Kiper DC, Beusmans JM, Carandini M, Zaidi Q, Movshon JA (1994) Chromatic properties of neurons in macaque MT. Vis Neurosci 11(3):455–466

Gegenfurtner KR, Rieger J (2000) Sensory and cognitive contributions of color to the recognition of natural scenes. Curr Biol 10(13):805–808

Jacobs GH (1993) The distribution and nature of colour vision among the mammals. Biol Rev Camb Philos Soc 68(3):413–471

Johnson EN, Hawken MJ, Shapley R (2001) The spatial transformation of color in the primary visual cortex of the macaque monkey. Nat Neurosci 4(4):409–416

Judd DB (1951) Report of U.S. Secretariat Committee on Colorimetry and Artificial Daylight. Paper presented at the Twelfth Session of the CIE, Stockholm

Kalesnykas RP, Hallett PE (1994) Retinal eccentricity and the latency of eye saccades. Vision Res 34(4):517–531

Kaplan E, Lee BB, Shapley R (1990) New views of primate retinal function. In: Osborne N, Chader G (eds) Progress in retinal research, Vol 9. Pergamon, Oxford, pp 273–336

Krauskopf J, Williams DR, Heeley DW (1982) Cardinal directions of color space. Vision Res 22(9):1123–1131

Livingstone M, Hubel D (1988) Segregation of form, color, movement, and depth: anatomy, physiology, and perception. Science 240(4853):740–749

Maunsell JH, Ghose GM, Assad JA, McAdams CJ, Boudreau CE, Noerager BD (1999) Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. Vis Neurosci 16(1):1–14

Maunsell JH, Gibson JR (1992) Visual response latencies in striate cortex of the macaque monkey. J Neurophysiol 68(4):1332–1344

Maunsell JH, Nealey TA, DePriest DD (1990) Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. J Neurosci 10(10):3323–3334

Merigan WH, Byrne CE, Maunsell JH (1991) Does primate motion perception depend on the magnocellular pathway? J Neurosci 11(11):3422–3429

Merigan WH, Maunsell JH (1993) How parallel are the primate visual pathways? Annu Rev Neurosci 16:369–402

Mollon JD (1989) "Tho' she kneel'd in that place where they grew..." The uses and origins of primate colour vision. J Exp Biol 146:21–38

Mullen KT, Kingdom FA (2002) Differential distributions of red–green and blue–yellow cone opponency across the visual field. Vis Neurosci 19(1):109–118

Nowak LG, Munk MH, Girard P, Bullier J (1995) Visual latencies in areas V1 and V2 of the macaque monkey. Vis Neurosci 12(2):371–384

Olds ES, Cowan WB, Jolicoeur P (1999) Stimulus-determined discrimination mechanisms for color search. Percept Psychophys 61(6):1038–1045

Perron C, Hallett PE (1995) Saccades to large coloured targets stepping in open fields. Vision Res 35(2):263–274

Posner MI (1980) Orienting of attention. Q J Exp Psychol 32(1):3–25

Robinson DL, McClurkin JW (1989) The visual superior colliculus and pulvinar. Rev Oculomot Res 3:337–360

Saito H, Tanaka K, Isono H, Yasuda M, Mikami A (1989) Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. Exp Brain Res 75(1):1–14

Satgunam P, Fogt N (2005) Saccadic latencies for achromatic and chromatic targets. Vision Res 45(27):3356–3364

Schiller PH, Logothetis NK, Charles ER (1990) Role of the color-opponent and broad-band channels in vision. Vis Neurosci 5(4):321–346

Schiller PH, Malpeli JG (1978) Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. J Neurophysiol 41(3):788–797

Schmidt T (2002) The finger in flight: real-time motor control by visually masked color stimuli. Psychol Sci 13(2):112–118

Schmolesky MT, Wang Y, Hanes DP, Thompson KG, Leutgeb S, Schall JD et al (1998) Signal timing across the macaque visual system. J Neurophysiol 79(6):3272–3278

Schwartz SH (1992) Reaction time distributions and their relationship to the transient/sustained nature of the neural discharge. Vision Res 32(11):2087–2092

Sincich LC, Horton JC (2005) The circuitry of V1 and V2: integration of color, form, and motion. Annu Rev Neurosci 28:303–326

Sommer MA, Wurtz RH (2004) The dialogue between cerebral cortex and superior colliculus: implications for saccadic target selection and corollary discharge. In: Chalupa LM, Werner JS (eds) The visual neurosciences, Vol 2. MIT, Cambridge

Sumner P, Adamjee T, Mollon JD (2002) Signals invisible to the collicular and magnocellular pathways can capture visual attention. Curr Biol 12(15):1312–1316

Toth LJ, Assad JA (2002) Dynamic coding of behaviourally relevant stimuli in parietal cortex. Nature 415(6868):165–168

Ungerleider JT, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Mansfield RJW, Goodale MS (eds) The analysis of visual behaviour. MIT, Cambridge pp 549–586

van Asten WN, Gielen CC, de Winkel ME (1988) The effect of isoluminant and isochromatic stimuli on latency and amplitude of saccades. Vision Res 28(7):827–840

Walker R, Deubel H, Schneider WX, Findlay JM (1997) Effect of remote distractors on saccade programming: evidence for an extended fixation zone. J Neurophysiol 78(2):1108–1119

Webster MA, Mollon JD (1993) Contrast adaptation dissociates different measures of luminous efficiency. J Opt Soc Am A 10(6):1332–1340

Wenban-Smith MG, Findlay JM (1991) Express saccades: is there a separate population in humans? Exp Brain Res 87(1):218–222

Wichmann FA, Hill NJ (2001a) The psychometric function: I. Fitting, sampling, and goodness of fit. Percept Psychophys 63(8):1293–1313

Wichmann FA, Hill NJ (2001b) The psychometric function: II. Bootstrap-based confidence intervals and sampling. Percept Psychophys 63(8):1314–1329

Wichmann FA, Sharpe LT, Gegenfurtner KR (2002) The contributions of color to recognition memory for natural scenes. J Exp Psychol Learn Mem Cogn 28(3):509–520

Zeki S (1983) The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. Proc R Soc Lond B Biol Sci 217(1209):449–470