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Color and motion: which is the tortoise and which is the hare? ☆

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Abstract

Recent psychophysical studies have been interpreted to indicate that the perception of motion temporally either lags or is synchronous with the perception of color. These results appear to be at odds with neurophysiological data, which show that the average response-onset latency is shorter in the cortical areas responsible for motion (e.g., MT and MST) than for color processing (e.g., V4). The purpose of this study was to compare the perceptual asynchrony between motion and color on two psychophysical tasks. In the *color correspondence* task, observers indicated the predominant color of an $18^\circ \times 18^\circ$ field of colored dots when they moved in a specific direction. On each trial, the dots periodically changed color from red to green and moved cyclically at 15, 30 or 60 deg/s in two directions separated by 180° , 135° , 90° or 45° . In the *temporal order judgment* task, observers indicated whether a change in color occurred before or after a change in motion, within a single cycle of the moving-dot stimulus. In the color correspondence task, we found that the perceptual asynchrony between color and motion depends on the difference in directions within the motion cycle, but does not depend on the dot velocity. In the temporal order judgment task, the perceptual asynchrony is substantially shorter than for the color correspondence task, and does not depend on the change in motion direction or the dot velocity. These findings suggest that it is inappropriate to interpret previous psychophysical results as evidence that motion perception generally lags color perception. We discuss our data in the context of a “two-stage sustained-transient” functional model for the processing of various perceptual attributes.

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1. Introduction

Understanding how neural activities give rise to perception is a fundamental problem in studies of the brain. The problem is complex because different attributes of a sensory stimulus are likely to be processed at different neuroanatomical sites (Livingstone & Hubel, 1988; Zeki, 1978). For example, cortical areas MT and MST in the monkey brain appear to be most relevant for the perception of motion (Parker & Newsome, 1998). Although

the neural substrates of color perception are not as well established, cortical area V4 is implicated as one important site for color processing (Livingstone & Hubel, 1988; Zeki, 1992). Neurophysiological investigations show that the average response-onset latency in cortical areas MT and MST is substantially shorter than the average response-onset latency in area V4 (Schmolesky et al., 1998). This difference in neural response timing for the processing of motion versus color would be expected to give rise to a similar difference at the perceptual level, resulting in the illusory perception that motion events lead color events in time. Contrary to this expectation, several recent psychophysical studies have been interpreted to indicate that the perception of motion temporally either *lags* (Arnold & Clifford, 2002; Arnold, Clifford, & Wenderoth, 2001; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002; Viviani & Aymoz, 2001) or is in synchrony (Nishida & Johnston, 2002) with the perception of color.

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Moutoussis and Zeki (1997) presented observers with an array of random dots that reversed motion-direction and changed color in a periodic temporal square-wave pattern. They manipulated the relative phase of motion and color changes and asked observers to judge the predominant color when the dots were moving in a specific direction (*color correspondence task*). The results indicate that color and motion appear perceptually in phase when physically the phase of the direction reversal was advanced approximately 80 ms with respect to the change in color. This striking reversal of timing between the perception of motion and color, as inferred from the psychophysical experiments cited above, could be explained if the processing of motion in areas MT and MST takes substantially longer than the processing of color signals in area V4, prior to perception (Moutoussis & Zeki, 1997). However, using a similar paradigm, Arnold and Clifford (2002) showed that the relative phase lag between motion and color that was required to achieve perceived correspondence varied systematically with the direction of motion change. Further, the results of another recent study imply that the perception of color and motion are temporally synchronous. Nishida and Johnston (2002) asked observers to judge whether a reversal of motion occurred before or after a change in color (*temporal order judgment task*). They found that motion and color changes were perceptually in phase when they were physically in phase. Based on this observation and others, Nishida and Johnston argued against the explanation that motion processing in the brain takes longer than color processing. They provide an alternative explanation that attributes the motion lag observed in previous experiments (Arnold & Clifford, 2002; Arnold et al., 2001; Moutoussis & Zeki, 1997; Viviani & Aymoz, 2001) not to motion processing delays but to a faulty correspondence-matching process between color transitions and position transitions (Nishida & Johnston, 2002).

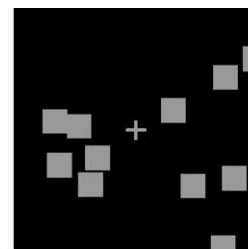
How can the contradictory findings among the various psychophysical studies be reconciled? And, how can the contrasting neurophysiological and psychophysical observations relating color and motion processing be explained?

We hypothesized that the contradictory findings of perceptual asynchronies between color and motion are due to the differences in the stimulus parameters and in the psychophysical tasks used. To test our hypothesis, we evaluated the perceptual asynchronies between color and motion using essentially the same stimulus, but for two different tasks, *viz.*, a *color correspondence task* and a *temporal order judgment task*. We tested a range of motion profiles, directions, and velocities in this study. We discuss the data reported here and elsewhere on the perceptual asynchrony between color and motion in the context of a two-stage sustained-transient functional model.

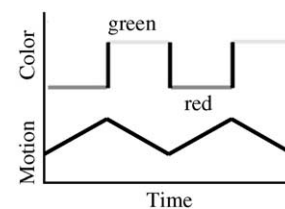
2. Methods

Each frame of the motion stimulus in the color correspondence and the temporal order judgment tasks consisted of a square field ($18^\circ \times 18^\circ$) of random dots ($1.6^\circ \times 1.6^\circ$) on a dark background (Fig. 1). The exact number (10–14) and positions of the dots varied from trial to trial. These stimulus parameters were chosen to closely match those of Moutoussis and Zeki (1997). The stimulus was presented on a 15 inch computer monitor using a Macintosh G3 computer, at a frame rate of 85 Hz. The duration of each frame of the stimulus was 11.8 ms. Observers viewed the monitor from a distance of 25 cm and were instructed to maintain fixation on a cross, presented at the center of the square field.

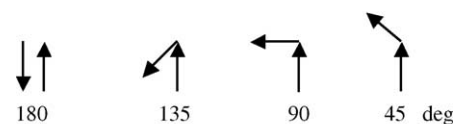
Within each block of trials, the velocity of the moving dots was 15, 30, or 60 deg/sec. Within each motion cycle, which consisted of several frames, the motion period was divided into two halves. In the first half-period, dots always moved upward. In the second half-period, dots moved in one of the following four directions in a block of trials: downward (180°), down and leftward (135°), leftward (90°), and up and leftward (45°). We examined four changes of direction between the first and second half-period because we suspected that observers may perform the color correspondence task using a steady-



A. A Frame of Random Dots



B. Temporal Profile



C. Directions in a Motion Cycle

Fig. 1. (A) A sample frame of random dots. (B) The temporal profile for the color and motion cycle, for the color correspondence task. (C) The four possible direction-changes during a motion cycle. Each pair of arrows specifies the directions of motion during the two halves of each motion cycle.

state signal of motion direction, obtained after spatio-temporal integration of motion signals along the motion trajectory. When the motion trajectory includes a direction change, the dynamics of spatio-temporal integration of motion signals is likely to be affected by the extent to which motion opponency mechanisms are engaged.

A color cycle was also divided into two half-periods. In each half-period, the color of all moving dots was either red or green. The luminances of red and green dots were set to equal multiples of the corresponding detection thresholds of each observer (average = 4.5 log units). Previously, Moutoussis and Zeki (1997) reported that departures from strict iso-luminance did not change the perceived motion lag in their experiments.

We used the method of constant stimuli to introduce a set of constant phase differences (for the color correspondence task) or a set of constant temporal asynchronies (for the temporal order judgment task) between the motion and the color cycles. The specific details for the two psychophysical tasks are given below.

For the *color correspondence task*, the set of phase differences between the motion and color cycle included 0°, 30°, 60°, 90°, 120°, 150°, 180°, 210°, 240°, 270°, 300°, and 330°. We presented each phase difference ten times within each block of trials, in a random order. Each trial consisted of presenting the motion cycle five times, after which the observer had to indicate which color (green or red) was more dominant during upward dot motion. To ensure that judgments were made when both the motion and color responses reached a steady-state condition, observers were asked to ignore the first cycle and base their judgments on the subsequent four cycles. The duration of each motion and color cycle was either 565 or 706 ms, similar to the two durations used in the study of Moutoussis and Zeki (1997). Each combination of cycle duration, dot velocity, and change in motion-direction was repeated at least twice for each observer.

For the *temporal order judgment task*, the set of 11 asynchrony differences between the change in motion direction and dot color straddled the point at which both motion-direction and color changed at the same time. This set of asynchrony differences spanned ± 118 ms. As in the color correspondence task, we presented each asynchrony difference ten times within each block of trials, in a random order. Each trial consisted of only one motion cycle, and the color only changed once during the motion cycle. The duration of the motion cycle was 706 ms. The task of the observers was to indicate whether the change in dot color occurred before or after the change in motion direction. Each combination of dot velocity and change in motion-direction was repeated at least twice for each observer. Because the observers viewed just a single cycle of motion and color change in the temporal order judgment task, a dissimilar outcome from the color correspondence task could conceivably be attributed to the reduced number

of motion- and color-change cycles, which may have resulted in a different adaptational state. Consequently, two of the observers performed additional temporal order judgments, which were made after five complete cycles of dot motion and color change. These five cycles were identical to those in the color correspondence task, except that the changes in dot motion and color always occurred physically in phase. Following a 353-ms interval with just the fixation cross (to serve as a cue), the observers were presented with a final cycle of dot motion and color change, about which they made their judgment of temporal order.

In addition to the set of four motion-direction changes, we also measured the observers' ability to indicate whether the change in dot color occurred before or after the onset and offset of motion. For these measurements, the random dots either stayed stationary and started to move upward half-way through each trial (*motion-onset condition*, as investigated previously by Viviani & Aymoz (2001)), or started moving upward at the beginning of each trial and stopped their motion half-way through (*motion-offset condition*).

Four observers participated in this study. Two were authors of this study and the other two were unaware of the purpose of the study. Observers gave informed consent after the procedures of the experiment were explained, and before the commencement of data collection. All had corrected-to-normal vision and wore corrective lenses for the experiment. Testing was binocular, in a dimly lit room.

3. Results

For the color correspondence task, the proportion of trials on which the observers indicated that the color of the dots was predominantly red during upward dot motion depended on the phase difference between the color and motion cycles. The relationship between the observer's responses and the phase difference between the color and motion cycles is more or less sinusoidal. Fig. 2 shows two sets of sample data presented in two ways: (1) as polar plots with the proportion of trials indicating red as the predominant color during upward dot motion on the radius, and the phase lag of the motion cycle relative to the color cycle in degrees on the circumference; and (2) as Cartesian plots with the proportion-of-trials plotted as a function of the phase difference between the color and motion cycles in degrees. The polar plots are presented in a way that is comparable with those presented by Moutoussis and Zeki (1997), where the major axis of the polygon that connects the data points represents the phase lag of the motion cycle relative to the color cycle that yields perceptual synchrony. To obtain quantitative measurement of the phase angle (k) between the motion and color

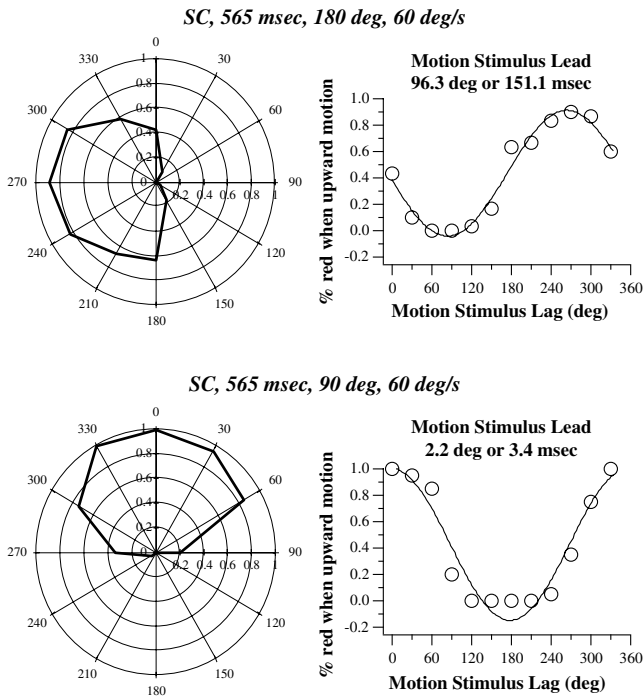


Fig. 2. Sample data plotted in (left) polar coordinates and (right) Cartesian coordinates. In the left hand polar plots, clockwise numbering on the circumference indicates the stimulus motion lag. The radial position indicates the proportion of trials on which the observer reported the dots as predominantly red when the direction of motion was upward. In the right hand Cartesian plots, a motion stimulus lag of zero indicates that the color of the dots is red when they are moving upward. Therefore, the phase angle at which each curve reaches its maximum value defines the phase delay of the motion cycle relative to the color cycle for perceiving the color and motion cycles in phase. Note the substantial difference in phase between color and motion for the two directions of motion change (180° top, 90° bottom) that are illustrated.

cycles, we fit each set of data plotted in Cartesian coordinates with a cosine function:

$$y = y_0 + A * \cos(x + k).$$

Here, A represents the amplitude of the function, y_0 is the offset, and x is the motion stimulus lag in radians. Positive values of k , for k less than π , indicate that the motion *stimulus leads* the color stimulus in time or, equivalently, that motion *perception lags* color perception. We converted these phase angles into temporal offsets (ms) by taking into account the motion period (565 or 706 ms).¹

The time of motion change compared to color change that yields perceptual synchrony is plotted as a function of the change of direction during the motion cycle in Fig. 3. Clearly, the time of motion change compared to

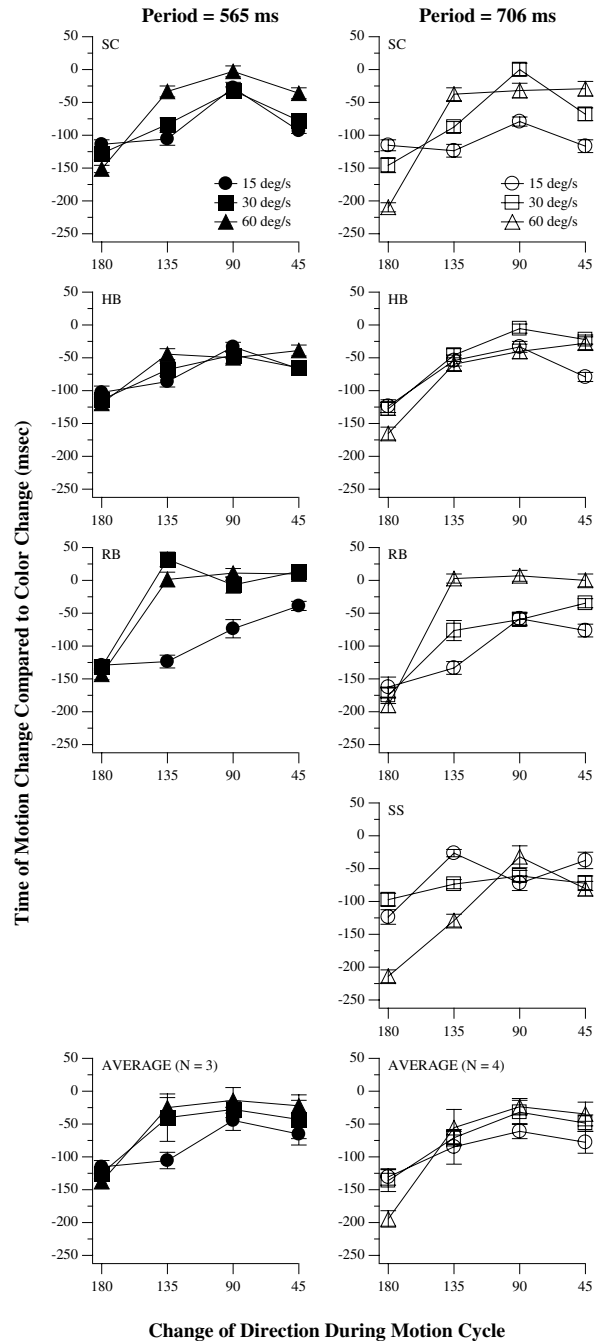


Fig. 3. Time of motion change compared to color change to yield perceptual synchrony is plotted as a function of the change of direction during the motion cycle, for the two motion cycle durations (left: 565 ms; right: 706 ms) in the *color correspondence* task. Each panel contains data for three dot velocities: 15, 30, and 60 deg/s. The top four rows are data from individual observers and the bottom row shows data averaged across all the observers. Negative (positive) times on the y -axis indicate that the motion cycle starts before (after) the color cycle. Thus, *negative times* in these plots can be interpreted to indicate that the perception of a change in the direction of motion *lags* the perception of a color change. The error bars in the top four rows represent ± 1 standard error of estimate of the perceptual asynchrony. The error bars in the bottom row represent the standard errors averaged across the observers, taking into account the within- as well as the between-observer differences.

¹ For example, in the top right panel of Fig. 2, the fitted equation is $y = 0.56 + 0.48 * \cos(x + 1.68)$. The phase angle (k) of 1.68 radians (96.3°), for a motion period of 565 ms, corresponds to a temporal offset of 151.1 ms.

color change depends on the change of direction during the motion cycle (repeated-measures ANOVA: $F_{(3,6)} = 28.03, p = 0.02$) but not on the velocity of dot motion (repeated-measures ANOVA: $F_{(2,4)} = 3.93, p = 0.17$) or the cycle duration (repeated-measures ANOVA: $F_{(1,2)} = 1.71, p = 0.30$).² For these plots, negative times indicate that the motion cycle starts before the color cycle and can therefore be interpreted to indicate that the perception of a change in the direction of motion *lags* the perception of a color change. Positive times imply a perceptual motion *lead*. Averaged across observers and dot velocity, the average temporal advance of the motion cycle relative to the color cycle, indicating that the change in motion is perceived to *lag* the change in color, is greatest (142 ± 29 (SD) ms) when the direction of motion reverses by 180° during the motion cycle. This perceptual lag of motion with respect to color decreases as the change in direction during the motion cycle becomes smaller. When the direction change is orthogonal (i.e. 90°), the perceptual lag of motion with respect to color reaches a minimum (31 ± 27 (SD) ms).

With respect to the temporal order judgment task, we fit each set of data (the proportion of trials on which the observer reported that the color change occurred before the change in motion direction, motion onset, or motion offset) with a cumulative-Gaussian psychometric curve. From the fitted psychometric function, we derived the point of subjective equality, which indicates when the observer perceived that the change in color and motion occurred simultaneously. These data are summarized in Fig. 4 for the conditions involving a change in motion direction, and in Fig. 5 for the motion-onset and motion-offset conditions. In these plots, positive (negative) times indicate that the change in the direction, motion onset, or motion offset occurs after (before) the color change. Thus, *positive* times in these plots can be interpreted to indicate that the perception of a motion change *leads* the perception of a color change. Although the time of motion change relative to color change in order for observers to perceive both simultaneously appears to occur earliest in the motion-offset condition, the difference between this and the other conditions of motion change (direction changes and motion-onset) is not statistically significant (repeated measures ANOVA: $F_{(5,10)} = 2.62, p = 0.09$). Neither does the time of motion change relative to color change to achieve perceived simultaneity depend on the velocity of dot motion (repeated measures ANOVA: $F_{(2,4)} = 0.13, p = 0.76$). Averaged across all the conditions and observers, the time of motion change relative to color change for

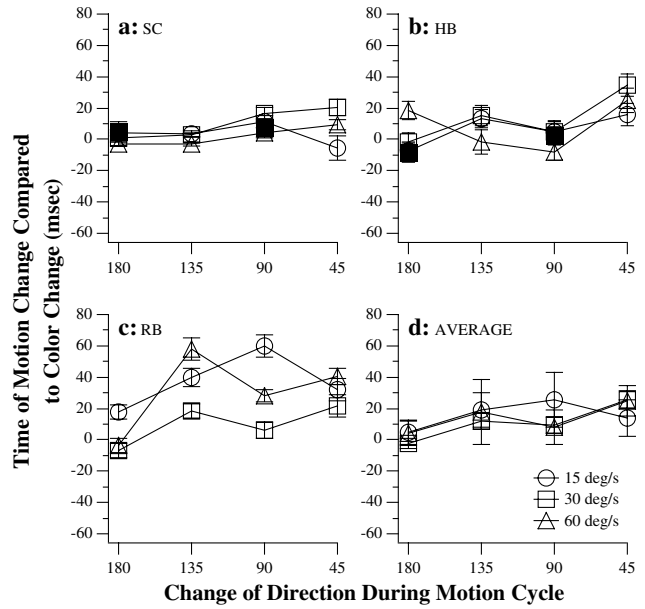


Fig. 4. Time of motion change compared to color change to yield perceptual synchrony is plotted as a function of the change of direction during a single motion cycle (unfilled symbols) in the *temporal order judgment* task. The motion cycle duration was 706 ms. Each panel contains data for three dot velocities: 15, 30, and 60 deg/s. Individual observers' data are plotted in panels a–c, and the average results of the three observers are given in panel d. As indicated by the filled squares in panels a and b, perceived temporal synchrony between changes in motion and color is not affected if the judgment is made after five instead of only a single cycle of continuous dot motion. In all panels, positive (negative) times on the y-axis indicate that the change in the direction of motion occurs after (before) the color change. Thus, *positive times* in these plots can be interpreted to indicate that the perception of a motion change *leads* the perception of a color change. The error bars in panels a–c represent ± 1 standard error of estimate for the perceptual asynchrony. The error bars in panel d represent the standard errors averaged across the observers, taking into account the within- as well as the between-observer differences.

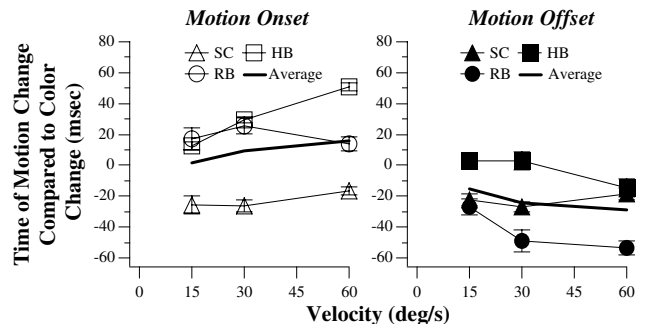


Fig. 5. Time of motion change compared to color change to yield perceptual synchrony is plotted as a function of the dot velocity for the motion-onset (left) and motion-offset (right) conditions, in the *temporal order judgment* task. The motion cycle duration was 706 ms. Data are shown for the three observers, as well as the averaged data (thicker line without symbols). Details of the plots are as in Fig. 4. The error bars in each panel represent ± 1 standard error of estimate of the perceptual asynchrony.

² We also performed separate ANOVAs on the three observers who completed all of the experimental conditions. Results of these individual ANOVAs confirm the significant main effect due to changes in motion direction during the motion cycle ($p < 0.0001$).

perceiving the two changes simultaneously is 6.4 ± 3.0 (SE) ms. Additional data obtained from observers SC and HB for a dot velocity of 30 deg/s (Fig. 4, filled symbols) confirmed that the temporal order judgments were unchanged if these judgments were made after five instead of a single cycle of motion and color change.

4. Discussion

The hypothesis we examined in this study is that the contradictory findings in previous psychophysical studies in relation to the perceptual asynchronies between color and motion are due to the differences in the stimulus parameters and tasks. To this end, we measured the perceptual asynchronies between color and motion for a range of motion profiles, directions and velocities, using the tasks of color correspondence and temporal order judgment. We found that the perceptual asynchrony between motion and color depends on the type of psychophysical task. This finding indicates that it is inappropriate to interpret previous results as evidence that motion perception generally lags color perception. We will discuss our data and the data reported previously in the context of the two-stage sustained-transient functional model that is outlined in the next section.

4.1. The “two-stage sustained-transient” functional model

Our explanation for the observed asynchronies between color and motion perception is based on the differential latency between color and motion processing in a “two-stage sustained-transient” model. As we will elaborate below, we propose that processing latencies depend on stimulus parameters as well as the experimental task. In the *first stage* of the model, the representations of stimulus characteristics (e.g., motion, color selectivity) are relatively stable and largely independent of the observer’s task, although modulation by internal factors, such as attention, is possible. We propose that two forms of information are available within this stage: time-dependent changes in stimulus attributes are encoded in the transient information, whereas steady-state stimulus attributes are encoded in the sustained information. For example, a sudden change in the direction of motion can be detected from transient information. On the other hand, the direction and duration of continuous motion can be determined from the sustained information. We postulate further that transient information about stimulus *changes* is available substantially earlier in time within this first processing stage than sustained information about stimulus attributes.

In the *second stage* of the model, the stimulus representations in the first stage are transformed (or read out) into another set of representations that satisfy the specific requirements of the observer’s task. The functional

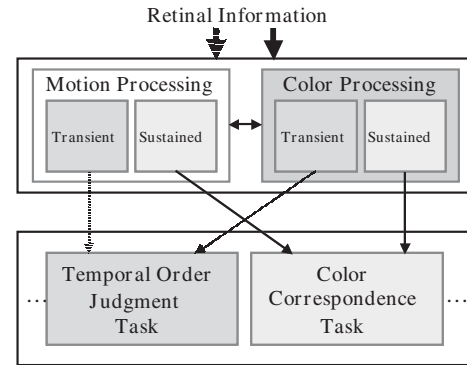


Fig. 6. Illustration of a two-stage sustained-transient functional model for the perception of motion and color. The first stage for both motion and color processing consists of transient and sustained processing components. The *temporal order judgment task* (e.g. Nishida & Johnston, 2002) uses information from the transient processing components while the *color correspondence task* (e.g. Moutoussis & Zeki, 1997) uses information from sustained processing components. In the *temporal order judgment task*, a temporal comparator within the second stage determines the temporal order of motion-change and color-change events that are detected in the first stage. In the *color correspondence task*, sustained color information from the first stage is further averaged in the second stage, within a temporal window that is defined by a stable signal of motion direction from the first stage. The temporal dynamics of the motion-direction signal are determined by a spatio-temporal integration process in the sustained component of the first stage. This integration process consists of averaging the signals from motion-detecting mechanisms tuned to various opponent and non-opponent directions.

architecture of this stage is assumed to be highly flexible so that relevant signals from the first stage can be combined following appropriate rules so as to satisfy the staggering number of complex tasks that human observers can carry out. A schematic representation of this two-stage sustained-transient model is shown in Fig. 6. The general framework for this “two-stage” approach, which addresses the question of how relatively simple and stable feature encoding can be transformed into rich behavioral outputs, can be traced back at least to Hebb (1949). A similar model with possible neural correlates has also been proposed by Van Wezel and Britten (2002).

4.2. Predictions of the “two-stage sustained-transient” functional model and comparisons with data

For the first set of predictions, we keep the observer’s task (and therefore the second stage in the model) constant while changing the stimulus so as to modify the activities in the first stage. Recall that in the color correspondence task, the observer is instructed to report the *predominant color* when stimulus dots are moving in one of two motion directions. Our explanation for the perceived motion lag in this task is based on the relative latency difference between the spatio-temporal integration of direction signals across opponent mechanisms (Recanzone, Wurtz, & Schwarz, 1997) and the compu-

tation of stimulus color. Consequently, varying the direction of the motion change, from say up-down to up-left, should influence the processing latency in the motion channel by affecting the extent to which motion opponency mechanisms are engaged. We therefore predict that the perceived motion lag should depend on the specific directions of motion that are used in the *color correspondence task*. If the magnitude of perceived motion lag reflects the differential latency between motion and color processing, then beyond a minimum period of the stimulus-attribute changes, the perceived motion lag should remain constant. The minimum period is defined as the period for which the responses of mechanisms responsible for motion and color perception have reached steady-state. Indeed, the data in Fig. 3 confirm that the perceived motion lag depends on the specific directions of motion change. Specifically, the perceived asynchrony between motion and color decreases as the difference between the two directions of the motion cycle is reduced. The velocity independence of the perceived motion lag can be explained in our model if we assume that the velocity-tuned mechanisms that respond to the moving stimuli that were used in our experiments have similar dynamic properties.

Previously, Nishida and Johnston (2002) proposed another model to account for the perceived temporal asynchrony between color and motion. According to their model, varying the direction of motion should not affect the perceived motion lag because a *change* in motion direction is a “second-order” property regardless of the specific directions of motion. Our data are not consistent with this model. However, our data are consistent with the data of Arnold and Clifford (2002), who also showed that the perceived motion lag decreases with a decrease in the difference between the directions of motion in the motion cycle. Another property of our data that cannot be readily accounted for by the model of Nishida and Johnston (2002) is that the perceived motion lag that we found is highly similar for the two cycle durations we examined. Like us, Moutoussis and Zeki (1997) also reported that the perceived motion lag is largely independent of the cycle duration, suggesting that it reflects fundamentally a temporal rather than a phase delay. In the absence of additional assumptions that make the positioning of the putative temporal-markers dependent on stimulus dynamics, the model of Nishida and Johnston (2002) makes a contrary prediction, namely that the perceived motion lag should increase systematically with the cycle duration. Additional aspects of the data from Nishida and Johnston (2002) are discussed below.

For the second set of predictions, we keep the stimulus (and therefore the first stage in the model) relatively constant while changing the observer’s task. If direction-change information is available from a separate transient motion mechanism in the first stage of the model,

then changing the observers’ task from reporting the predominant color to reporting the temporal order of attribute-changes is predicted to result in a read out from a different subset of activities in the first stage and, therefore, in a different perceived motion lag. Further, if this subset of activities is based on transient responses as postulated in the model, the perceived motion lag in the *temporal order judgment task* should be independent of the specific directions and velocities of motion that are used in the task. Note that the *color correspondence task* requires a stable signal of motion direction (i.e., the observer judges the predominant color when the motion is upward) whereas the *temporal order judgment task* only requires information about a direction change. The data in Fig. 4 are consistent with these predictions: (1) the perceived color-motion asynchrony is smaller in the temporal order judgment task than in the color correspondence task and (2) the perceived color-motion asynchrony in the temporal order judgment task does not depend on the specific directions of motion change or velocity. Our data are consistent with the data for the temporal order judgment task reported by Nishida and Johnston (2002). Note that the magnitude of the color-motion asynchrony in both tasks should depend also on the detectability of the stimuli for each observer (Purushothaman, Patel, Bedell, & Ogmen, 1998). Individual differences in the detectability of the motion and color stimuli might account for the larger magnitude of color-motion asynchrony found in our color correspondence task (as well as for the two practiced subjects reported by Arnold & Clifford, 2002), compared to that reported elsewhere in the literature (Arnold & Clifford, 2002; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002).

Nishida and Johnston (2002) argued that the dissociation that they observed between reaction time (RT) and “perceptual-simultaneity” measures provides evidence against an explanation for color-motion asynchronies based on processing latencies. The stimuli in these experiments consisted of randomly ordered intervals with different colors (blue, green, yellow, and red) or with different directions of motion (upward, downward, leftward, and rightward). In the RT experiment, observers were shown one of these stimulus sequences (color or motion) and were required to press a mouse button immediately when they detected the target (a predetermined color or direction of motion). The resulting RTs for color and motion were approximately equal. In the “perceptual-simultaneity” experiment, the color and motion sequences used in the RT experiment were displayed simultaneously at two different spatial locations. Within a given session, either a specific color or a specific direction of motion was designated as the target stimulus and the stimuli within the other sequence were designated as the test. The observers’ task was to “decide which of the four test stimuli was concurrent with the target.” For example, if the designated target was the

color red, then the observer judged which of the four directions of *motion* in the test stimulus occurred synchronously with “red” in the *color* sequence. Nishida and Johnston (2002) reported substantial motion lags for this task, that were similar in magnitude regardless of whether the target was a specific color or direction of motion.

One possible way that we can account for these results is as follows. With respect to the RT experiments, a large body of neurophysiological, perceptual, and behavioral evidence shows at least a partial dissociation between perceptual and visuo-motor responses, which has been interpreted to indicate that these two types of responses are mediated largely by different visual processing streams (Milner & Goodale, 1995; Goodale & Humphrey, 1998). For example, a backward mask that reduces or eliminates the perception of a target stimulus may have little or no effect on the motor RT or on the accuracy of the motor responses to the same target stimulus (e.g., Fehrer & Raab, 1962; Ogmen, Breitmeyer, & Melvin, 2003; Schiller & Smith, 1966; Taylor & McCloskey, 1996). Therefore, whereas the two-stage architecture that we proposed above may apply equally to both the visuo-motor and perceptual systems, the neural structures that constitute these stages are likely to be different. These differences in architecture could explain why the timing differences across different stimulus attributes that are measured by RTs or other motor tasks differ from those based on perceptual judgments.

There is also a second way that we can account for the data reported by Nishida and Johnston. Specifically, the nature of the temporal integration required in Nishida’s and Johnston’s RT experiment is likely to be different from that required in their “perceptual-simultaneity” experiment. In the RT experiment, a motor response needs to be produced as fast as possible. Consequently, the second-stage in our model needs to integrate information from the initial part of the first-stage response only until a criterion level is reached at which the identity of the stimulus within the specified dimension (color or direction of motion) is determined. However, in the “perceptual-simultaneity” experiment, the second stage needs to integrate information for close to the entire target interval in order to establish the degree of temporal synchrony between different stimulus features on the color and motion dimensions. Consequently, Nishida’s and Johnston’s “perceptual simultaneity” task is more similar to a color-correspondence task than to a temporal-order task. As outlined above, we propose that the perceived motion-lag in color-correspondence experiments is attributable to the relative latency difference between the computation of stimulus color and the spatio-temporal integration of direction signals across opponent motion mechanisms. If this proposal is correct, then the same magnitude of motion lag would *not* be expected for RT and “perceptual-simultaneity” experiments, because the tasks in these experiments

involve different types of temporal integration. Quantitatively however, our model predicts that the motion lag in Nishida’s and Johnston’s “perceptual-simultaneity” experiment (in which opponent directions of motion occur sequentially only on the average of every third trial) should be smaller than in their color-correspondence experiment (in which the motion stimulus alternates between opponent directions). Additional experiments to evaluate the effects of interleaving multiple stimulus colors and multiple directions of motion are needed to make a more precise comparison between these two paradigms.

Nishida and Johnston (2002) reported that the perceived motion lag in their color-correspondence experiment decreases systematically with the cycle duration whereas our data indicate that the perceived motion lag is independent of cycle duration. One important difference between the experiment of Nishida and Johnston and the experiments of Moutoussis and Zeki (1997) and ours is the instruction given to the observer. Nishida and Johnston asked their observers to indicate with a yes–no response whether “the oscillation of color and that of direction were perfectly in phase.” Different cues may have been utilized to infer phase synchrony in their experiments, depending on the duration of the motion cycle. When the cycle duration was short, their observers may have performed a color correspondence task because of the large number of rapid color and motion direction transitions. On the other hand, when the cycle duration was longer, their observers may have shifted to using a temporal order judgment to infer phase synchrony between the transitions in color and motion. In the study of Moutoussis and Zeki (1997) and in the current study, the observers were instructed specifically to report the predominant color when the motion was in a certain direction. Our model predicts that for long cycle durations the outcome of the color correspondence task should indicate little or no color-motion asynchrony. For example, for long cycle durations such as those used by Nishida and Johnston (2002), the color-motion asynchronies that are present only near the points when color and motion change in the cycle, will be masked by the large proportion of the cycle that is perceived to be in color-motion synchrony. In other words, because the color correspondence task is based on sustained motion and color information, it is relatively insensitive to color-motion asynchrony in the presence of large intervals of color-motion synchrony.

Viviani and Aymoz (2001) also used a temporal order judgment task and reported that motion perception lags color perception by about 50 ms. In their experiments, observers reported whether a change in color occurred before or after the onset of motion. We performed similar experiments in which the observer reported whether a change in color occurred before or after motion onset (like Viviani & Aymoz, 2001) or motion

offset. Consistent with the predictions of our model for a temporal order judgment task, the data (Fig. 5) do not show a statistically significant motion lag in either the motion-onset (two-tail t -test: $t_{(df=2)} = -0.55$, $p = 0.64$) or the motion-offset (two-tail t -test: $t_{(df=2)} = 1.96$, $p = 0.19$) conditions. Although the difference in color-motion asynchrony between the motion-onset and motion-offset conditions is not statistically significant for our three observers, a small difference in asynchrony remains possible. If so, we would attribute this difference to dissimilar dynamics of the transient motion signals for motion onset vs. offset, for example, because of a persistence of motion signals at motion offset (Shioiri & Cavanagh, 1992).

How can we account for the difference in results in the motion onset condition reported by Viviani and Aymoz (2001), compared to our experiment? An important difference between our experiment and the one reported by Viviani and Aymoz is the stimulus. Viviani's and Aymoz's stimulus was either a large homogeneous circle (diameter = 9.9°) or a square (side = 8.8°). Because the stimuli were homogeneous, the initial movement signals were generated only at eccentric retinal locations. However, these stimuli provide color signals at both eccentric and foveal locations. Thus, the perceived motion lag reported by Viviani and Aymoz (2001) may reflect additional motion processing delays that are introduced when motion signals from the periphery are compared with color signals from the fovea. In our stimulus, on the other hand, the motion and color signals are generated at the same retinal locations and are present simultaneously in the fovea and the periphery.

4.3. Additional psychophysical evidence for the "two-stage sustained-transient" model

The perceived misalignment between a continuously moving and a flashed target (the flash-lag effect) depends on the angle of the motion change (compare the data in Whitney, Cavanagh, & Murakami (2000a) to the data in Whitney, Murakami, & Cavanagh (2000b)), a finding that parallels our data on color-motion asynchrony. Our explanation for the perceived misalignment between the moving and the flashed targets in this paradigm is based on the differential latency between the two neural populations that respond to the moving and to the flashed target (Patel, Ogmen, Bedell, & Sampath, 2000; Purushothaman et al., 1998). Similar to the spatio-temporal integration of the direction of motion, the temporal integration of position information for a moving object would also be expected to depend on the extent to which motion opponency mechanisms are engaged. Therefore, as for the color-motion asynchrony experiments reported here and by Arnold and Clifford (2002), our model accounts also for the dependence of the flash-lag effect on the angle of motion change.

Sheth, Nijhawan, and Shimojo (2000) reported a task-dependent perceptual asynchrony between one stimulus disk that continuously changed its color and a second, flashed disk of a single color. When their observers were asked to perform a color matching task, the results indicate about a 330 ms lag between the perceived color of the continuously changing disk and the perceived color of the flashed disk. However, when the observers were asked to perform a temporal order judgment task, the color change and the flash were perceived to occur simultaneously if, in fact, they occurred physically at almost the same time.

Finally, Clifford, Pearson, and Arnold (2002b) and Clifford, Arnold, and Pearson (2002a) showed that the perceived asynchrony between color and orientation depends on stimulus parameters (the frequency of the attribute changes) as well as whether the observers were instructed to perform a correspondence or a temporal-order judgment. For the correspondence judgment, the perception of orientation lagged the perception of color by approximately 50 ms when the frequency of attribute change was low. This lag decreased with an increase in the frequency of change and vanished at 10 Hz. No significant perceptual lag was observed for the temporal-order judgment task.

Each of the aforementioned findings was obtained for comparisons between different sets of stimulus attributes. In the aggregate, they indicate that the extent of perceptual asynchrony depends on the degree and the frequency of attribute change and on the observers' task. That all of these previous findings can be accounted for qualitatively by our two-stage sustained-transient model provides additional support for the generality of this model.

5. Conclusions

The primate parvocellular and magnocellular pathways provide sustained and transient information to the visual cortex. Sustained and transient mechanisms have been shown to play distinct and often complementary roles in the processing of luminance information by the human visual system (Breitmeyer, 1984; Breitmeyer & Ogmen, 2000). We propose that sustained and transient mechanisms are utilized also within the color and motion (as well as other) processing systems. The task-dependent variations observed in the magnitude of the temporal asynchrony between the perception of color and motion is a direct reflection of this organization, which provides a unified framework to account for the apparent conflict between previous neurophysiological and psychophysical observations. We conclude that various illusory phenomena related to stimulus timing reflect the brain's parallel multiple-input, multiple-output type of computational architecture (stage 1 in our

model) and its remarkable ability to rapidly reconfigure based on the demand placed by the observer's task (stage 2 in our model).

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