

# Competition between color and luminance for target selection in smooth pursuit and saccadic eye movements

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Visual processing of color and luminance for smooth pursuit and saccadic eye movements was investigated using a target selection paradigm. In two experiments, stimuli were varied along the dimensions color and luminance, and selection of the more salient target was compared in pursuit and saccades. Initial pursuit was biased in the direction of the luminance component whereas saccades showed a relative preference for color. An early pursuit response toward luminance was often reversed to color by a later saccade. Observers' perceptual judgments of stimulus salience, obtained in two control experiments, were clearly biased toward luminance. This choice bias in perceptual data implies that the initial short-latency pursuit response agrees with perceptual judgments. In contrast, saccades, which have a longer latency than pursuit, do not seem to follow the perceptual judgment of salience but instead show a stronger relative preference for color. These substantial differences in target selection imply that target selection processes for pursuit and saccadic eye movements use distinctly different weights for color and luminance stimuli.

Keywords: smooth pursuit, saccades, color, luminance, contrast, visual motion, salience, target selection

Citation: Spering, M., Montagnini, A., & Gegenfurtner, K. R. (2008). Competition between color and luminance for target selection in smooth pursuit and saccadic eye movements. *Journal of Vision*, 8(15):16, 1–19, <http://journalofvision.org/8/15/16/>, doi:10.1167/8.15.16.

## Introduction

When viewing a visual scene, we often direct our gaze to the location that appears most salient. The salience or conspicuousness of a location or object is determined by the presence of local features (e.g., color or orientation) and their perceptual weight relative to each other and relative to the visual context (Nothdurft, 1992, 2000). The salience of an object in a visual scene can be represented in a bottom-up salience map in primary visual cortex (Itti & Koch, 2001; Li, 2002). This information has to be extracted from the salience map to drive the selection of a visual target by actual motor behavior such as eye movements. Accordingly, characteristics of a visual salience map have been found in visual motor areas related to eye movement control, for example in the frontal eye fields (FEF; Thompson & Bichot, 2005; Thompson, Bichot, & Sato, 2005), and lateral intraparietal area (LIP; Goldberg, Bisley, Powell, & Gottlieb, 2006). Here, we ask whether there is a single salience map for perception and for different types of oculomotor behavior, by which a target can be selected.

## Evidence for similarity in smooth pursuit and saccadic eye movements

The present study focuses on the comparison of visual processing of color and luminance information for the selection of a visual object of interest in two different types of eye movements. In everyday situations, a combination of smooth pursuit and saccadic eye movements is used to select and track a moving visual object. Pursuit and saccades are voluntary, goal-directed movements that serve to bring a visual object of interest close to the fovea. Although the two types of movement differ in timing and kinematics, pursuit and saccades share many response properties on the behavioral and neuronal level (Krauzlis, 2004, 2005).

The interaction between pursuit and saccades starts on the level of the visual input. Saccades are mainly guided by position signals, whereas pursuit mostly relies on velocity signals. But there is also evidence for velocity input to the saccadic system for the control of catch-up saccades during pursuit (Blohm, Missal, & Lefèvre, 2005a; de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002), and for position input to the pursuit system (Blohm, Missal, & Lefèvre, 2005b; Missal, Lefèvre,

Delinte, Crommelinck, & Roucoux, 1996). Pursuit and saccades differ substantially in latency. In humans, pursuit is usually initiated at a latency of about 100–150 ms, whereas saccades take considerably longer, about 200–250 ms (Krauzlis, 2004; Rashbass, 1961). However, the time to movement onset can be influenced in the same way and to the same extent by task and visual stimulus used. Pursuit and saccade latencies are reduced by a gap between fixation-point offset and target onset to a similar degree (gap paradigm; Krauzlis & Miles, 1996a, 1996b). When the target appears before the disappearance of the fixation point, pursuit latency is prolonged and pursuit and saccadic latencies are highly correlated (overlap paradigm; Erkelens, 2006). Pursuit and saccade tracking are also similarly influenced by visual spatial attention (Adler, Bala, & Krauzlis, 2002; Krauzlis, Zivotofsky, & Miles, 1999; Madelain, Krauzlis, & Wallman, 2005). Furthermore, pursuit and saccades are tightly coupled with regard to the selection of a visual target (Gardner & Lisberger, 2001; Liston & Krauzlis, 2003, 2005) and share processing at the level of response preparation (Joiner & Shelhamer, 2006). Evidence from neurophysiological studies in monkeys and functional imaging studies in humans supports these behavioral similarities in visual processing, target selection, and response preparation. Pursuit and saccades are processed in parallel cortical pathways. They share processing in premotor and motor areas (e.g., Dicke, Barash, Ilg, & Thier, 2004; Gardner & Lisberger, 2002; Keller & Missal, 2003; Krauzlis & Dill, 2002; Krauzlis & Miles, 1996b; Missal & Keller, 2002; for reviews, see Krauzlis, 2004, 2005) but are controlled by distinct subregions (Petit & Haxby, 1999; Rosano et al., 2002).

The resemblance between pursuit and saccadic eye movements has been taken to imply that both types of movement are merely different motor outcomes of a common visuomotor processing stage (Joiner & Shelhamer, 2006; Krauzlis, 2004), and that the same visual signals drive target selection in pursuit and saccades (Liston & Krauzlis, 2005). However, there are profound differences between pursuit and saccades with regard to the visual input. The saccadic system is largely driven by position signals. Although position-error signals certainly play a role in pursuit control, the pursuit system critically depends on visual motion signals (Beutter & Stone, 1998; Madelain & Krauzlis, 2003; Masson & Stone, 2002; Steinbach, 1976; Thier & Ilg, 2005).

## Processing of color and luminance information for pursuit and saccades

In the primate brain, visual motion information is primarily processed in a cortical brain area in the medial temporal sulcus: the middle temporal cortex (MT). Neurons in area MT have large receptive fields and are selective for the direction of visual motion (Born & Bradley, 2005). Activity in area MT is closely related to the

perception of visual motion and to the control of smooth pursuit eye movements (Newsome, Wurtz, Dürsteler, Mikami, 1985). Generally, it is assumed that cortical processing of visual information is obtained in distinct, parallel visual pathways from retina to primary visual cortex (V1). In their classic, simplified parallel processing model, Livingstone and Hubel (1988) assume two pathways—a “motion pathway” that is controlled by input from magnocellular layers of the lateral geniculate nucleus (LGN) and a “color and form pathway” that is dominated by input from parvocellular layers of the LGN (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Ungerleider & Mishkin, 1982). Area MT is part of the “motion pathway” and receives most of its inputs from V1 layer 4B. The response properties of MT neurons indicate that this input is largely magnocellular: MT neurons are highly sensitive to contrast, respond at short latencies, and lack color preference (Maunsell & van Essen, 1983; Zeki, 1974).

In line with physiological data, behavioral studies reported that visual attributes, such as color and luminance contrast, are processed differently for the detection of a visual stimulus and the discrimination of its motion direction (Cavanagh & Anstis, 1991; Cavanagh, Tyler, & Favreau, 1984), especially at low stimulus speed (Gegenfurtner & Hawken, 1995, 1996; Hawken, Gegenfurtner, & Tang, 1994). It is now beyond dispute that motion perception of isoluminant chromatic targets is possible and that, maybe due to interaction between the two visual pathways and due to minor parvocellular inputs to area MT (Maunsell, Nealey, & DePriest, 1990), the motion pathway is not completely color blind (Gegenfurtner et al., 1994; Saito, Tanaka, Isono, Yasuda, & Mikami, 1989). However, there are differences in the mechanisms for processing motion information from chromatic and luminance targets. Krauskopf and Li (1999) have suggested that the mechanism responsible for motion perception of chromatic stimuli is based on the assessment of relative target position, whereas motion perception in luminance stimuli is based on relative target motion or retinal image motion (see also Seiffert & Cavanagh, 1999). Eye movement studies support these assumptions. Pursuit latency to isoluminant targets is delayed by about 50 ms in comparison with luminance targets (Braun et al., 2008). No such impairment for color processing was found for saccades (White, Kerzel, & Gegenfurtner, 2006). Based on these facts, it cannot generally be assumed that the same visual signals are used to drive smooth pursuit and saccadic eye movements, in particular when visual targets vary in chromatic and luminance properties, which might be processed differently in the brain.

## Aims of the present study

We compared visual processing of color and luminance information for target selection in pursuit and saccades. Understanding how pursuit and saccades select one of two

potential targets can reveal the mechanisms by which the two oculomotor systems are coordinated. We studied pursuit and saccadic eye movements separately in a paradigm in which a moving stimulus split into a color-defined and a luminance-defined component. After the split, the stimuli either moved smoothly into different diagonal directions, requiring a pursuit response, or stepped to two different peripheral locations, requiring a saccade. Observers were instructed to choose the more salient of the two stimuli by making an eye movement. We also tested observers' perceptual judgments of salience and asked which of the two stimuli was perceived as more conspicuous.

Based on what is known about differences in processing color and luminance in stationary and moving stimuli, this study can reveal differences between pursuit and saccades in their preference for physical stimulus properties. A systematic comparison between perceptual and motor responses to color and luminance stimuli will also allow examining the assumed close relationship between perceptual salience and eye movements.

## Methods

We conducted four experiments. In the first two experiments, we examined pursuit ([Experiment 1](#)) and saccadic eye movements ([Experiment 2](#)) to stimuli differing along the visual dimensions color and luminance. Observers were instructed to choose the stimulus that was more conspicuous (salient). In control experiments, we asked observers to perceptually compare and judge stimulus salience of two moving ([Experiment 3](#)) or stationary ([Experiment 4](#)) stimuli.

### Observers

Six to eight observers from a pool of nine female subjects and one male subject (mean age  $25.9 \pm 3.4$  years) participated in each of the experiments. Eight observers were undergraduate students from the University of Giessen, Germany, and were naive as to the purpose of the experiment. Authors AM and MS participated in the first two experiments. All observers had normal or corrected-to-normal visual acuity. For each of the four experiments, data were collected in 60-minute sessions. Observers completed one or two sessions with a total of two to six blocks of 128 trials per experiment.

### Stimuli and setup

Stimuli were spots with a Gaussian luminance profile ( $SD = 0.3^\circ$ ) that were either defined by color or luminance and were presented on a uniform gray background with

mean luminance of  $32 \text{ cd/m}^2$ . Luminance contrast of the luminance-defined stimuli was varied between  $32.6$  and  $34.6 \text{ cd/m}^2$ , resulting in Weber contrasts of approximately 1 to 8% for the range of luminance contrasts used. Color stimuli were isoluminant to the background, and color saturation was varied along the L–M (“red–green”) isoluminant axis of the DKL color space (Derrington, Krauskopf, & Lennie, 1984). Using corrected color matching functions (Judd, 1951), the CIE chromaticity coordinates ( $x$ ,  $y$ ) of the color stimuli at maximum saturation were 0.343 and 0.297 for red, and 0.226 and 0.348 for green. Chromaticity values of the gray background were 0.289 and 0.321. The maximum modulation in color saturation (100%) corresponds to a 9% root mean squared contrast in the L- and M-cones. Color saturation/contrast in our experiments ranged from 20 to 80%. Color and luminance stimuli were approximately equated for cone contrast in order to grant a similar range of saliency (Gegenfurtner & Hawken, 1996). The setup for stimulus presentation was identical to that described in our previous studies (Spering, Gegenfurtner, & Kerzel, 2006). Briefly, stimuli were presented on a 21-inch CRT monitor with a refresh rate of 100 Hz and a spatial resolution of 1280 (H)  $\times$  1024 (V) pixels. Observers viewed stimuli from a distance of 47 cm in a dimly lit room.

### Procedure and design

Each trial began with a black fixation spot (diameter  $0.15^\circ$ ), presented in the center of the monitor. Observers initiated the trial by pressing a button, and the eye tracking system performed a drift correction for head movements while observers held fixation. The basic paradigm, used in [Experiments 1](#) and [2](#), is depicted in [Figure 1](#). A stimulus appeared to the left or right of fixation and moved horizontally toward the center of the monitor at  $10.6^\circ/\text{s}$ . Observers were instructed to make a saccade to the stimulus once it appeared in the periphery and to smoothly track its motion. Shortly before or after the stimulus crossed the center of the monitor, in a time window of 400–700 ms after stimulus motion onset, the stimulus was split into two components. After the split, the stimulus was presented for 1000 ms. The stimulus before the split was defined by the sum of the two independent properties, color and luminance, of the following stimuli. The two stimulus components after the split differed in luminance and chromatic contrast.

In [Experiment 1](#), the initial horizontally moving stimulus was split into two components that continued to move smoothly into two different diagonal directions,  $45^\circ$  upwards or downwards, at horizontal and vertical velocity components of  $7.5^\circ/\text{s}$ . In [Experiment 2](#), the smoothly moving stimulus was split into two components that stepped to two diagonal positions  $6^\circ$  peripheral from the location of stimulus split. [Experiment 1](#) required a smooth

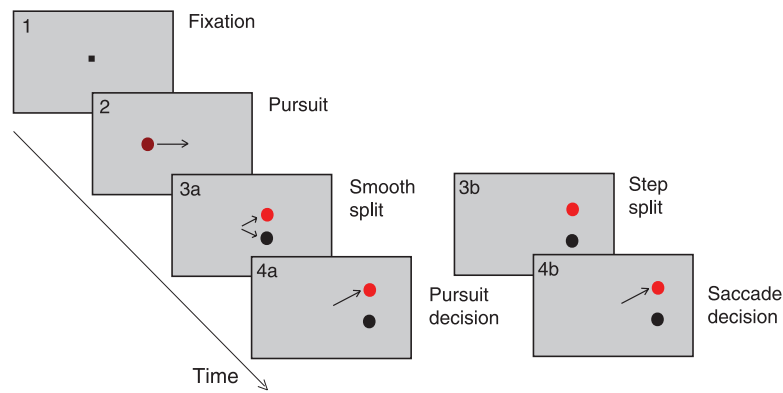


Figure 1. Schematic diagram of a trial sequence in [Experiments 1](#) (left) and [2](#) (right). (1) Fixation and drift correction of the eye tracker. (2) Stimulus appearance to the left or right of fixation. Observers made a saccade to the stimulus and tracked its smooth motion for 400–700 ms. (3) The target split into two new stimuli that either moved diagonally up or down (exp. 1, 3.a) or stepped to two peripheral positions (exp. 2, 3.b). (4) Observers were instructed to pursue (exp. 1, 4.a) or saccade (exp. 2, 4.b) to the more salient of the two stimuli. Stimulus presentation duration after the split was 1000 ms.

pursuit response to one of the two diagonally moving stimuli. [Experiment 2](#) required a saccadic response to one of the two new peripheral stimulus locations. Observers were instructed to choose the more salient stimulus by moving the eyes to that stimulus. To keep visual processing comparable, stimulus presentation in both experiments was identical up to the time of the stimulus split. Weber contrasts of the stimuli were at 2, 4, 6, 8% (luminance) and 20, 40, 60, 80% (color), resulting in 32 conditions (4 luminance  $\times$  4 color contrasts  $\times$  2 directions).

In two control experiments, we used the same visual stimuli as in [Experiments 1](#) and [2](#), and asked observers to judge which stimulus was more salient. [Experiment 3](#) was similar to [Experiment 1](#), except that observers were asked to maintain fixation at the point where the stimuli had split. The purpose of fixation before giving the judgment was to avoid a judgment bias in the direction of the eye movement. In [Experiment 4](#), a stationary target with the same visual properties as the initial target in [Experiments 1](#) and [2](#) was initially presented in the center of the visual display. To control for effects of retinal motion on perceptual judgments, observers were asked to maintain fixation throughout the entire trial. After a random period of fixation the stationary target disappeared and two new stimuli reappeared in the same peripheral locations as in [Experiment 2](#).

## Eye movement recordings and analysis

### Recording of eye movements

Eye position was continuously monitored in all four experiments. Eye movement recording, calibration procedures, and the processing of eye position data followed routines described in our previous studies (Spering et al., 2006; Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005). Eye position signals were recorded with a

head-mounted, video-based eye tracker (EyeLink II, SR Research, Osgoode, Ontario, Canada) and were sampled at 250 Hz. The apparatus was calibrated at the beginning of the experiment and recalibrated after each block of trials. The system automatically chose the eye with the better calibration result (i.e., the lower mean deviation from the calibration points). We then recorded from the chosen eye. In addition to calibration, at the beginning of each trial, the EyeLink II system performed a drift correction to correct for shifts of the head-mounted tracking system. Observers were seated with their heads stabilized with a chin rest, and viewed the display binocularly.

### Velocity filtering

For pursuit analysis, all traces were first aligned to the split of the stimulus. Most of the analysis was based on eye velocity, which was obtained by digital differentiation of eye position signals over time, and filtered using a low-pass filter with a cutoff at 40 Hz.

### Saccade detection

Saccades in the horizontal and vertical eye velocity traces were detected separately and removed from the unfiltered traces. The algorithm for detecting saccade onsets and offsets follows a routine introduced by Wyatt (1998) and was based on the third derivative of eye position over time (jerk). Eye acceleration and jerk were obtained by differentiating unfiltered eye velocity and acceleration, respectively. Four consecutive samples had to exceed a fixed criterion of  $60000^\circ/s^3$  to be counted as saccade samples. We compared this routine to other detection algorithms based on an acceleration criterion only, or a combined velocity and acceleration criterion. All algorithms yielded the same results, with the algorithm

based on jerk detecting some of the very small saccades that were missed by the other routines. All traces were visually inspected. Traces with eye blinks or trials in which the saccade detection algorithm missed a saccade were excluded from further analysis (<1% of all trials in any experiment).

### Pursuit latency

We were interested in timing and direction of target selection after the stimulus split. We analyzed the latency of the pursuit direction change by identifying the onset in the vertical component of the pursuit eye movement after the split (termed “pursuit onset” or “latency” in the following). The algorithm for detecting the onset of the vertical pursuit response was based on the analysis by Carl and Gellman (1987) and has been successfully used in onset detection at velocities higher than  $1^\circ/\text{s}$  (Spering et al., 2005, 2006). Two regression lines were fit to the vertical eye velocity trace within two sliding 80-ms windows with an offset of 80 ms (Figure 2b). The

difference between the slopes of the two regression lines had to exceed a fixed velocity criterion (25% of target velocity) to qualify as smooth pursuit onset. The latency of the pursuit direction change was defined as the intercept of the two sliding regression lines (Figures 2a and 2b). In addition, we introduced a time window for identifying valid latencies to avoid including trials, in which observers made an early decision based on top-down processes. Latencies were considered as valid that occurred more than 60 ms after the stimulus split. To allow for the calculation of pursuit target selection direction, vertical pursuit onsets were only counted as valid if they occurred at least 40 ms before the first saccade. Less than 1% of all trials with a pursuit onset had to be excluded based on these two timing criteria.

### Target selection criteria

In Experiment 1, the pursuit target selection direction (upward or downward) was defined as the sign of the eye velocity in a 40-ms interval after pursuit onset. In

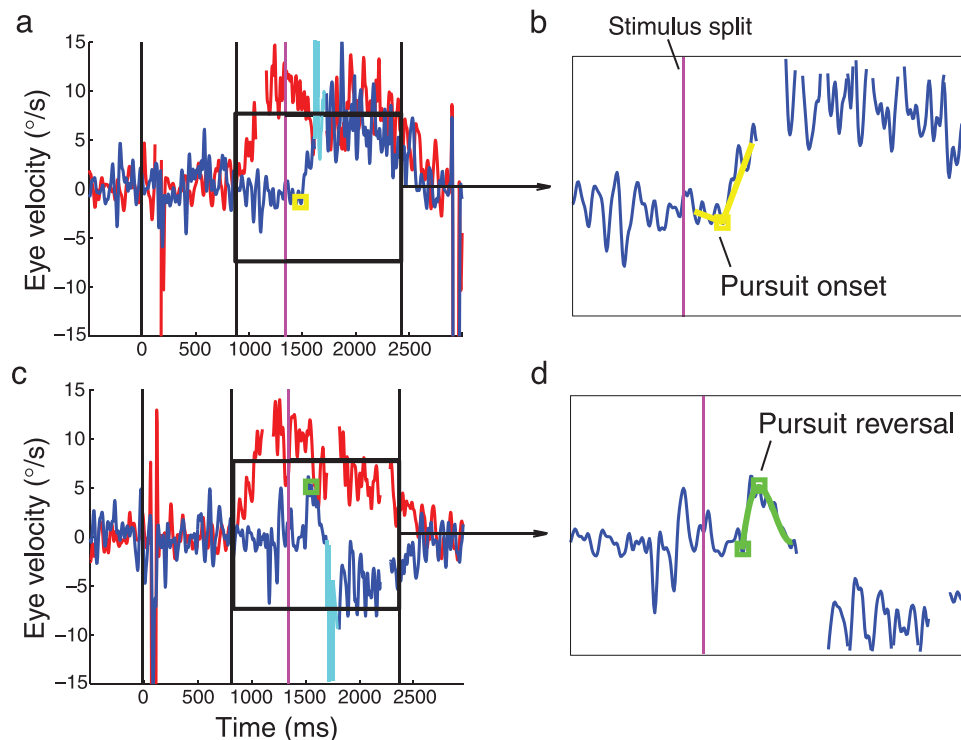


Figure 2. Representative single eye movement traces to an upward luminance and a downward color target in Experiment 1 from observer EB. Horizontal (red) and vertical (blue) filtered eye velocity traces are plotted as a function of time with respect to the beginning of the trial. Gaps in the traces are intervals in which a saccade was removed from the velocity profile. Cyan markings denote initial or first catch-up saccade after split. Black vertical lines denote trial start, target motion onset and offset. Magenta line denotes stimulus split. (a) Pursuit and catch-up saccade to luminance. Yellow square marks pursuit onset. (b) Magnified pursuit trace from (a), motion onset to offset, demonstrates algorithm for detecting pursuit onset. Yellow lines are two sliding regression lines with 80 ms offset, yellow square marks intersection of lines and pursuit onset. (c) Pursuit reversal trial. Pursuit first went to luminance, followed by a smooth reversal to color and a saccade to color. The green square denotes reversal point. (d) Magnified pursuit trace from (c), motion onset to offset, depicts algorithm for detecting pursuit reversal. Green line denotes fit of third-order polynomial (see Liston & Krauzlis, 2003; p. 11307, Fig. 2).



combined with luminance contrast at either 2 (minimum) or 8% (maximum). For each color–luminance stimulus pair, the luminance stimulus could either move upwards or downwards. When the color stimulus was paired with a stimulus at low luminance contrast, the eye movement went in the direction of the color stimulus, as indicated by the direction of the vertical eye velocity (Figure 3a). When paired with a high-contrast luminance stimulus, the eye followed the luminance stimulus on most trials (Figure 3b).

After the initial increase in eye velocity toward luminance with a peak at about 200 ms after the split, eye acceleration decreased and the observer tracked color or luminance, depending on the relative contrast, at a constant velocity. Horizontal eye velocity traces (Figures 3c and 3d) revealed no difference between the four conditions. Horizontal eye velocity generally slowed down after the stimulus split and initially undershot stimulus velocity. The slow-down in the horizontal velocity data was expected, because stimulus velocity decreased from  $10.6^\circ/\text{s}$  before the split to  $7.5^\circ/\text{s}$  after the split. The initial undershoot resembles the overshoot that is often observed in pursuit velocity during the transition from open loop to sustained pursuit or after a velocity change (Krauzlis &

Lisberger, 1989; Robinson, Gordon, & Gordon, 1986). The decision-making process (the change in vertical eye direction), which takes up to about 200 ms (see vertical eye movement trace), could have further added to the slow-down in horizontal eye velocity.

Figure 4 shows pursuit decision direction in vertical eye velocity responses, averaged across six observers, as a function of luminance contrast for different color contrasts. For this figure and all following statistical analyses, responses to the luminance stimulus going upward were pooled with inverted traces for downward stimulus motion of the according condition. Across conditions, vertical pursuit direction changed with a mean latency of 165.7 ms ( $SD = 42.0$ ). A repeated-measures ANOVA showed that the latency of the vertical direction change was significantly affected by luminance contrast ( $F(3,15) = 5.97$ ,  $p = 0.007$ ) but not by color contrast ( $F(3,15) = 0.81$ , n.s.). For a given color contrast, pursuit latency varied systematically with luminance contrast and was shorter for higher luminance contrasts. Pursuit decision direction was influenced by both color and luminance contrasts. When the luminance stimulus had a low contrast, the eye generally followed the color stimulus, irrespective of its contrast (green curves). For high luminance contrasts, irrespective

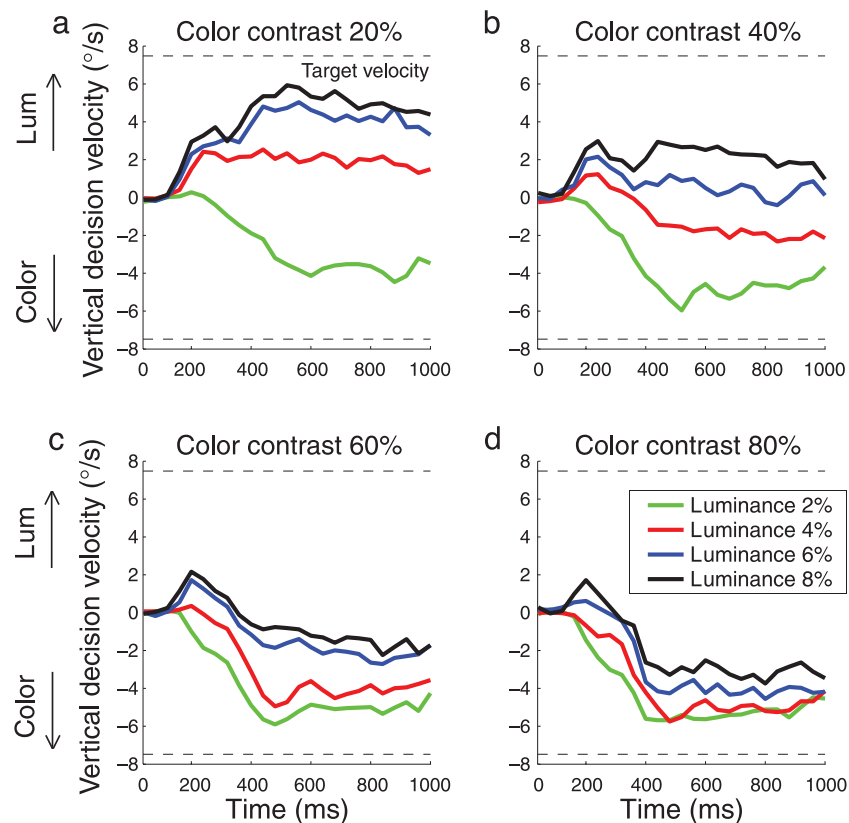


Figure 4. Pursuit target selection in Experiment 1. A combined color and luminance stimulus splits into a separate color and luminance target differing in contrast ( $N = 6$ ). Shown are mean filtered and desaccaded eye velocity traces to upward luminance stimulus motion pooled with inverted traces for downward luminance stimulus motion, plotted as a function of time with respect to stimulus split. Upward traces reflect a choice for luminance, and downward traces reflect a choice for color. Luminance contrast is denoted by line color.

of color contrast, the eye initially went to the luminance stimulus (black curves). At about 100–150 ms after pursuit onset (detected in  $n = 1509$  trials, 59.2%), depending on the contrast of the color stimulus, the eye started to reverse toward the color stimulus (peak and dip in black, blue, and some red curves). On average, in 505 (33.5%) out of all trials with a valid pursuit onset and a subsequent saccade ( $n = 1507$ ), the initial pursuit direction and the direction of the catch-up saccade disagreed. In most of these trials (473 or 93.7%), the eye reversed from luminance to color, meaning that pursuit was initiated toward the luminance stimulus and corrected to continue in the direction of the color stimulus. When the vertical direction change was initiated by a saccade ( $n = 1007$  trials with an initial saccade in which no pursuit onset was detected), this saccade was almost always biased toward color (Figure 5), except when color contrast was low, at 20%, and luminance contrast was high, at 6 or 8% (Figure 5a).

These differences in pursuit and saccadic choice patterns might point to a difference in visual processing for target selection in the two types of eye movements. Alternatively, our results could be caused by differences in neuronal processing time for color and luminance stimuli, in combination with an inherent difference in pursuit and saccadic latencies. However, these latency differences

alone cannot explain the results. If visual signals of color and luminance stimuli were processed at different speeds to drive pursuit eye movements, as reported in Braun et al. (2008), pursuit direction changes to the luminance stimulus should have occurred earlier than direction changes to color. However, across all contrast conditions, pursuit choices to luminance and color did not occur at significantly different times ( $F(1,5) = 0.65$ , n.s.). Moreover, latency distributions (see Figures 6a and 6b) show that on average, across observers and trials, pursuit and saccades had a marked tendency to prefer different stimuli at the same time after the stimulus split. For instance, in the time interval of 250–350 ms after split a larger number of pursuit responses went to luminance (black), whereas initial saccades preferred color (red). Relative preference did not depend on the time at which a pursuit or saccadic decision was made.

In Experiment 1, we observed four different patterns of eye movement choice behavior. The two most common cases were (a) a pursuit onset in the direction of the luminance stimulus, followed by a catch-up saccade into that same direction (see Figure 2a) and (b) a saccade onset into the direction of the color stimulus with a second saccade also in that direction. On some other trials the pursuit direction reversed, either by a smooth reversal in the pursuit response (see Figure 2c) or by a saccade into

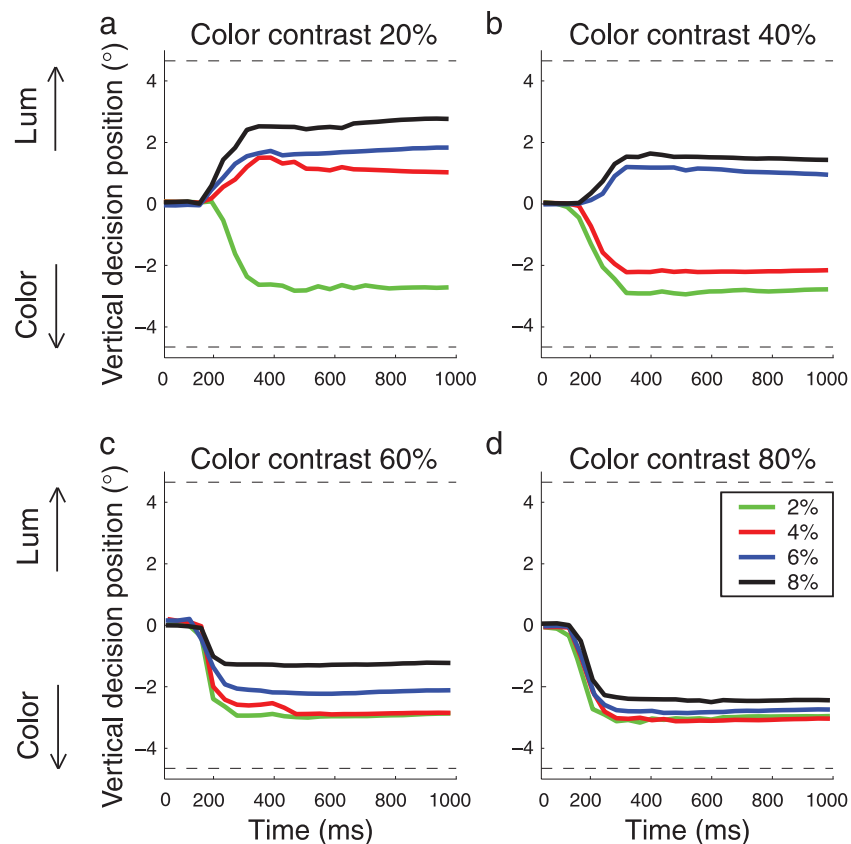


Figure 5. Target selection by initial saccades in Experiment 1. Shown are mean filtered velocity traces from trials in which no pursuit onset was detected and vertical direction change was initiated by a saccade. Presentation follows the same pattern as in Figure 4.



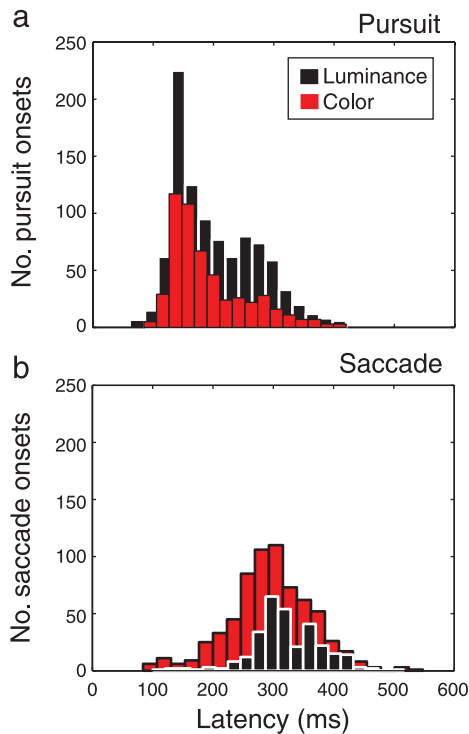


Figure 6. Latency distribution in [Experiment 1](#) as a function of time relative to the stimulus split across all contrast conditions for (a) pursuit ( $n = 1509$  trials) and (b) saccades in 1007 trials in which smooth tracking was initiated by a saccade. Pursuit and saccade target selection direction is denoted by color, with black for luminance choice and red for color choice.

the opposite direction to the initial pursuit choice. Overall, the rate of trials with opposite decision directions in pursuit and saccadic eye movements (incongruent trials) observed here was much higher than the rate of incongruent trials found by others ([Liston & Krauzlis, 2003, 2005](#)). These authors report that in most trials, in which pursuit and saccadic decision differed, the initial pursuit response was corrected by a reversal in the pursuit response before the onset of the first saccade. In contrast, in [Experiment 1](#) of the current study, only 127 out of 505 incongruent trials (25.1%) were due to a smooth reversal in the pursuit response. With respect to the total number of 1509 trials with a pursuit onset, and in comparison to data obtained by [Liston and Krauzlis \(2003\)](#), this is only a small number. One explanation for the small number of trials with a pursuit reversal in our study could be that the catch-up saccade, which was likely to be caused by the required change in pursuit direction, left too little time for pursuit to reverse. The time difference between mean pursuit onset and mean onset of the first catch-up saccade was 218 ms on pursuit reversal trials versus 166 ms on trials in which pursuit and saccade agreed (congruent trials). However, the mean latency of pursuit reversals relative to pursuit onset in our study was only 65.7 ( $\pm 18.3$ ) ms. Thus, there would have been ample time for pursuit to

reverse in congruent trials with earlier saccades occurring at around 166 ms. The small number of pursuit reversals detected here cannot be solely due to task requirements. In our data, incongruent trials were mostly due to a saccade made into the opposite direction to the initial pursuit response. After a saccade reversal, pursuit decision was always in agreement with the reversal saccade direction (i.e., there were no trials with two consecutive reversals).

[Figure 7](#) shows that, in accordance with the overall high rate of saccadic reversal trials, initial pursuit and consecutive saccade preferred different stimuli. For all color contrasts, the proportion of choices to the luminance stimulus increased with increasing luminance contrast. This difference in preference was particularly prevalent for color contrast equal to or higher than 40%, and luminance contrast equal to or higher than 4% ([Figures 7b–7d](#)). Accordingly, a paired samples  $t$ -test (two-tailed) between pursuit choices and catch-up saccades showed that preferences differed significantly for all contrast conditions with at least 40% color contrast and 4% luminance contrast (see [Figure 7](#)). At the lowest color contrast, luminance preference was still higher for pursuit than for saccades, but there was no significant difference for different luminance contrasts, except that preferences differed significantly for the lowest color and luminance contrast condition (20% color, 2% luminance, see [Figure 7a](#)). Preferences in initial saccades and catch-up saccades were very similar and only differed significantly in a paired samples  $t$ -test for color contrast of 80% and luminance contrast of 6% ( $t(5) = 3.35$ ,  $p = 0.02$ ). Pursuit choice with pursuit reversal trials included did not differ significantly from pursuit choice without pursuit reversal trials for any of the contrast conditions.

[Figure 8](#) shows that the number of incongruent trials varied with stimulus contrast. The analysis is based on trials with a valid pursuit onset and a subsequent saccade, in which no pursuit reversal was detected ( $n = 1375$ ). For 20% color contrast ([Figure 8a](#)), the number of incongruent trials was small: At low luminance contrast, pursuit and saccades went to color; at high luminance contrast, both types of eye movements preferred luminance. The pattern of results for the remaining color contrasts was similar: For each of the panels in [Figure 8](#), as luminance contrast increased from 2 to 8%, the number of trials in which both types of movement went toward luminance increased (black line), and the number of decisions to color decreased (blue line). At the same time, the number of trials with a reversal from luminance to color increased (red line). Note that the peak of occurrence of the luminance-to-color reversals changed with color contrast (across panels in [Figure 8](#)), suggesting that the pattern of saccadic reversal decisions reflects the cone-contrast matching criterion (namely, a factor of 10 has to be accounted for by a quantitative match between color and luminance contrasts, see [Methods](#) section). Overall, there were only very few reversals from color to luminance (green curve).

We next analyzed incongruent trials on a trial-by-trial basis, following parts of the analysis by [Liston and](#)

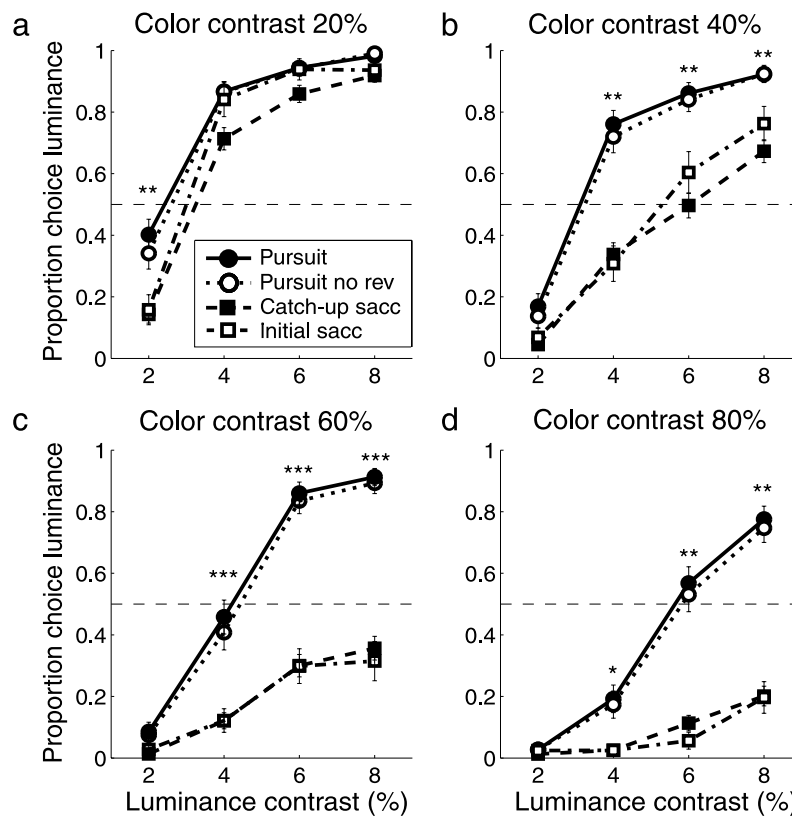


Figure 7. Proportion of trials in which the luminance target was chosen in [Experiment 1](#). Plotted are means ( $\pm$ SEM) of initial eye movement direction ( $N = 6$ ). Symbol types denote type of eye movement to the luminance stimulus: initial pursuit response in trials with a valid direction change in the vertical pursuit response (filled circles;  $n = 1509$  trials), initial pursuit response in trials without a pursuit reversal (open circles;  $n = 1377$  trials), first catch-up saccade following pursuit direction change (filled squares;  $n = 1507$ ), initial saccade in trials that started with a saccade, and where no pursuit direction change was detected (open squares;  $n = 1007$ ). The horizontal dashed black line denotes equal probability of choosing color and luminance. Stars denote significant pairwise comparisons between pursuit and catch-up saccade choices in a two-tailed  $t$ -test,  $*p \leq 0.05$ ,  $**p \leq 0.01$ ,  $***p \leq 0.001$ .

Krauzlis (2003). We divided the data set of trials with valid pursuit onsets into fractions of trials in which pursuit and saccadic decisions agreed (both went to luminance or color, respectively) or disagreed for each contrast condition. Next, for each individual observer, the fraction of “same” responses was compared with predictions from two different models. The “dependent” model assumes that pursuit and saccade choices are dependent. Because, by definition, the “dependent” model predicts pursuit and saccades to agree on each trial, the prediction is unity (dotted line in [Figure 9](#)).

The prediction of the “independent” model was calculated from the following equation by Liston and Krauzlis (2003, p. 11310):  $F_{\text{independent}} = F_{\text{pursuit}} * F_{\text{saccades}} + (1 - F_{\text{pursuit}}) * (1 - F_{\text{saccades}})$ , where  $F$  denotes the fraction of choices in pursuit or saccadic to the luminance stimulus (dashed line in [Figure 9](#)). Clearly, the fraction of same pursuit and saccade responses was much closer to the “independent” than to the “dependent” model for all observers. Regression coefficients calculated separately for the color contrasts were all significantly different from zero in a two-tailed partial  $t$ -test (20%:  $B = 0.98$ ,  $t = 6.9$ ,

$p = 0.02$ ; 40%:  $B = 0.95$ ,  $t = 4.3$ ,  $p = 0.05$ ; 60%:  $B = 0.99$ ,  $t = 23.5$ ,  $p = 0.002$ ; 80%:  $B = 0.99$ ,  $t = 11.1$ ,  $p = 0.008$ ). In line with our assumptions, the observed fraction of same responses was always significantly different from the predictions of the “dependent” model ( $\chi^2$ ,  $p < 0.0001$ ).

Overall, data from [Experiment 1](#) show that pursuit and saccades differ markedly in target selection when confronted with two physically unequal stimuli. Pursuit showed a relative preference for luminance ([Figure 4](#)), whereas initial saccades ([Figure 5](#)) and catch-up saccades went to the color stimulus more often (see summary in [Figure 7](#)). One potential problem in the interpretation of these results could be that we compared pursuit responses and initial and catch-up saccades to moving stimuli. The purpose of catch-up saccades is to bring a moving stimulus closer to the fovea when the eye falls behind, because the stimulus is not tracked fast enough. Catch-up saccades to moving stimuli might be driven by different visual signals than saccades to stationary targets (Orban de Xivry & Lefèvre, 2007). Initial saccades in [Experiment 1](#) (e.g., see comparison to catch-up saccades and pursuit in [Figure 7](#)) were also made in response to moving targets.

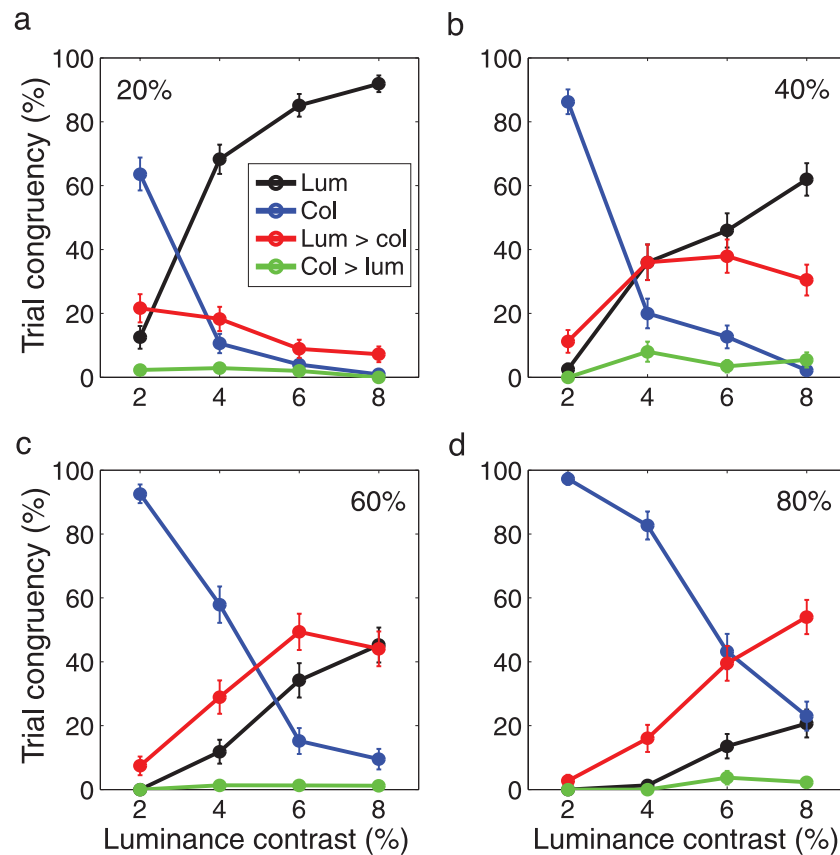


Figure 8. Percentage of congruent and incongruent trials in [Experiment 1](#) as a function of luminance contrast ( $N = 6$ ). For each condition, in a given trial, initial pursuit and subsequent saccade were either congruent (black: luminance, blue: color) or incongruent (red: pursuit to luminance, saccade to color, green: pursuit to color, saccade to luminance). Data are means ( $\pm$ SEM).

We therefore conducted a second experiment, in which a saccade had to be made to one of two stationary targets.

## Experiment 2: Saccade target selection between color and luminance

This experiment was identical to [Experiment 1](#) in stimulus conditions, except that the two stimuli stepped to a position  $6^\circ$  peripheral, along the diagonal directions, from the position where the split had occurred. Six observers were asked to make a saccade to the more salient of the two stimuli after the split. [Figure 10](#) shows the direction of the saccadic decision as reflected in the vertical eye position responses (based on a total of  $n = 2681$  trials) to different levels of contrast in the color stimulus ([Figures 10a–10d](#)) and the luminance stimulus (different line colors). The pattern of saccadic decisions in [Experiment 2](#) differs from the data on pursuit decision direction obtained in [Experiment 1](#) but is very similar to the pattern found for initial saccades and catch-up saccades in [Experiment 1](#) (compare [Figure 10](#) to [Figure 5](#)). Generally, color played a stronger role in driving saccadic eye movements than pursuit. Saccades almost always preferred color, except when color contrast was lowest

(20%) and luminance contrast was highest (6 or 8%). Overall, 2061 out of 2681 valid saccades (76.9%) went to the color stimulus.

This result is reflected in the proportion of trials in which observers chose luminance over color by making a saccade ([Figure 11](#)). Saccadic choice patterns in [Experiment 2](#) are very similar to saccadic choice patterns obtained in the pursuit experiment (shown in [Figures 5](#) and [7](#), and dashed and dotted lines in [Figure 11](#)). When choices were solely made by a saccade, as requested in [Experiment 2](#), choice patterns were even more strongly biased toward color than for catch-up saccades in [Experiment 1](#). The difference between saccadic choice in [Experiments 1](#) and [2](#) is likely to be due to a general difference between saccades to stationary stimuli ([Experiment 2](#)) and saccades during pursuit ([Experiment 1](#)). Saccades occurring early after pursuit onset were either reversal saccades (being responsible for the difference in pursuit and saccadic choice patterns), or catch-up saccades in the direction of pursuit, therefore sharing information with the pursuit system. This explains why the result pattern for saccades during pursuit is somewhere in between pure pursuit and pure saccadic choices. To further test the assumption that pursuit and saccades differ with respect to the processing of visual stimulus properties, we conducted two control

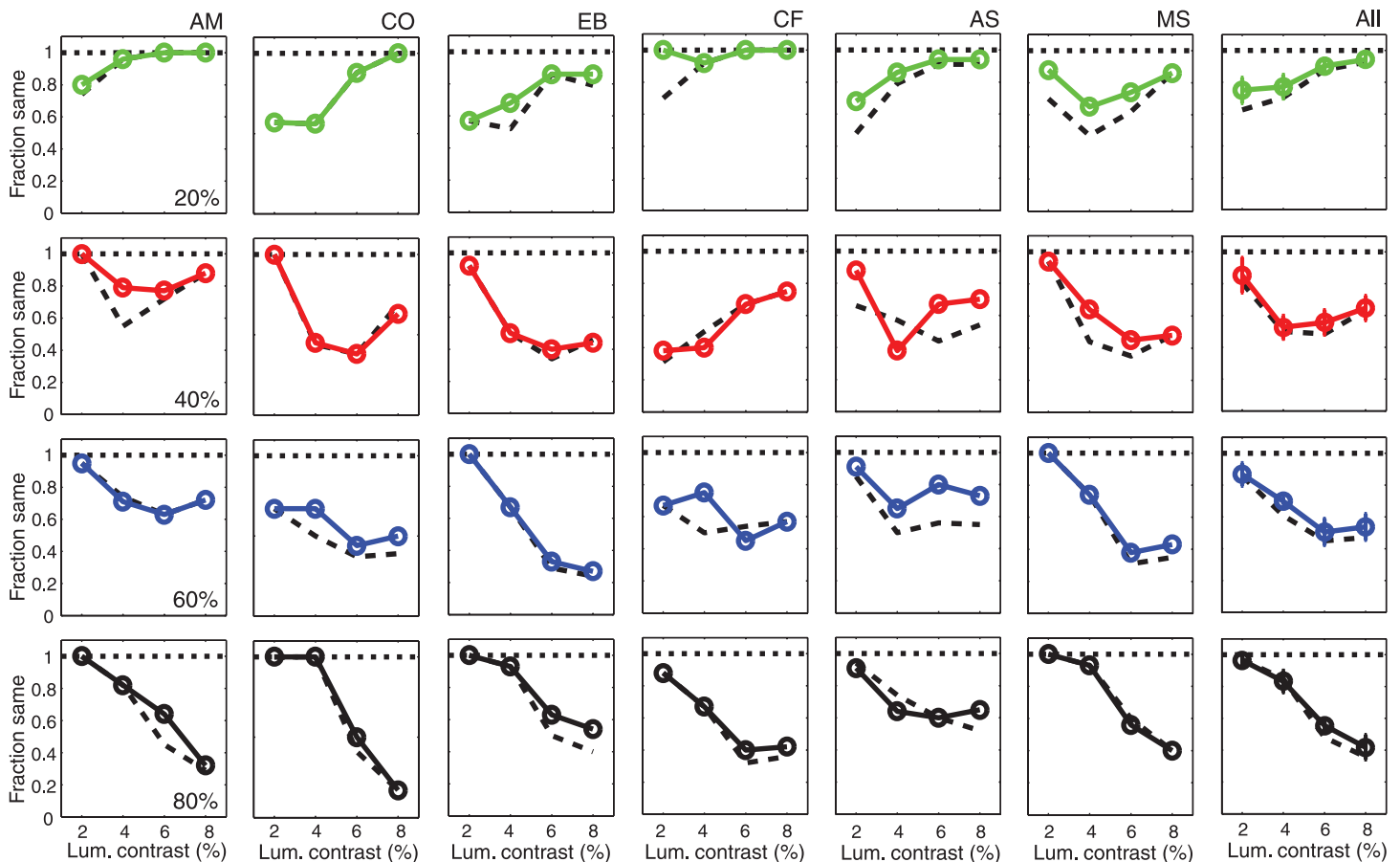


Figure 9. Trial-by-trial analysis of agreement in pursuit and saccade choices in [Experiment 1](#) as a function of luminance contrast. Each column represents data for one observer, with the average across all observers in the last column. The dashed line denotes the prediction of the “independent” model, the dotted line denotes the prediction of the “dependent” model, which is, by definition, at unity.

experiments. These experiments were specifically designed to investigate how pursuit and saccades relate to perceptual judgments of stimulus salience.

### Experiment 3: Perceptual judgment of salience in moving color and luminance targets

Observers ( $N = 8$ ) perceptually judged stimulus salience in a paradigm that was identical to [Experiment 1](#), except that after an initial period of pursuit, observers were instructed to fixate at stimulus split (see [Methods](#) section). Eye position was continuously monitored and we verified that eye position did not deviate systematically from fixation. Trials in which observers pursued one of the two stimuli after the split were excluded from analysis (less than 1% of all trials). Perceptual judgments are shown in [Figure 12a](#). Judgments from trials with upward moving luminance stimulus were pooled with inverted judgments from trials with downward moving luminance stimulus, so that an upward judgment is identical to reporting a more salient luminance stimulus, and a downward judgment corresponds to reporting a more salient color stimulus. Results clearly show a bias toward luminance in salience

judgments. For the lowest color contrast (green line), in almost 100% of all trials the luminance stimulus was perceived as more salient, irrespective of luminance contrast. For 40% (red line) and 60% color contrast (blue line), color was only preferred when luminance contrast was lowest. For the highest color contrast (black line), color was only chosen more often than luminance when luminance contrast was 2 or 4%. In all other conditions, luminance was preferred. These perceptual results are similar to pursuit choices for luminance obtained in [Experiment 1](#) (see solid line for pursuit in [Figure 11](#) across panels a–d).

We conducted a second control experiment to rule out that the close similarity between perception and pursuit was confounded by observers’ pursuit of the horizontally moving stimulus before the split. During the second control experiment, observers therefore maintained fixation.

### Experiment 4: Perceptual judgment of salience in stationary color and luminance targets

In [Experiment 4](#), observers ( $N = 6$ ) gave a salience judgment after keeping fixation for the duration of the trial



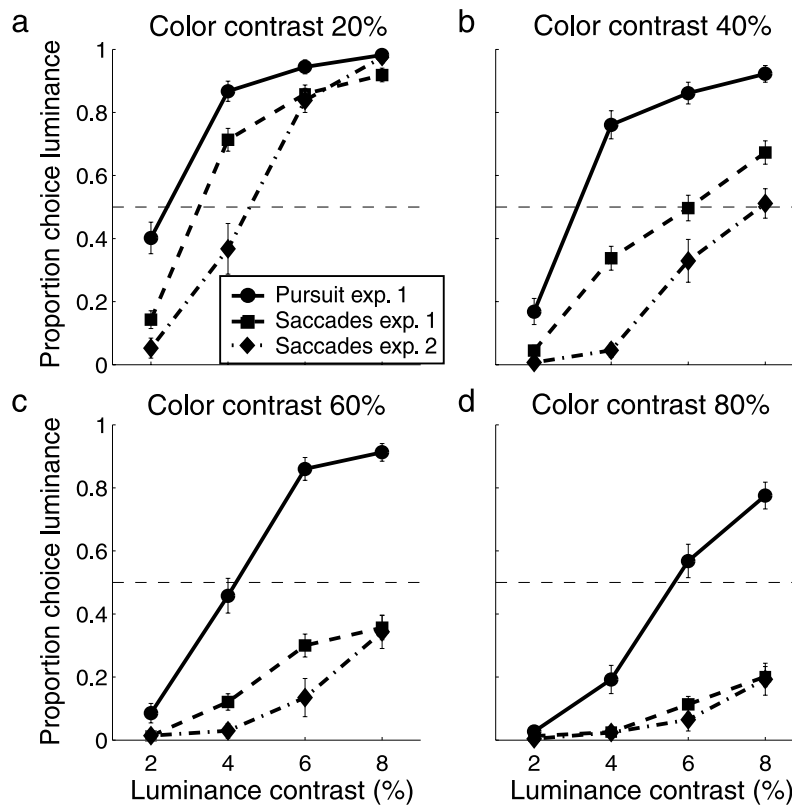


Figure 11. Comparison of proportion choice luminance in Experiments 1 and 2 as a function of luminance contrast. Saccade choice towards luminance in Experiment 2 (diamond symbols) is compared to data from Experiment 1 (see Figure 7) for initial pursuit direction change (circles) and direction of the first catch-up saccade (squares).

processing, whereas the longer latency saccadic response might be made on the basis of a perceptual judgment of salience. Following this alternative explanation, pursuit and saccades would not rely on differences in visual information processing per se. Rather, given the differences in response latencies, pursuit and saccades might be based on the availability of visual information at different stages of the same visual processing mechanism. In two control experiments, one mimicking Experiment 1, and the

other Experiment 2, we showed that the perceptual judgment of stimulus salience was more similar to pursuit than to saccadic choices. The finding that pursuit eye movements showed similar choice preferences to perception, but that saccades did not, is surprising. Pursuit eye movements, despite their short latency, agree with perceptual judgments of stimulus salience, whereas saccades in our Experiments 1 and 2 seem to be based on a different weighting of color and luminance inputs.

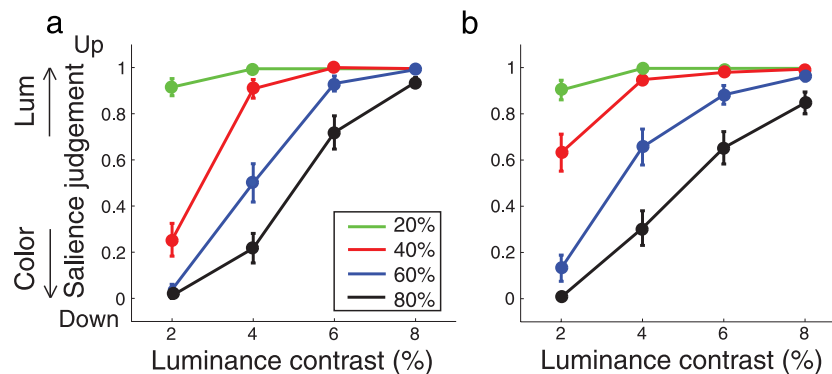


Figure 12. Perceptual judgments of stimulus salience. (a) Results of Experiment 3 (pursuit, stimuli moving after split, fixation upon split). (b) Results of Experiment 4 (fixation, stimuli stationary after split). Luminance moving/stepping upward, color downward. Color contrast denoted by line color.

## Reconciling salience perception with eye movement results

Overwhelming evidence from behavioral studies in monkeys and humans shows that target selection in saccades is driven to a large degree by stimulus salience. Neurophysiological studies revealed salience maps in areas LIP (Goldberg et al., 2006) and FEF (Thompson & Bichot, 2005), two cortical areas that are closely related to the generation of saccadic eye movements.

The correspondence between saccades and perception of salient stimuli was also shown in a series of behavioral studies in humans, using a visual search paradigm (Beutter, Eckstein, & Stone, 2003; Eckstein, Beutter, Pham, Shimozaki, & Stone, 2007). Eckstein et al. (2007) claim that perception and saccadic target selection are controlled by the same neural mechanisms. However, in many of these studies, stimulus salience is poorly defined. The theoretical notion of a salience map (e.g., Itti & Koch, 2001) consists of multiple maps encoding contrast of single visual features such as luminance or color, therefore reflecting physical properties of visual stimuli. Accordingly, salience is often defined bottom-up, based on the intrinsic conspicuousness of the visual stimulus, as the stimulus with unique features that pops out relative to its visual environment (Thompson & Bichot, 2005), or simply based on signal-to-noise ratio (Beutter et al., 2003). Alternatively, stimulus salience is defined top-down as the behaviorally relevant target (as opposed to the task-irrelevant distractor), or as the stimulus that exogenously attracts attention (Goldberg et al., 2006).

Observers in the current study were asked to select the stimulus that appeared more salient. Here, salience must therefore be defined as a subjective property of a visual stimulus that makes one of the two stimuli more conspicuous than the other (see Nothdurft, 1992, 2000). A comparison between target selection in pursuit and saccadic eye movements with perception of salience revealed findings that are strikingly different from the view of a close overlap between saccades and perception that is commonly assumed in the literature. We show that pursuit and perception overlap, whereas the saccadic choice differs from the perceptual judgment. Saccades generally prefer the color stimulus, although this stimulus appears perceptually less salient.

## Different processing mechanisms for pursuit and saccades?

Different types of eye movements such as pursuit and saccades are generally performed to serve the same purpose, namely to keep an object of interest close to the fovea, thereby enabling the observer to perceive details and to precisely plan consecutive movements (Land, 2006). It is therefore not surprising that recent studies on pursuit and saccades have focused on similar-

ities rather than differences between the two types of movements (for an overview, see Orban de Xivry & Lefèvre, 2007). A similar trend can be observed in the comparison of saccadic eye movements and reaching or pointing movements (Neggers & Bekkering, 2000; Scherberger & Anderson, 2007; Scherberger, Goodale, & Anderson, 2003).

The results reported in the present study are not in agreement with the general conclusion that the same processing mechanisms underlie target selection in pursuit and saccades. It is important to note that most of the studies that reported similarities in pursuit and saccadic response patterns in decision-making situations used stimuli that differed along one dimension only, either in luminance contrast, color, form, or direction of motion (Adler et al., 2002; Gardner & Lisberger, 2001, 2002; Krauzlis et al., 1999; Liston & Krauzlis, 2003, 2005). Observers were usually instructed or cued to choose a predefined target and had to indicate their decision by making a combined pursuit and saccadic eye movement. For instance, Liston and Krauzlis (2005) had human observers discriminate between two vertically offset and horizontally moving textured patterns of different luminance contrast, which moved into opposite directions. Starting from central fixation, observers had to make an eye movement to the higher contrast texture and to subsequently track the chosen target. In over 90% of all trials the pursuit and the saccadic system reached a concordant directional decision with a similar trade-off between speed and accuracy. In the remaining trials, the pursuit response reversed direction before the first saccade was made. The authors suggest that this disagreement in motor choice is due to an inherently lower response threshold in the pursuit system and that pursuit and saccadic decisions are driven by a common decision signal (Liston & Krauzlis, 2003, 2005).

In a study by Case and Ferrera (2007), monkeys were rewarded for making an eye movement to either a red or green moving stimulus in a two-target selection paradigm. The rewarded target color was varied from session to session, and monkeys were allowed 100 trials at the beginning of each session to learn reward contingencies. A comparison of the direction of pre-saccadic pursuit, the first saccade, and post-saccadic pursuit showed that on more than 80% of all trials pursuit and saccades agreed in choice. The authors came to a similar conclusion than Liston and Krauzlis (2003, 2005) and added that the visual information that controls target selection in saccades was available to the pursuit system at the same time or even before the saccade was made. These results are therefore evidence for a parallel selection mechanism in pursuit and saccades. Again, this paradigm differs from ours in two important aspects: First, stimuli were only varied along one dimension (i.e., color), and second, the monkey received a reward for choosing a particular stimulus.

We propose that target selection mechanisms might be different in more complex situations with a richer visual







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