Interaction of motion and color in the visual pathways

Karl R. Gegenfurtner and Michael J. Hawken

In recent years the idea of parallel and independent processing streams for different visual attributes has become a guiding principle for linking the organization, architecture and function of the visual system. Findings concerning the segregation of motion and color information have been at the forefront of the evidence in favor of the parallel processing scheme. A number of studies have shown that motion perception is impaired for isoluminant stimuli, which are thought to isolate the color system. However, there are now many studies, the results of which are incompatible with the simple idea of segregated pathways. We propose two processing streams for motion that differ mostly in their temporal characteristics. Although neither of the two motion streams is color-blind, as was originally suggested, they differ radically in the way they process color information. The view that we propose provides a framework that reconciles a number of seemingly contradictory results. Evidence to support the new framework comes from psychophysical, physiological and lesion studies.

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THE SEPARATION of color and motion has always been a cornerstone in the argument for separate processing pathways[1–3]. The characteristics of neuronal responses in the extrastriate cortical areas MT and V4, with their strong selectivity for motion and color, respectively[1], seem to reflect closely the properties of magnocellular (M) and parvocellular (P) neurons at the level of the retina and lateral geniculate nucleus (LGN)[4–6]. In areas V1 and V2, the anatomical segregation into compartments with differential staining for the mitochondrial enzyme cytochrome oxidase (CO) suggests a 1–1 correspondence between geniculate and extrastriate pathways[7–10]. According to this proposal the M-pathway processes motion while the P-pathway processes color and form information. Because magnocellular neurons show poor color selectivity[4–6], it was assumed that a pure chromatic contrast invisible to M-cells would also be invisible to the motion pathway.

Pure chromatic contrast is an attribute of isoluminant stimuli, which are defined exclusively by variations in chromaticity and do not have any luminance contrast (see Box 1). If the motion system receives input from neurons in the visual pathway that only respond to luminance modulation and not to isoluminant modulation, then an isoluminant stimulus will effectively silence or 'lesion' the motion pathway. The idea of making a selective functional 'lesion' of specific brain areas by using a simple visual manipulation was novel and potentially very revealing, since the corresponding anatomical lesion experiments are extremely difficult to accomplish[11,12]. However, the past two decades have seen a large number of experiments investigating the responses of the motion system (and other systems) to isoluminant stimuli, and the results have called the simple notion of a color-blind motion system into question. On one hand, there are experiments showing that motion processing is impaired at isoluminance or that it is qualitatively different from the processing of luminance-defined motion[13–22]. Isoluminant stimuli appear to move slower than luminance stimuli, and their direction of motion cannot be identified at the threshold for seeing these patterns. On the other hand, there are experiments that conclusively show that, under certain conditions, color and motion interact suggesting that they share a common neuronal pathway[14,23–30]. For example, isoluminant stimuli can induce a motion after-effect on luminance stimuli[23–25], or they can cancel the motion of luminance stimuli drifting in the opposite direction[29]. All these perceptual results together are not compatible with the notion of a single motion pathway that is color-blind. We will present the results of psychophysical and physiological experiments, which show that there is no strict separation between color and motion *per se*. Rather, we will argue there are two functional streams that differ mostly in their temporal properties. Both process color and motion information, but in fundamentally different ways. There is a fast motion pathway that veridically represents the velocity of moving patterns, and that also gives a response to isoluminant patterns but might not code the color of such patterns. A second slow pathway has a high sensitivity to color, and signals the direction of slowly moving patterns, but its coding of stimulus velocity is not veridical.

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Psychophysics: threshold measurements

One procedure that has been widely used in psychophysics to indicate the involvement of a specific perceptual mechanism is to have subjects perform a dual detection and identification task. For example, when subjects view a moving sinusoidal grating defined by luminance they can identify its direction of motion as soon they can detect the grating[31]. If the detection and identification thresholds are the same

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Box 1. What is luminance?

Luminance is a photometric quantity that forms the basis for light measurement. Since such measurements are usually carried out by physical devices (photometers), it is often overlooked that the definition of luminance is derived from psychophysical measurements on humans. Such measurements were obtained by the Commission Internationale de l'Eclairage (C.I.E.) in 1924 to define the relative luminous efficiency of a human standard observer under photopic conditions. The definition takes the form of a curve, called V(λ), that specifies how efficient light of each wavelength is in exciting the visual system. Luminance is then defined as the integral over wavelength of the radiance of a source, weighted by the spectral luminosity V(λ). This definition implies that luminance is additive and transitive. A paradigm to compare lights of different wavelength, that also has these required properties, is heterochromatic flicker photometry (HFP), in which the observer adjusts the intensity of two flickering lights until the perceived flicker is minimized. This method formed the basis for the C.I.E. 1924 standard[a,b].

Clearly many different wavelength distributions can lead to the same luminance. One can add light of a long wavelength to a stimulus, and subtract the same amount of light at a shorter wavelength. The result will most likely have a different color, but might well have the same luminance as the original. The two stimuli are therefore said to be equi-luminant, or isoluminant, and will have the same effect on any system that uses a sensor based on luminance. Furthermore, if an image consists of only isoluminant variations, then it should appear uniform to any such system.

The above says nothing about a physiological correlate of luminance in the visual system. Interestingly, one can obtain the V(λ) curve by adding the spectral sensitivities of the medium wavelength-sensitive (M) cones and the long wavelength-sensitive (L) cones, weighting the L cones by a factor of two. The short wavelength-sensitive (S) cones do not seem to contribute significantly to luminance. The summation of L-cones and M-cones in the ratio of 2:1 is similar to the way magnocellular retinal ganglion cells sum their cone inputs[c].

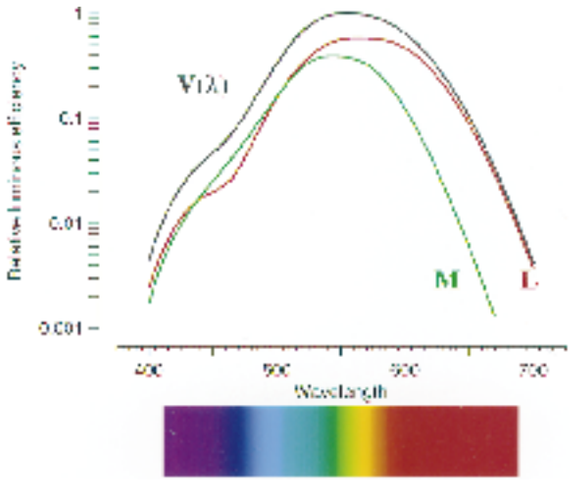

Fig. ***Human luminous efficiency curve V(λ) and cone spectral sensitivity curves.*** *The black curve shows the relative luminous efficiency as defined by the Commission Internationale de l'Eclairage (C.I.E.) in 1924 for a small field (2°) observer. The red and green curves show relative cone spectral sensitivities for the long wavelength-sensitive (L) and the medium wavelength-sensitive (M) cones, respectively[d]. They are scaled at an L:M ratio of 2:1, so that their sum closely approximates the V(λ) curve.*

References

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then this is evidence that movement-selective mechanisms underlie the detection of the stimuli. If the thresholds for detection are lower than for identification then this is evidence for separate mechanisms. We have applied the detection–identification paradigm to tease apart the contributions of luminance and color to the perception of motion. The results of such an experiment are illustrated in Fig. 1A which gives the psychophysically determined thresholds of a human observer for detecting a sinusoidal luminance grating of 1 cycle degree^{-1} (open circles) and for identifying its direction of motion (filled circles) as a function of temporal frequency. For these stimuli of a constant spatial frequency, the temporal frequency and velocity values are equivalent. Sensitivity, defined as the inverse of threshold contrast, is high: at 4 Hz the grating can be seen at 0.5% contrast. It is also quite clear that the threshold for identifying the direction of motion is equal to the detection threshold. Results are different for isoluminant gratings[16–18,20], as is shown in Fig. 1B. At low temporal frequencies, sensitivity for direction of motion (filled circles) is considerably lower than for detection (open circles). One common interpretation of this result is that the color pathway is sensitive to the color of the stimulus, but not to its motion. The sensitivity for motion – at sufficiently high contrasts the motion of the isoluminant grating can be seen – is often attributed to residual processing by the luminance-based motion mechanism[33].

In many studies sensitivity of the color system is defined in terms of the modulations of the phosphors on a color TV monitor. This definition is hardly a meaningful measure when dealing with the visual system. It obscures the fact that isoluminant stimuli generally present lower excitations for the retinal cones, which are the input stage to the visual system. When contrast is defined in terms of cone contrast[32,34–36], as in Fig. 1B, it is found that the sensitivities for isoluminant stimuli exceed those for luminance stimuli. This makes it highly improbable that a luminance-based mechanism would underlie motion identification of isoluminant stimuli. In the next section we will investigate the chromatic nature of the underlying motion mechanism in more detail. Figure 2A illustrates the color space spanned by the contrasts in the long and middle wavelength-sensitive cones. We can reasonably neglect the short wavelength-sensitive cones here, since their contribution to motion perception is known to be very small[32,37]. For a luminance stimulus the contrasts of L- and M-cones are of equal sign and magnitude (positive diagonal). For isoluminant stimuli any increase in L-cone excitation has to be balanced

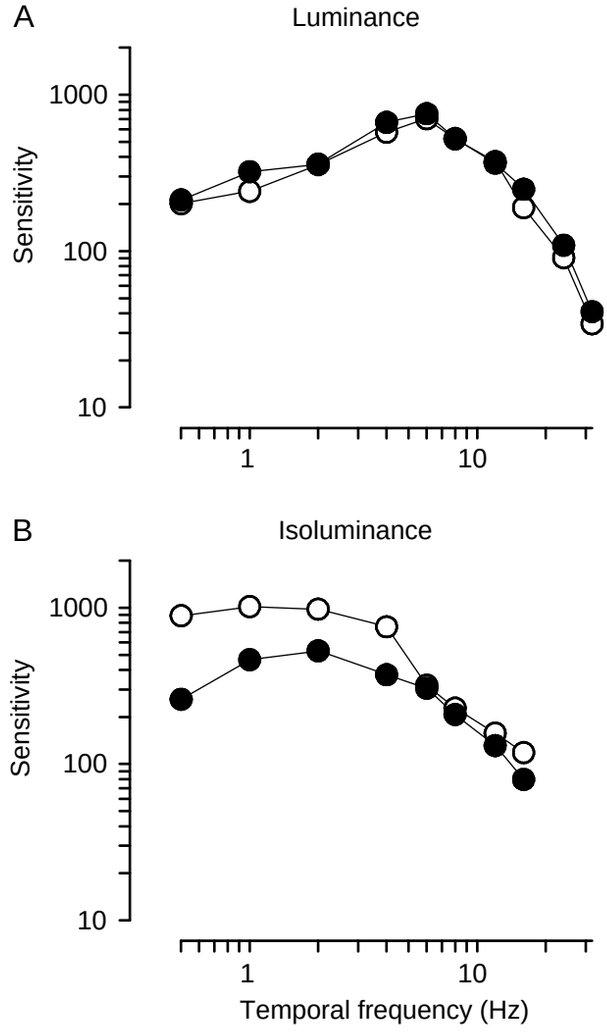

Fig. 1. ***Psychophysical thresholds for detecting moving patterns and identifying their direction of motion.*** **(A)** *Luminance gratings.* **(B)** *Isoluminant red–green gratings. Cone contrast sensitivity is given as a function of temporal frequency for the detection (open symbols) and identification (filled symbols) of a foveally presented sinewave grating of 1 cycle degree^{-1} for subject CT. Cone contrast sensitivity is the reciprocal of the root-mean-squared (RMS) cone contrast of the L- and M-cones at threshold: RMS = $[((\Delta L/L)^2 + (\Delta M/M)^2)/2]^{1/2}$, where L and M are the average cone excitations, and ΔL and ΔM are the differences between the peak excitations and the mean excitations for the L- and M-cones, respectively. For luminance stimuli the L- and M-cone contrasts are equal and therefore identical to the RMS cone contrast.* Figure reproduced from Ref. 32.

by a decrease in M-cone excitation. Therefore the cone contributions have different signs (line with negative slope). The colored insets in Fig. 2A show the appearance of stimuli that differentially modulate the L- (x-axis) or M-cones (y-axis). Both appear as red–green modulations; the similarity in their appearance is due to the overlap of their absorption spectra[38]. Therefore the maximum cone contrast that can be produced for isoluminant gratings modulated symmetrically around a neutral white point is about 30% for the L- and M-cones, much lower than the 100% contrast that can be attained for luminance stimuli. This narrower range is illustrated in Fig. 2A by the length of the arrow along the isoluminance direction; the even narrower range that can be produced on typical CRT monitors is indicated by the closed contour running close to the luminance direction.

The lower graphs show the results of our threshold measurements in this cone contrast space. Figure 2B shows the results for slow-moving gratings. In accordance with Fig. 1 thresholds are lowest in the isoluminance direction, and thresholds for detection (open symbols) are consistently lower than thresholds for identification of direction of motion (filled symbols) for most color directions close to isoluminance. What is even more remarkable is that the contour is running parallel to the luminance direction. For the majority of stimuli in Fig. 2B only the magnitude of the difference in L- and M-cone contrasts determines their visibility, whether for detection (open circles) or for motion identification (closed circles). In other words, the mechanism that underlies the detection and identification of these stimuli is color-opponent. As temporal frequency increases, the sensitivity to luminance patterns increases, while the sensitivity to isoluminant patterns decreases. The point of equal sensitivity is reached at about 4 Hz (Ref. 32). Only at high temporal frequencies (16 Hz; Fig. 2C) do the results conform to the conventional expectation, high sensitivity for luminance stimuli, and low sensitivity for isoluminant stimuli. At high temporal frequencies the thresholds for detection and motion identification are equal[32].

Recently Cropper and Derrington[39] have also convincingly shown that a color-opponent mechanism can underlie direction of motion judgements for isoluminant stimuli. In their experiments the motion of an isoluminant grating could not be masked by a luminance grating, and was visible at extremely short presentation durations (17 ms). Furthermore, their experiments show that a mechanism with a response to unsigned image contrasts, such as the frequency-doubled response which is observed in magnocellular LGN neurons[40], could not underlie the identification of motion. Therefore we can conclusively refute the idea that the color system is blind to motion, and that the motion system is blind to color. Not only is the sensitivity for the motion of slowly moving isoluminant stimuli quite exquisite, the underlying mechanism is also chromatically opponent. It is only at higher temporal frequencies that the sensitivity of the luminance-based mechanism increases differentially.

Psychophysics: perceived speed

The relevance of threshold measurements to perception is often questioned. Some caution is required in drawing strong conclusions based on threshold measurements alone. And, in fact, the most impressive evidence for a separation of color and motion actually comes from measurements of the perceived speed of suprathreshold stimuli. Cavanagh, Tyler and Favreau[14] showed that perceived speed is dramatically reduced for isoluminant stimuli. In their experiments the subjects had to adjust the speed of a 10% contrast luminance grating so that it matched the speed of a highly saturated red–green grating moving at a constant speed. They varied the luminance contrast of the red–green grating and found that at the point of isoluminance (when the red and green grating bars had the same luminance), the red–green grating was perceived to move at about 40% of the speed of the luminance grating. As mentioned previously, the difficulty in making a straightforward conclusion from this experiment is that the contrast of luminance and isoluminant

gratings cannot be readily compared. The problem of unmatched contrasts is compounded by the observation that contrast can have a marked effect on the perceived speed of luminance stimuli; a black and white grating of low contrast is perceived to be moving at a lower speed than a grating with a higher contrast[41,42]. Since the maximum contrast attainable in the cones is limited under isoluminant conditions, it might well be that isoluminant stimuli are perceived to move slower simply owing to their lower contrast. What if we compare a luminance grating of lower contrast to isoluminant gratings of even higher chromatic contrast? Rather than trying out all possible combinations of contrasts, comparing the perceived speed of luminance to isoluminant stimuli, we chose to examine perceived speed as a function of contrast for both luminance and isoluminant gratings[43]. Since earlier experiments[14,32,36,41,44] suggested an effect of temporal frequency as well, this variable was also systematically varied in our experiments.

Figure 3A presents the results for slowly moving luminance and isoluminant gratings of 1 Hz. If speed perception was indeed contrast invariant, then all data points should fall on the dashed horizontal line. The positive slopes indicate that stimuli of higher contrast are perceived to move faster. However, the slope is different for luminance and isoluminant gratings. The contrast dependence is much steeper for isoluminant gratings. Since the slope of the contrast versus perceived speed line is independent of the contrast scale on log coordinates, the comparison of slopes is a meaningful procedure. The difference in slopes implies that isoluminant stimuli do not act simply as low-contrast luminance stimuli. At some point the isoluminant stimuli must actually be processed by different neural pathways from the luminance stimuli.

Figure 3B shows that for fast-moving stimuli of 8 Hz the results are quite different from those obtained for slowly moving targets. Speed perception is contrast invariant for both luminance and isoluminant stimuli, suggesting that there is no difference in the processing of luminance and isoluminant stimuli. Remarkably, once luminance stimuli are above the detection–discrimination threshold then the speed judgements remain constant across about 2 log units of contrast[43]. The invariance of speed judgements with stimulus contrast and chromaticity is consistent with the idea of a motion pathway that is invariant to any changes in stimulus parameters other than speed and direction[45].

The results of our experiments on perceived speed are consistent with our threshold experiments.

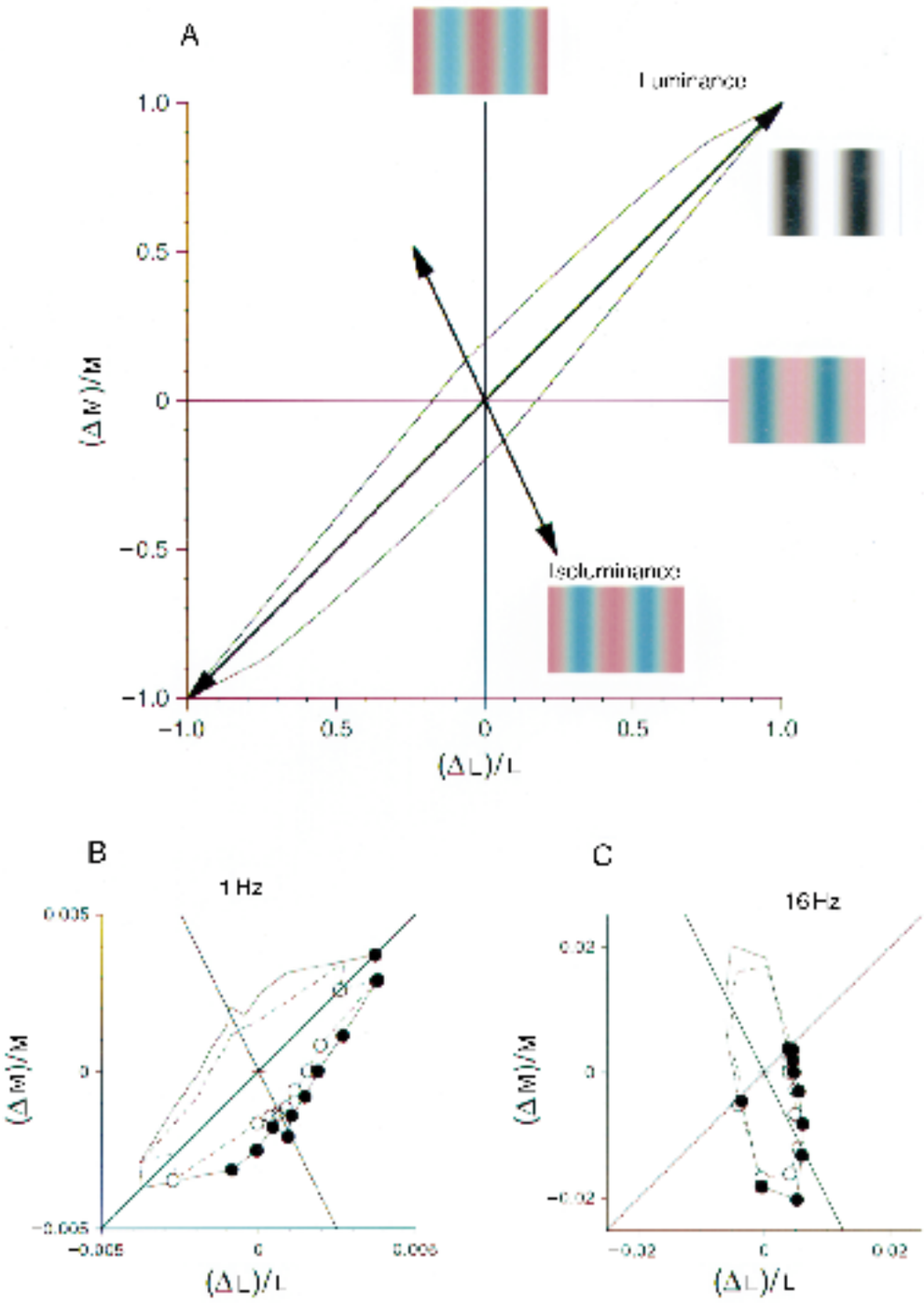

Fig. 2. ***Psychophysical threshold contours in a cone contrast space.*** **(A)** *Illustration of the color space used for threshold measurements. The horizontal axis shows the contrast of the long wavelength-sensitive (L) cones, the vertical axis shows the contrast of the middle wavelength-sensitive (M) cones. The thick lines through the origin indicate the directions for which luminance was kept constant (all points on the thick line with negative slope are isoluminant) and for which stimuli had no chromatic component (points on the thick positive diagonal are black–white with only luminance contrast). The arrows show the maximum possible contrast in the luminance and isoluminant directions under the constraint of symmetrically modulating around a neutral white point. The closed contour shows the contrasts achievable on a typical CRT monitor.* **(B)** *Threshold contours for subject KG for the detection (open symbols) and identification of the direction of motion (filled symbols) of a foveally presented grating with a temporal frequency of 1 Hz (Ref. 32). Because of the symmetry of the stimuli the contour is reflected around the origin.* **(C)** *Same as in* B, *but for a temporal frequency of 16 Hz.*

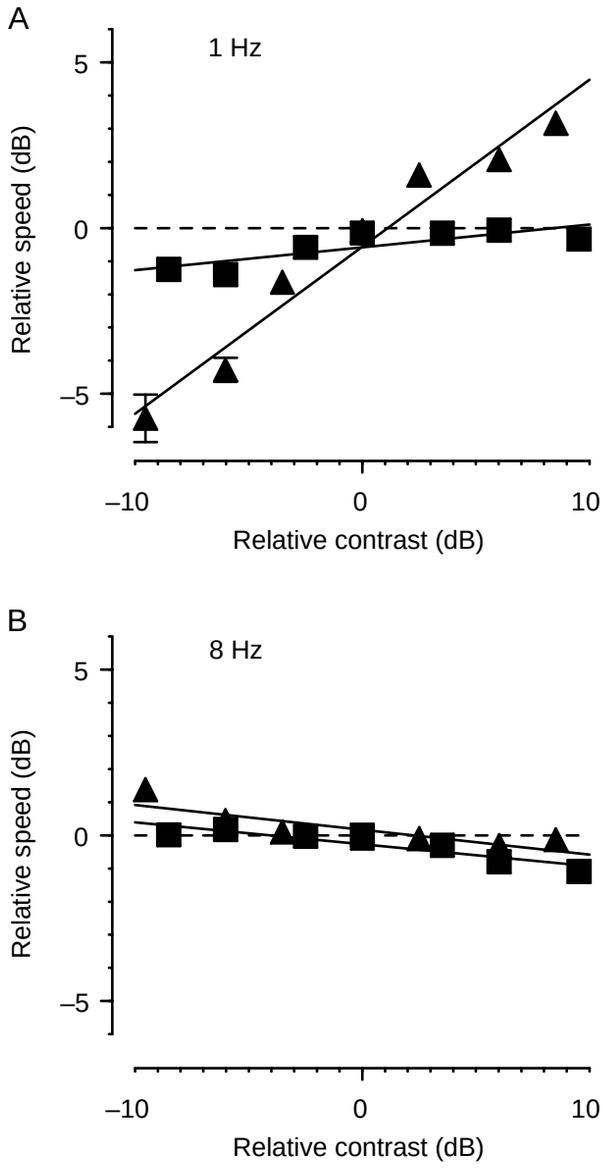

Fig. 3. ***Perceived speed as a function of contrast.*** *The relationship between perceived velocity and contrast for luminance (squares) and isoluminant (triangles) sinewave gratings. All the data are for a single observer MH, who matched the perceived speed of seven comparison gratings of different contrasts to the perceived speed of a standard grating with fixed contrast. The speed of each of the comparison gratings was adjusted by a staircase procedure. The ratio of the contrast of the comparison to the contrast of the standard grating is given on the x-axis in dB (decibels), which is expressed as* $20 \times \log_{10}$*(comparison contrast/standard contrast). Relative speed, the standard grating's velocity divided by the comparison grating's velocity at the match point, is plotted on the y-axis in dB, which is expressed as* $20 \times \log_{10}$*(comparison velocity/standard velocity). A positive value indicates that the actual velocity of the comparison was lower than that of the standard when the subject judged the velocities as equal. A negative value means that the real velocity of the comparison was higher than that of the standard when the perceived velocities were equal. For this experiment both the standard and comparison were vertically oriented gratings with a spatial frequency of 1 cycle deg*$^{-1}$ *(cpd). The standard and comparison gratings differed either only in luminance (squares) or in color (isoluminant, triangles). Contrasts of the standard gratings were chosen so that the perceived speed of the luminance standard (4% contrast) and the isoluminant standard (8% root-mean-squared cone contrast) approximately matched.* **(A)** *Slow-moving standard grating of 1 Hz and 1 cpd.* **(B)** *Fast-moving standard grating of 8 Hz and 1 cpd.* Figure reproduced from Ref. 41.

Processing at slow speeds is very different from processing at high speeds. At slow speeds there is evidence for different mechanisms for luminance and color, but not at high speeds. The mechanism that underlies perception of slowly moving isoluminant gratings is sensitive to the direction of motion and to color, but is inadequate for coding velocity. At high speeds processing is similar for luminance and color, and velocity is coded veridically.

Physiology: area MT

The next section focuses on the brain areas that underlie these mechanisms and discusses the range of neuronal properties that would support perception. The usual suspect of the neural substrate for a motion mechanism is the middle temporal area (MT or V5). Extrastriate visual area MT is a relatively small brain region which is of great importance in the processing of visual motion and in the generation of signals for the guidance of smooth-pursuit eye movements[46–48]. The proportion of directionally selective neurons, about 90% in MT, is higher than in any other area of visual cortex. Experiments by Newsome and colleagues[49] have shown that the activity of neurons in area MT is closely correlated with perceptual decisions made by awake behaving monkeys about the direction of motion. Furthermore, they have shown that microstimulation of a group of neurons in MT can actively bias perceptual decisions. Whereas early reports[46] indicated no response at all to color in area MT, more recent and systematic investigations have found responses of MT neurons to isoluminant stimuli[50–53]. Our goal was to determine whether these signals could form the basis for the psychophysically observed motion mechanisms. The question here is not simply whether the firing rate of MT neurons differs for luminance and isoluminant stimuli. We want to know whether MT neurons behave qualitatively like the slow mechanism identified psychophysically, which is color-opponent and has high sensitivity to chromatic contrast at low temporal frequencies, or whether it matches the behavior of the fast mechanism, which processes luminance and isoluminant stimuli in a similar manner.

Single neurons were recorded in anesthetized and paralysed macaque monkeys[53], whose color vision is known to be quite similar to the human[54]. When we investigated the contrast sensitivity of these cells to isoluminant gratings we found that sensitivity was not great enough to account for the excellent behavioral sensitivity to slowly moving isoluminant gratings. Figure 4 shows the average contrast response of the 18 neurons in our sample with the best response to chromatic gratings and compares it with the average response the same cells gave to stimuli defined by luminance contrast. All the measurements were made using the cells optimal temporal frequencies, which were between 3 Hz and 8 Hz, as is typical for MT cells. The arrows show the results of behavioral measurements for identification of direction of motion in macaque monkeys, under the same experimental conditions the physiological measurements were made. As expected, neuronal sensitivity approximately matched behavioral sensitivity to fast-moving gratings. For slowly moving luminance gratings behavioral sensitivity decreases, whereas sensitivity increases for

slowly moving isoluminant gratings. There is no response from MT cells to contrasts that lie at the level of behavioral threshold (left open arrow) for slowly moving isoluminant gratings. Thus the sensitivity of neurons in area MT cannot account for behavioral responses to slowly moving isoluminant stimuli.

To explore further the nature of the chromatic inputs to MT cells, we compared the neuronal responses to black and white grating stimuli of increasing contrast (luminance gratings) with those to red and green grating stimuli (chromatic gratings), whose luminance contrast matched that of the black and white stimuli. In these experiments each black and white stimulus had two matching red and green stimuli, one with bright red and dark green bars, the other one with bright green and dark red bars. The rationale of the experiment was that if MT neurons respond to the luminance component of the stimuli only, then the response curves for the black and white and for the red and green stimuli should overlap completely. Furthermore, the response to the chromatic gratings should be zero at isoluminance, which corresponds to a zero-contrast luminance stimulus.

Indeed, most of the neurons we recorded from in area MT behaved as if they only responded to the luminance component of the gratings. A typical cell's response is illustrated in Fig. 5A. Responses to red–green stimuli were virtually identical to the luminance responses. The cell responded to the luminance component only, and therefore did not respond at all at isoluminance. We found that 82% (37 of 45) of all cells showed a complete null response at or near isoluminance. In some of these cases (12 of the above 37), however, like the one presented in Fig. 5B, the response curve to chromatic stimuli was shifted slightly leftward or rightward away from isoluminance. In terms of the V(λ) curve (see Box 1), this response can be thought of as an additive combination of L- and M-cones not in the normal ratio of 2:1. In addition, a few cells did show signs of color-opponent inputs (8 of 45), but all of these cells responded at least equally strongly to black and white stimuli. The population response, virtually identical to what other investigators have reported[52], is shown in Fig. 5C. Variations in the isoluminant points of individual cells lead to a significant response at photometric isoluminance. The small advantage for color at non-zero luminance contrasts reflects residual color-opponent inputs to some cells.

In summary, the characteristics of MT responses are very different from the chromatically opponent response of the slow-motion mechanism observed psychophysically. MT cells are not color-opponent, and they cannot match behavioral sensitivity to slowly moving isoluminant gratings. Since MT neurons do give a response to isoluminant stimuli and their sensitivity to fast-moving luminance stimuli is sufficiently high, area MT is a likely candidate for the fast-motion pathway. However, it can be rejected as the neuronal substrate for the slow-motion pathway which requires a sensitive color-opponent motion mechanism.

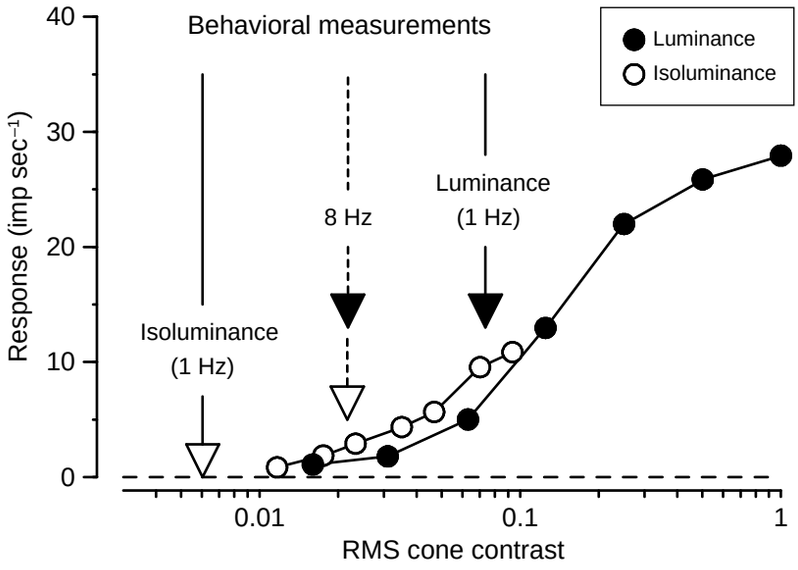

Fig. 4. ***Average contrast response of MT neurons.*** *The root-mean-squared (RMS) cone contrast is plotted on the x-axis. The y-axis shows the response in impulses per second. The open circles show the average contrast response of the 18 neurons with the best response to isoluminant red–green chromatic gratings. The filled circles show the average response of the same cells to stimuli defined by luminance contrast. All measurements were made using the cells' optimal temporal frequencies, which were between 3 Hz and 8 Hz. Because of the band-pass nature of the temporal frequency tuning curve of MT cells, the responses at all lower temporal frequencies would be smaller. The arrows show the results of behavioral measurements for identification of direction of motion in monkeys of the same species, under the same experimental conditions as in the physiological measurements[53].*

What is the purpose of two pathways?

We have identified two processing streams for moving targets that differ mostly in their temporal properties. The 'slow' channel has a high sensitivity for color contrast, but does not code velocity in a contrast-invariant manner. Neuronal processing of these stimuli does not appear to occur in area MT. The functional properties of this slow stream, in particular its color-opponency, make it quite suitable for the assignment of surface characteristics, for example color, to objects; a task that is typically associated with the infero–temporal cortical processing stream[55,56].

The 'fast' channel, on the other hand, has a high sensitivity to luminance-defined stimuli. Color variations are processed like small luminance variations without actually signifying color itself. Motion coding is contrast-invariant and veridical. The neuronal substrate of this channel is very likely to be the magnocellular-processing stream including area MT. One of the known important functions of area MT, and the dorsal stream in general, is the co-ordination of oriented behavior in space, and in particular the control of eye movements[48]. It is known that area MT plays an important role in the generation of the visual signals that control smooth-pursuit eye movements. Such signals need to be processed quickly to enable a fast and proper reaction to environmental stimuli. A fast neuronal pathway is advantageous, where there is little mixing of signals about different stimulus attributes, and therefore less synaptic integration is required. The magnocellularly dominated pathway via layer 4Cα and 4B in V1 that projects directly to area MT fulfils these requirements. The small variations of the isoluminant points of individual cells in area MT might be an elegant and efficient implementation of cue-invariance[45].

There is clinical support for the idea that area MT is not the only area underlying visual motion perception. The finding of a patient with selective disturbance of motion perception[57] (cerebral akinetopsia)

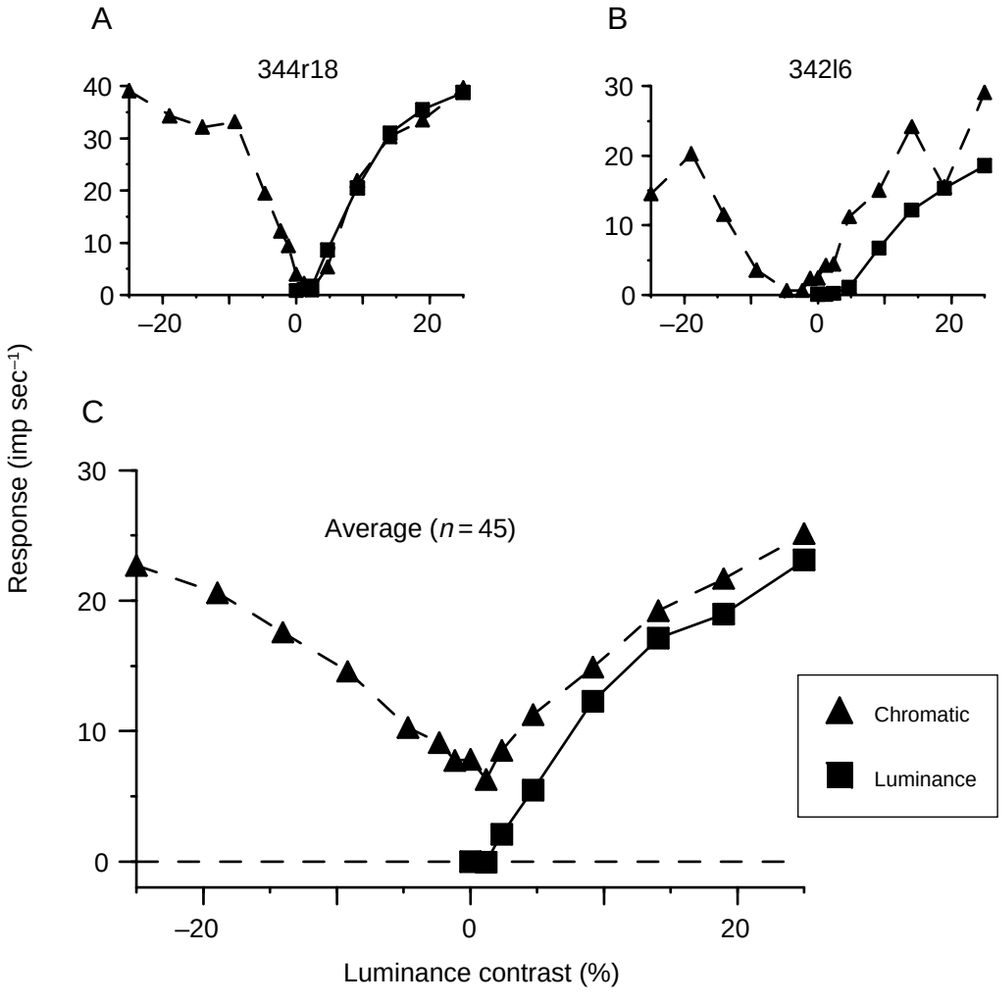

Fig. 5. ***Responses of cells in macaque area MT to luminance and color.*** *The squares indicate the responses (in impulses per second) of MT neurons to black and white luminance stimuli of varying contrast. The triangles indicate the response to stimuli having an added constant chromatic component. Baseline responses were subtracted. For chromatic stimuli, the contrast of the chromatic component was fixed at 75% of the maximum of our monitor (10% root-mean-squared cone contrast). Each cell's preferred temporal frequency was used, 7.5 Hz for the two examples shown here.* **(A)** *This cell (344r18) is representative of the most common type. It has a complete null very close to the photometric isoluminant point. The response is fully explained by the luminance component of the stimulus.* **(B)** *This cell (342l6) has a null at a contrast close to photometric isoluminance. Its response can also be attributed solely to the luminance component of the stimulus, but because of the horizontal shift of its response curve it gives a significant response at isoluminance.* **(C)** *Average response of a population of 45 neurons. Variations in individual cells' isoluminant point (as in* B*) led to a significant response at photometric isoluminance. The small upward shift of the chromatic response curve is caused by weak color-opponent inputs to some of the cells.*

was considered to be a major piece of evidence in support of a dedicated motion-processing center in the brain. This patient is suffering from bilateral damage to a circumscribed region of the lateral temporo–occipital cortex, including the human counterpart of area MT. However, motion processing for this patient is impaired only for fast-moving stimuli, and no deficit can be found for slowly moving stimuli below 4 Hz (Ref. 58).

What could be the neural substrate then for the slow motion mechanism? In the patient with cerebral akinetopsia significant residual responses in area V3 to motion stimuli were reported in a study using positron emission tomography[59]. Single-unit recordings on macaque monkeys revealed neurons in area V3 that are jointly selective for the color and the motion of stimuli[60]. Since V3 projects to areas MT and V4, the pathway via V3 and V4 might be a good candidate for the neuronal substrate of the slow motion pathway. There are populations of neurons in area V4 that do respond to color[61] and to motion[62]. Unfortunately, no quantitative data exist yet of the combined chromatic and directional properties of single neurons in area V4.

From our studies a picture is starting to emerge of two processing streams for the motion of one-dimensional patterns. Each stream has clear-cut functional properties. More generally there is mounting support for the idea that there are a number of separate mechanisms that operate in parallel to give a percept of motion; fast and slow motion that we discussed in this article, second-order motion[63], motion through attentional tracking[64], or motion in depth[65,66]. It will be very revealing to determine how luminance and color interact across the whole range of motion systems. In summary, there is no simple segregation into different stimulus attributes, but rather stimulus attributes are combined in ways that are optimally suited for particular functions such as object recognition and space-oriented behavior[67].

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Varieties of vision: from blind responses to conscious recognition

Petra Stoerig

Lesions in consecutive parts of the visual system cause visual deficits that spare increasingly complex residual functions. Patients with lesions up to and including primary visual cortex can show neuroendocrine, reflexive, implicit and forced-choice responses to visual stimulation but no conscious vision. In contrast, patients with lesions in higher visual cortical areas have conscious vision. Its lowest level is that of phenomenal vision, followed by object vision and recognition. These levels are dissociable. They require the integrity of different parts of the system.

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MOST NEUROSCIENTISTS who study the neuronal correlate(s) of consciousness assume that a consciously represented neuronal process must in some measurable way be different from the simultaneously ongoing processes which are not, now or in principle, represented in this form. The visual system, as the best-studied sensory system, has been the focus of such empirical approaches. If organizational principles are discovered in one, they might well apply to the other sensory systems, no matter whether direct projections to prefrontal areas[1], back-projections from higher cortical areas to primary sensory cortex[2], synchronization of neuronal firing[3], certain cortical[4] or subcortical areas of the brain[5], particular neurones[1,6], or neurotransmitters[7] are needed for the sensory information to be consciously represented.

Neuropsychological evidence demonstrates that visual processes come in conscious as well as unconscious forms; both shape the patients' behaviour. In addition, the evidence demonstrates that different stages of blind as well as conscious vision must be distinguished, and that they require the functional integrity of different parts of the system. Consequently one needs to clarify which of the dissociable conscious visual processes one refers to when suggesting a particular neuronal correlate.

Unconscious vision

In contrast to the legal definition of blindness, which refers to a reduction of visual acuity to an incapacitating fraction, absolute blindness is a total absence of visual-information processing (see Box 1). A baby born prematurely without eyes is an example of this rare condition. In contrast, an adult who has lost the function of his eyes is not, because once the visual system has worked normally it might remain capable of endogenous vision, as shown by reports of visual hallucinations in blindness from ocular and retinal pathology[8]. Closest to an absence of all visual function is the form of blindness that can be observed in patients who have lost their vision through damage that destroys the parallel retinofugal projections, with the exception of the pathway to the hypothalamus. Although neither a pupil reflex nor any dim perception of light can be elicited, these patients might still suppress the secretion of melatonin when exposed to bright light[9].

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