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Neural Correlates of Chromatic Motion Perception

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Summary

A variety of psychophysical and neurophysiological studies suggest that chromatic motion perception in the primate brain may be performed outside the classical motion processing pathway. We addressed this provocative proposal directly by assessing the sensitivity of neurons in motion area MT to moving colored stimuli while simultaneously determining perceptual sensitivity in nonhuman primate observers. The results of these studies demonstrate a strong correspondence between neuronal and perceptual measures. Our findings testify that area MT is indeed a principal component of the neuronal substrate for color-based motion processing.

Introduction

Although chromatic motion perception has been studied extensively throughout the past 20 years, its neural basis remains controversial. On the one hand, it is widely agreed upon that the difference between the color of a moving object and the color of the background over which it moves is a potentially valuable cue for detection of motion direction. On the other hand, early reports suggested that the primate visual motion system fails to exploit this cue (Ramachandran and Gregory, 1978; Zeki, 1978; Livingstone and Hubel, 1987). More recent studies, however, have provided compelling psychophysical evidence for color-based motion processing (Cavanagh and Anstis, 1991; Chichilnisky et al., 1993; Cropper and Derrington, 1996; Dobkins and Albright, 1993; Dougherty et al., 1999; Gegenfurtner and Hawken, 1995, 1996; Hawken et al., 1994; Stromeyer et al., 1995; Rezec et al., 2000). Attempts to understand the neuronal basis of this phenomenon have focused on the middle temporal visual area (area MT) of primate cerebral cortex, an area believed to play a key role in motion perception. Several studies have revealed that MT neurons can signal the motion of chromatically defined stimuli (Saito et al., 1989; Dobkins and Albright, 1994, 1998; Gegenfurtner et al., 1994; Seidemann et al., 1999; Thiele et al., 1999). However, a number of differences have been reported to exist between chromatic motion perception in human observers and the sensitivity of MT neurons in nonhuman primates. Such differences have led to the hypothesis that neural activity in area MT is not sufficient to account for chromatic motion processing revealed perceptually, and that other brain regions must contribute significantly to this phenomenon (Cavanagh and Anstis, 1991; Gegenfurtner et al., 1994; Hawken, et al., 1994; Gegenfurtner and Hawken, 1995, 1996; Stromeyer et al., 1995; Cropper and Derrington, 1996).

To address this issue directly, we assessed the sensitivities of individual MT neurons and observers to the motion of chromatically defined stimuli in the same nonhuman primates (rhesus monkeys). For this purpose, we employed an equivalent luminance contrast (EqLC) paradigm, which enables precise quantification of sensitivity for chromatic motion and has previously been applied in human psychophysical studies (Cavanagh and Anstis, 1991; Chichilnisky et al., 1993; Rezec et al., 2000; Thiele et al., 1999) and neurophysiological studies in monkey area MT (Thiele et al., 1999).

The logic behind this EqLC procedure can be understood by considering two patterns of moving stripes (referred to as "gratings"), one of which is yellow/black (achromatic) and the other of which is dark-red/bright-green (heterochromatic). If the luminance contrast is the same in the two gratings, differences in the response of a motion detector to these two stimuli must be due to the chromatic component of the heterochromatic grating. Response differences observed can be eliminated by adjusting the luminance contrast of the achromatic grating. The amount of luminance contrast so added or subtracted represents the sensitivity of the motion detector to chromatic contrast, scaled in units of luminance contrast, i.e., the equivalent luminance contrast of the chromatic (i.e., red/green) component. In practice, this scaling can be performed by superimposing achromatic and heterochromatic gratings and moving them in opposite directions (Figure 1A). If oppositely tuned motion detectors are equivalently sensitive to the two gratings, no motion will be perceived. The luminance contrast difference between the two gratings required to reach this motion "null point" constitutes the EqLC of the chromatic component of the heterochromatic grating (Figure 1B).

In human observers, EqLC is constant over a range of luminance contrasts in the heterochromatic grating (Cavanagh and Anstis, 1991; Chichilnisky et al., 1993; Rezec et al., 2000; Thiele et al., 1999), which means that perceptual sensitivity to chromatic motion does not depend upon the quantity of luminance variation present. In light of this perceptual invariance, we were surprised to discover previously that the EqLC of directionally selective neurons in area MT of monkeys declines precipitously with increasing luminance contrast (See Figure 9 in Thiele et al., 1999). These neurons are, in other words, highly sensitive to the direction of chromatic motion when there is no luminance contrast present, but chromatic contrast has little positive effect (indeed, it often has a negative effect) on neuronal motion

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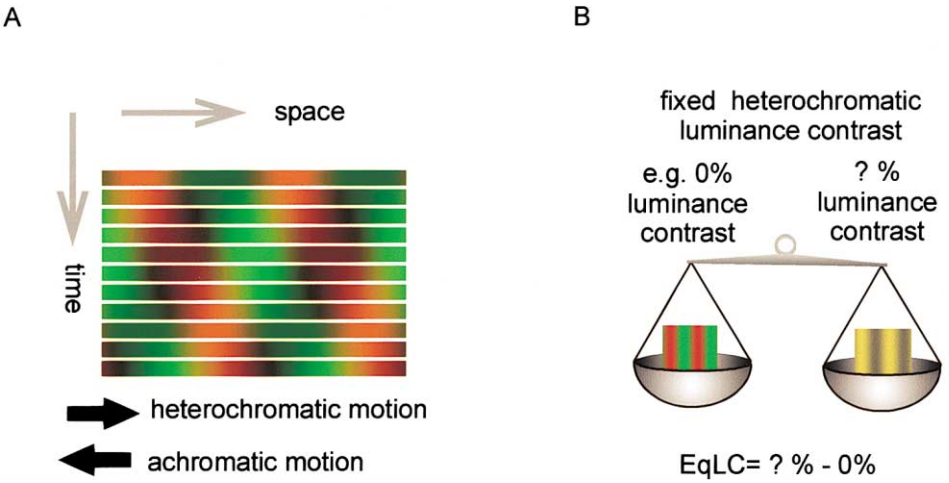


Figure 1. Equivalent Luminance Contrast Paradigm

(A) Space-time plot of the "opposed motion" stimulus. Two superimposed sinusoidal gratings (yellow/black [achromatic] and red/green [heterochromatic]) were moved in opposite direction. (B) EqLC describes the driving power of the chromatic portion of a heterochromatic stimulus, scaled in units of luminance contrast. In practice, EqLC is determined by adjusting luminance contrast of heterochromatic (left side of scale) and achromatic (right side of scale) components until they yield balanced responses (perceptual or neuronal). For the case illustrated, this determination amounts to identifying the achromatic luminance contrast that precisely balances an oppositely moving heterochromatic component of 0% luminance contrast.

detection when accompanying luminance contrast becomes large ($>\sim$20%). This marked difference between EqLC values obtained perceptually in humans and neuronally in monkeys could be due to any of the following: (1) species differences (human versus monkey) in chromatic motion processing, (2) differences in task requirements (humans reported direction, monkeys passively viewed stimuli), or (3) perceptual sensitivity to chromatic motion is not mediated by area MT. In order to distinguish among these possibilities, it was necessary to extend our previous study (Thiele et al., 1999) and obtain perceptual reports from rhesus monkeys while simultaneously recording neuronal activity from area MT (Figure 2).

Results

Example Data

Data from a typical neuron are shown in Figure 3, along with psychophysical data obtained concurrently. Neuronal and perceptual EqLCs were determined using red/green gratings of three different luminance contrasts: 0%, perceptual isoluminance (Figure 3B), −25% (red more luminous than green, R > G, Figure 3A), and +25% (green more luminous than red, G > R, Figure 3C). When the red/green luminance contrast was nil (0%), neuronal EqLC was 11.60% and perceptual EqLC was 10.70%. The magnitude of these values confirms previous findings that chromatic contrast contributes significantly to detection of motion direction when luminance contrast is small or nonexistent (Saito et al., 1989; Dobkins and Albright, 1994, 1998; Seidemann et al., 1999; Thiele et al., 1999). When luminance contrast in the heterochromatic grating was large, however, such that red was more luminous than green (−25%), both neuronal (6.20%) and perceptual EqLC (6.85%) declined markedly. Similarly, when heterochromatic luminance contrast was such that green was more luminous than red (+25%), neuronal EqLC was −0.40% and perceptual EqLC was −3.25%. A close match between neuronal and perceptual EqLC thus existed at all luminance contrast levels tested. Moreover, in contrast to previous findings in human psychophysical observers, perceptual EqLC decreased with increasing luminance contrast, and did so in conjunction with neuronal EqLC.

Population Data

Sixty-two MT neurons from two monkeys were studied precisely as described for the example shown in Figure

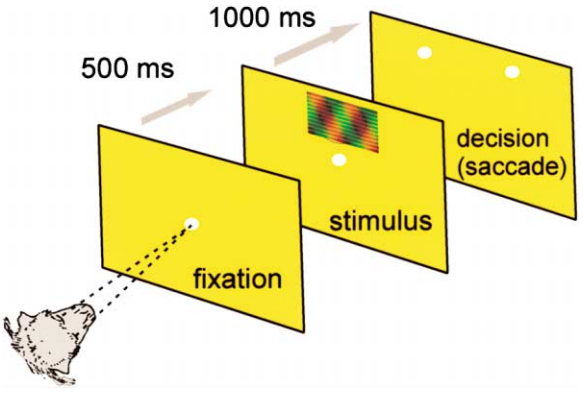


Figure 2. Paradigm for Receptive Field Stimulation and EqLC Determination

Animals were required to fixate a 0.2° target for the duration of each trial. Following a 500 ms prestimulus period, the opposed motion stimulus appeared for 1000 ms, centered on receptive field (small outlined circle) of the neuron under study and with stimulus motion direction aligned with preferred axis of motion. Each successfully fixated trial concluded with the appearance of two peripheral targets placed along the axis of stimulus motion direction. Animals were required to indicate perceived direction via an eye movement to the appropriate target. (The opposed motion stimulus is illustrated in space-time. Subjects actually viewed a 2D spatial configuration that varied in time, i.e., moved.)

3. A plot of the neuronal EqLC for each neuron versus the simultaneously obtained perceptual EqLC appears in Figure 4A. Three data points are shown for each neuron, one for each heterochromatic luminance condition (coded by color). Individual neurons may have higher or lower EqLC values than the monkey observer, as revealed by the variability of these measures. On average, however, both neuronal and perceptual measures were influenced by stimulus changes, and they were so to a similar degree. This point is further emphasized in Figure 4B, wherein mean neuronal and perceptual EqLCs are plotted as a function of heterochromatic luminance contrast. Consistent with the example shown (Figure 3), the effective driving power of chromatic contrast was high, both neuronally (mean EqLC = 11.64 ± 6.62) and perceptually (mean EqLC = 9.58 ± 1.69), when there was little or no accompanying luminance contrast. This power declined as luminance contrast was added to the heterochromatic component (−25% contrast (R > G): neuronal EqLC = 2.92 ± 5.92, perceptual EqLC = 1.97 ± 3.45; 25% contrast (G > R): neuronal EqLC = 2.02 ± 5.14, perceptual EqLC = −0.33 ± 3.21), and this effect was significant [two-factor ANOVA (factor 1: luminance contrast, factor 2: EqLC type, i.e., perceptual versus neuronal EqLC), main effect of luminance contrast: $p < 0.001$]. In addition, there was a small but significant difference between perceptual and neuronal EqLC measures (main effect of EqLC type: $p < 0.05$). Most importantly, however, the effect of luminance contrast on EqLC was similar for both neuronal and perceptual measures, as evidenced by the absence of a significant interaction between luminance contrast and EqLC ($p > 0.05$).

An additional 53 MT neurons were studied using a procedure that differed slightly from that described above (see Figure 3), and which permitted a more direct comparison to previous reports of MT neuronal EqLC (Thiele et al., 1999). For these neurons, the luminance contrast in the achromatic grating was fixed (15% and 25%), while the luminance contrast in the heterochromatic grating was adjusted to obtain the point of equivalence with the achromatic grating. This second approach is a complement of the first and the data obtained were qualitatively similar: For the 15% achromatic luminance contrast condition, the mean neuronal and perceptual EqLCs were 3.41 ± 4.28 and 2.42 ± 1.86, respectively. Neuronal and perceptual EqLC values for the 25% contrast condition were 1.91 ± 3.10 and 0.14 ± 2.18, respectively, which reflects a significant decline as a function of increasing luminance contrast (2-factor ANOVA, main effect of luminance contrast, $p < 0.001$). Notably, neuronal EqLC values were nearly identical to those obtained using this stimulus approach in our previous study (Thiele et al., 1999), in which animals were not required to perform the motion discrimination task.

Effects of Temporal Frequency

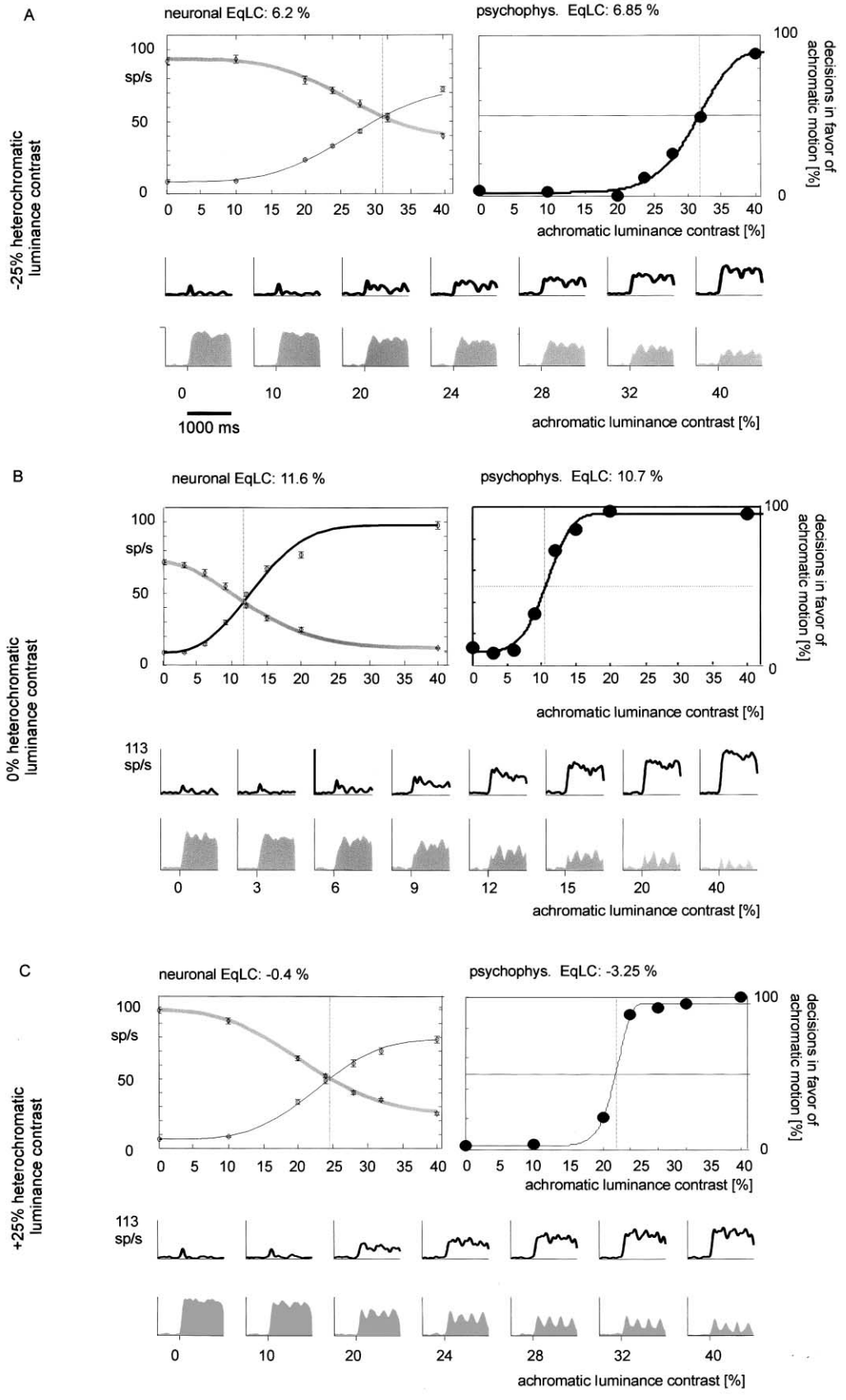
Psychophysical studies have suggested that two different mechanisms of chromatic motion processing exist in the primate brain (Gorea et al., 1993; Gegenfurtner and Hawken, 1995), one active at low temporal frequency and the other active at high temporal frequency. We therefore investigated whether the correspondence between neuronal and psychophysical data was dependent upon temporal frequency. The data presented above (Figures 3 and 4) were obtained using stimuli of relatively low temporal frequency (2 Hz). An additional sample of neurons (n = 11) was tested using stimuli of higher temporal frequency (8 Hz). Under these latter conditions, neuronal (12.9 ± 3.49) and perceptual (9.70 ± 2.16) EqLCs were high at isoluminance, and declined significantly when luminance contrast was added to the red/green grating (−25% contrast (R > G): neuronal EqLC = 0.27 ± 7.21, perceptual EqLC = −1.60 ± 3.91; 25% luminance contrast (G > R): neuronal EqLC = −2.86 ± 5.83, perceptual EqLC = −3.50 ± 4.23 [two factor ANOVA, $p < 0.05$]). This similarity of neuronal and perceptual EqLC across different temporal frequencies does not support the proposal that different mechanisms underlie chromatic motion processing at high versus low temporal frequencies (Gorea et al., 1993; Gegenfurtner and Hawken, 1995). Furthermore, the marked similarity between patterns of neuronal and perceptual EqLCs reported here forestalls the need to assign chromatic motion processing to brain regions other than MT or to higher order mechanisms (but see Discussion).

Human Perceptual EqLC

Our finding of a negative interdependence between the effects of chrominance and luminance cues on detection of motion direction in monkeys lies in stark contrast to human psychophysical data (Cavanagh and Anstis, 1991; Chichilnisky et al., 1993; Rezec et al., 2000; Thiele et al., 1999). To rule out the possibility that this discrepancy is due to unintended stimulus differences, and to facilitate comparison of the present results with published human psychophysical data, we conducted an additional experiment to assess human perceptual EqLC. Under stimulus conditions identical to those used for the monkey study reported herein, human EqLC was found to be near 10% (Figure 4B, stippled line) at all contrast levels tested (−25% luminance contrast (R > G): EqLC = 10.55%; 0% luminance contrast (perceptual isoluminance): EqLC = 10.8%; +25% luminance contrast (G > R): EqLC = 8.25%), which confirms previous reports (Cavanagh and Anstis, 1991; Chichilnisky et al., 1993; Thiele et al., 1999; Rezec et al., 2000).

Discussion

By eliminating species and behavioral task differences, we have revealed a close match between patterns of neuronal and perceptual sensitivity to the motion of chromatically defined stimuli. Our results thus provide direct evidence that neuronal activity in MT is sufficient to account for perception of both luminance and chromatically defined stimuli under the current task conditions. It might nevertheless be argued that MT is not sufficient to account for psychophysical sensitivity under different task conditions, e.g., when contrast sensitivity for direction of motion is tested. It has, for example, been reported that sensitivity of MT neurons to chromatic motion at slow speeds is substantially lower than behavioral sensitivity (Gegenfurtner et al., 1994). An additional argument against the claim that MT is crucial for all aspects of chromatic motion processing comes


A
neuronal EqLC: 6.2 %
psychophys. EqLC: 6.85 %
-25% heterochromatic luminance contrast
100
sp/s
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0 5 10 15 20 25 30 35 40
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B
neuronal EqLC: 11.6 %
psychophys. EqLC: 10.7 %
0% heterochromatic luminance contrast
100
sp/s
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psychophys. EqLC: -3.25 %
+25% heterochromatic luminance contrast
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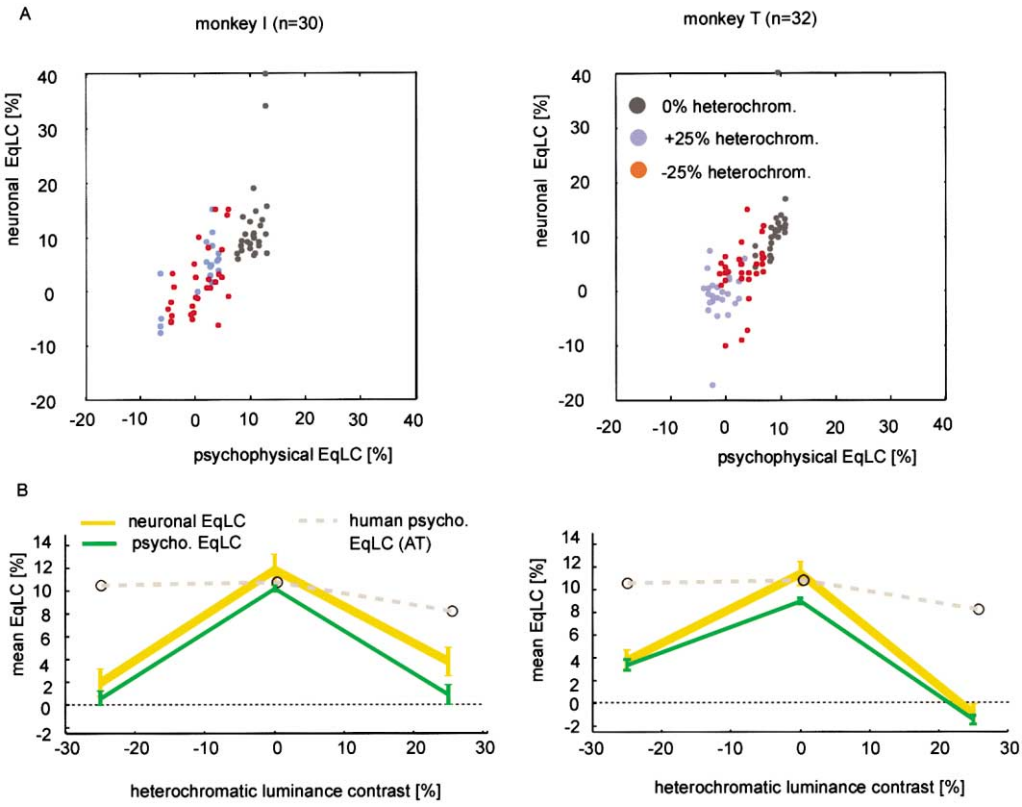

Figure 4. Relationship between Neuronal and Perceptual EqLC

(A) Data are plotted separately for each of two animals. Each data point represents a pair of simultaneously determined neuronal and perceptual EqLCs. Three such measures were obtained for each neuron sampled, one for each of three heterochromatic luminance contrasts. In response to these different stimulus conditions, neuronal and perceptual EqLC values varied in parallel. (B) Comparison of average perceptual and neuronal EqLC as a function of heterochromatic luminance contrast. Yellow line denotes neuronal EqLC; green line denotes perceptual EqLC. Both decreased significantly with increased heterochromatic luminance contrast (two way ANOVA, factor luminance, $p < 0.001$). Gray line indicates human EqLC (subject AT) obtained under same stimulus conditions.

from the finding that, in humans, the most sensitive mechanism for identifying direction of motion exhibits color opponent properties (Stromeyer et al., 1995), whereas MT neurons appear to lack such opponency.

These arguments advise caution when interpreting the generality of our findings. Nonetheless, we emphasize that our discovery of a strong correlation between neuronal and perceptual measures of chromatic motion sensitivity was a product of a study in which neuronal and psychophysical data were obtained simultaneously from the same subjects. Further studies of this latter type are needed to determine whether a similar association between MT and perceptual responses exists for a wider range of chromatic motion stimuli.

Motion Processing Differences between Humans and Monkeys?

Having equated stimulus and task conditions, our data reveal a surprising difference in chromatic motion processing for humans and rhesus monkeys. We can now speculate on the causes for this difference. One possibility is that it reflects a fundamental and heretofore unrevealed difference in the organization and function of the visual systems between the two species. Although this explanation is impossible to discount at present, it is not particularly compelling in view of the substantial body of behavioral, anatomical, physiological, and functional imaging data that demonstrate strong similarities between the visual systems of humans and monkeys.

Figure 3. Neuronal and Perceptual Responses to the Opposed Motion Stimulus

Each neuronal/perceptual EqLC comparison was performed at three heterochromatic luminance contrasts: (A) −25% luminance contrast (R > G), (B) 0% luminance contrast (perceptual isoluminance—see Experimental Procedures), (C) +25% luminance contrast (G > R). Gray PSTHs illustrate activity recorded when heterochromatic component moved in preferred direction (achromatic component moved simultaneously in antipreferred direction). Black outlined PSTHs illustrate activity for opposite directional polarity. *Upper-left graph in each panel*: mean and standard error of neuronal response (sp/s) as a function of achromatic luminance contrast. Neuronal EqLC was determined from intersections of Weibull fits to these data points. *Upper-right graph in each panel*: psychophysical data obtained simultaneously with neuronal data. Depicted is the proportion of decisions in favor of achromatic motion direction, as a function of luminance contrast in achromatic grating. Perceptual EqLC was determined from null point (point at which perceived direction of motion was equally likely in favor of either stimulus component).

Nonetheless, some quantitative differences between humans and monkeys do exist as early as the retina (Mollon and Bowmaker, 1992; Jacobs and Deegan, 1997; Dobkins et al., 2000), and it would perhaps not be surprising to encounter differences in the organization of chromatic motion processing. A second, but not mutually exclusive, possibility is that the observed behavioral difference reflects use of different strategies to solve the motion discrimination task. For example, it is possible that monkeys attend globally to the motion stimulus, whereas humans focus on individual features, and that this difference affects EqLC values. Final resolution of this issue will likely come from imaging of neuronal signals in human observers, as well as efforts to ensure that humans and monkeys adopt the same behavioral strategy.

Source of Chromatic Signals for Motion Detection

Signals carrying information about chromatic motion could arise in the magnocellular (M) and/or parvocellular (P) pathways. The largest fraction of input to area MT arises from the M pathway, although some contribution stems from the P-pathway (Maunsell et al., 1990). In order to determine the likely source of signals that govern perceptual EqLC, Cavanagh and Anstis (1991) tested whether a model based upon the variance of M cell isoluminant points or, alternatively, a model based upon color-opponent P cell responses predicted perceptual EqLC (see also Thiele et al., 1999). While the M cell model predicted that EqLC should decrease with increasing luminance contrast, the P cell model predicted EqLC to be independent of luminance contrast, which is a property characteristic of human psychophysical data (Cavanagh and Anstis, 1991; Thiele et al., 1999). Cavanagh and Anstis argued from this analysis that P cells contribute substantially to chromatic motion perception. Other recent psychophysical evidence from human observers appears to support this interpretation (Stromeyer et al., 1995; Gegenfurtner and Hawken, 1995; Cropper and Derrington, 1996). By contrast, the results of our previous neurophysiological studies in monkeys (Dobkins and Albright, 1994, 1998; Thiele et al., 1999) point to a significant M cell contribution. The M cell model also offers the most parsimonious explanation for the perceptual and neuronal effects in monkeys reported herein (for a detailed discussion, see Thiele et al., 1999). Full resolution of this discrepancy will require a better understanding of the reasons for the observed perceptual EqLC differences between humans and monkeys (see above).

Is Chromatic Motion Processing a Product of an Attention-Based System?

A variety of psychophysical studies have demonstrated that attention plays a prominent role in human chromatic motion perception (Cavanagh, 1992; Lu et al., 1999; Rezec et al., 2000). Lu et al. (1999) have even argued that chromatic motion perception is exclusively a product of an attention-based ("third-order") motion system. To address this provocative proposal, we have compared neuronal EqLC data obtained under the conditions of the present experiment (which required attention to the opposed motion stimulus) to those previously obtained under "fixation only" conditions (which did not require attention to the motion stimulus, Thiele et al., 1999, mean EqLC values: approximately 5% when the red/green grating was near isoluminance and approximately −2% when it contained 25% luminance contrast). These different attentional conditions yielded nearly identical neuronal EqLC values, as well as similar effects of luminance contrast on EqLC values, suggesting that low level motion mechanisms are sufficient to account for chromatic motion perception of the type studied. Although sufficiency is not equivalent to proof, our data are thus unsupportive of the proposal that chromatic motion perception is exclusively a product of an attention-based motion subsystem (Lu et al., 1999).

Experimental Procedures

Experiments were conducted, in part, using methods described previously (e.g., Thiele et al., 1999). In brief, rhesus monkeys (*M. mulatta*) were trained to fixate gaze upon a small spot on a video display, and to maintain fixation during the presentation of a moving visual stimulus. Following each stimulus presentation, animals were required to indicate direction of perceived motion by a saccadic eye movement to a peripheral target. During stimulus presentation, we recorded the responses of single isolated neurons in the middle temporal area (area MT) using microelectrodes lowered into that region of visual cortex. Additional details and exceptions to these general procedures are provided below. Protocols for all experiments were approved by the Salk Institute Animal Care and Use Committee, and conformed to USDA regulation and NIH guidelines for the humane care and use of laboratory animals.

Apparatus

Visual stimuli were generated using a SGT Pepper Graphics board (Number Nine Computer Corporation: 640 × 480 pixel resolution, 60 Hz frame rate) residing in a Pentium II-based PC, and were displayed on a 20″ analog RGB monitor (Sony GDM 2000TC, 60 Hz, noninterlaced). Linearization of monitor output was achieved for each of the three phosphors independently. Stimuli were generated under the charge of CORTEX 5.7 (Lab of Neuropsychology, NIMH), which was also used for data acquisition and behavioral control.

Visual Stimuli

For a detailed description of stimulus properties, see Thiele et al. (1999). Briefly, visual stimuli were of three basic types: (1) achromatic gratings, (2) heterochromatic gratings, and (3) "opposed motion" stimuli. Achromatic and heterochromatic gratings were generated by conventional means (Dobkins and Albright, 1994; Thiele et al., 1999). The achromatic gratings were used for initial characterization of the directional tuning of each cell. Both achromatic and heterochromatic gratings of various luminance contrasts provided a set of "directionally unambiguous" stimuli that were interleaved with near-threshold opposed motion stimuli to maintain behavioral control in the direction discrimination task (see Behavioral Paradigm, below).

The opposed motion stimuli were the principal experimental stimuli used to determine neuronal and perceptual EqLC values. These stimuli were generated by spatial superimposition of achromatic (yellow/black) and heterochromatic (red/green) sinusoidal gratings (Figure 1A) moving in opposite directions. Component gratings were 0.4 cyc/°, and were moved at 2 Hz (or 8 Hz in some experiments). Mean stimulus luminance was 24 cd/m^2, on a yellow background of equal luminance. Stimuli were viewed through a 4.7° rectangular window from a distance of 60 cm.

Stimulus Conditions

Either the heterochromatic or achromatic component of the opposed motion stimulus could move in the preferred direction of the neuron under study. This "directional polarity" was one of three independent variables. The luminance contrasts of the achromatic and heterochromatic component gratings constituted the two addi-

tional independent variables. These three variables were manipulated to create a set of stimulus conditions that enabled determination of neuronal and perceptual EqLC values. Different stimulus conditions appeared in a pseudo-random sequence.

In practice, EqLC was determined perceptually and for each neuron by response nulling procedures (described below). Two complementary sets of stimulus conditions were used to obtain these EqLC measures:

- Stimulus Set #1: Heterochromatic luminance contrast was fixed (i.e., "reference grating") at one of three values: 0%: red and green isoluminant (see below); −25%: red more luminous than green (R > G); +25%: green more luminous than red (G > R). EqLC was determined for each of these conditions by pitting them against achromatic gratings of various contrasts (i.e., "test gratings"), optimized individually for each condition (see Figures 3 and 4). Seventy-three neurons were tested under these conditions.
- Stimulus Set #2: Reference and test grating types were swapped, relative to Stimulus Set #1. Thus achromatic luminance contrast was fixed at 15% or 25%. EqLC was determined by pitting each of these reference components against heterochromatic test gratings of various luminance contrasts, which ranged from −45% (R > G) to +45% (G > R). This method yielded two null points: one occurring when the heterochromatic grating was such that red was more luminous than green, the other occurring when green was more luminous than red (see reference 13 for details). Fifty-three neurons were so tested.

Heterochromatic luminance contrast was referenced to each animal's perceptual isoluminance point. The latter was predetermined by obtaining psychophysical data using Stimulus Set #2. Specifically, the two heterochromatic stimuli of opposite luminance polarity that each yielded a null point were considered of equal salience. Hence, the luminance contrast determined to be midway between these points was defined as the point of perceptual isoluminance.

MT Recordings

We studied a total of 126 MT neurons in two monkeys (*M. Mulatta*). All data reported here were taken under conditions of single-unit isolation. For each MT neuron tested, the receptive field was mapped initially using a white bar moving on a gray background. The preferred direction for the neuron was determined from its directional tuning curve, obtained by presenting moving achromatic gratings (0.7 cycles/°, 4 Hz, 100% Michelson contrast) in eight different directions.

Behavioral Paradigm

Behavioral task conditions and requirements are described here for experiments conducted using monkeys as subjects. The paradigm used for human psychophysics was similar; significant exceptions are noted below.

Visual stimuli were presented in a trial format (see Figure 2). Each trial began with the appearance of a small (0.2°) fixation target at the center of the video display. After the animal stably directed gaze to the fixation target, a visual stimulus appeared and remained present in the visual field for an additional 1000 ms. Following stimulus presentation, two targets appeared equidistant from the moving stimulus, aligned with the axis of motion, and each corresponding to one of the two possible directions of motion. Following target appearance, monkeys indicated perceived direction of motion via a saccadic eye movement to one of the targets. "Correct" responses (see below for definition of "correct") were rewarded with a drop of juice, and followed by a brief (1–2 s) inter-trial interval. Error trials were terminated without reward. Trials were aborted if eye position deviated from the fixation target (fixation window = ±0.7°) at any time prior to appearance of the saccade-choice targets.

In practice, only approximately two-thirds of the moving stimuli were "unambiguous," in the sense that the correct behavioral response could be defined objectively. Single heterochromatic and achromatic gratings of various luminance contrasts constituted the majority of unambiguous stimuli presented. Their presence ensured that monkeys reliably reported perceived direction of motion. In addition, opposed motion stimuli were considered unambiguous if they yielded >90% decisions in favor of one of the components upon first day encounter after extensive exposure to single moving gratings. The reward schedule employed on each trial depended upon whether the stimulus was ambiguous or unambiguous: upon presentation of ambiguous stimuli, animals were allowed to choose either target to obtain reward. By contrast, correct decisions were enforced upon presentation of unambiguous stimuli.

Computing Neuronal EqLC

These measures were obtained by calculating the average spike rate during stimulus presentation. Weibull functions were fitted to these means, separately for each heterochromatic luminance contrast and for each directional polarity of the opposed motion stimulus. Using Stimulus Set #1, the two directional polarities yielded oppositely directed response functions (one increasing with luminance contrast, the other decreasing; see Figures 3A, 3B, 3C, gray and black lines in the upper left inset). Neuronal "motion null" points were interpolated from the intersections of the fitted Weibull functions. Each intersection corresponds to a luminance balance in the opposed motion stimulus that rendered the neuron insensitive to directional polarity of that stimulus. Neuronal EqLC was calculated as the difference between the luminance contrasts of reference and test gratings at which motion null occurred.

Using Stimulus Set #2, two motion null points were obtained (one each for red-brighter-than-green and green-brighter-than-red); EqLC was computed as the mean of the absolute difference between the luminance contrasts of reference and test gratings.

Computing Perceptual EqLC

Perceptual motion null was defined as the point at which perceived direction was equally likely in favor of either component of the opposed motion stimulus. Similar to neuronal EqLC, perceptual EqLC was computed as the difference between the luminance contrasts of reference and test gratings at which motion null occurred.

Data used to compute neuronal and perceptual EqLC values were obtained on concurrent trials. A pair of neuronal/perceptual EqLC values was retained in the data pool if (1) the neuron was directionally selective, (2) at least ten trials were recorded for each stimulus conditions, and (3) Weibull "Goodness of fit" was acceptable for neuronal and perceptual data sets, based on chi-square fitting procedure.

Human Psychophysics

Stimulus conditions and display methods for our human subject were identical to those employed for monkeys (see above). Stimuli were 4.7° × 4.7°, presented at an eccentricity of 2.3°, which corresponded to the mean eccentricity of the neuronal RFs sampled. The human observer reported perceived direction of motion by a keypress.

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