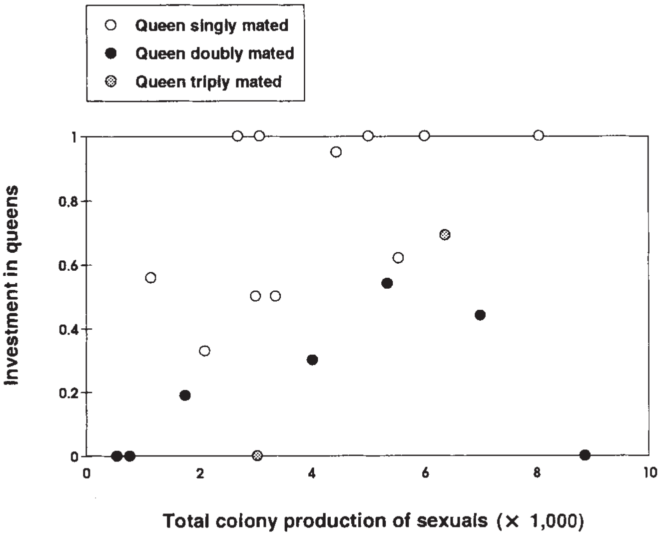

FIG. 2 Sex allocation in relation to colony productivity and queen mating frequency. The number of sexual pupae produced was determined twice by marking–recapturing in 1992. Marking was done with a waterproof filter pen and pupae were recaptured 2 days later. The amount of female bias depended mainly on colony type (singly or multiply mated queen), but also on colony productivity (ANOVA/analysis of covariance (ANCOVA)): number of mates per queen, $F=26.7$, $P=0.0001$; with colony productivity as a covariate, $F=7.1$, $P=0.02$, $n=20$). Colony type and productivity together explain 66% ($F=17.1$, $P=0.0001$) of the total variation in sex ratios, and when productivity is factored out there is virtually no overlap in sex ratios between colony types. The association between colony productivity and sex ratio was confirmed by a non-parametric analysis on data adjusted for differences in means between the two categories (Spearmann rank correlation $r=0.56$, $P=0.01$) as well as without this adjustment (Spearmann rank correlation $r=0.43$, $P=0.04$). These results were checked for their robustness assuming that two of the colony queens assessed as singly mated were in fact multiply mated (see Fig. 1 legend). All possible pairs of colonies producing an all-female brood were selected and assigned to the multiply mated class. The ANOVA/ANCOVA above was repeated for each of the 10 pairs (ANOVA for number of mates per queen: the range of $F$ values was 13.7–5.7, and the range of significance levels was $P=0.002$–$0.03$; ANCOVA for productivity: $F=8.4$–$2.7$, $P=0.01$–$0.12$, $n=20$). In addition, the difference in sex ratios between the singly and multiply mated groups was tested with two randomly selected colonies producting an all-female brood reassigned to the multiply mated class and without productivity as a covariate (Mann–Whitney rank sum test, $P=0.03$). There were no differences in the total number of sexuals produced between colonies with singly mated and multiply mated queens (4,030 ± 2,000 and 4,190 ± 2,900, respectively, Mann–Whitney, $P=1$).

ratios in response to the relative relatedness asymmetry in their colonies[5,12]. This is a further example of the complexity and sophistication of worker reproductive strategies in social insects. It also implies that workers have a mechanism for accurately determining queen mating frequency, possibly using some phenotypic expression of the genetic diversity of their nestmates, such as genetically determined odour cues[19,22]. The accuracy of the results further suggests that the diversity of such genetically determined cues is reasonably high[19,22]. □

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# Contrast dependence of colour and luminance motion mechanisms in human vision

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**CONVENTIONAL views of visual perception propose a colour-blind pathway conveying motion information and a motion-blind pathway carrying colour information[1,2]. Recent studies show that motion perception is not always colour blind[3,4], is partially dependent on attention[5,6], can show considerable perceptual slowing around isoluminance[7–9] and is contrast-dependent[10,11]. If there is a single motion pathway, receiving luminance and chromatic input, then the dependence of relative perceived velocity on relative stimulus contrast should be the same for both luminance and chromatic targets. Here we provide a distinctive characterization of the motion mechanisms using a robust velocity-matching task. A relative contrast scale allows direct comparison of the performance with luminance and chromatic targets. The results show that the perceived speed of slowly moving coloured targets at isoluminance has a steep contrast dependence. The perceived speed of slowly moving luminance targets shows a much lower contrast dependence. At high speeds the contrast dependence is low for both luminance and isoluminant stimuli, although the behaviour is unlike either of the slow mechanisms. The results suggest two independent pathways that perceive slowly moving targets: one is luminance-sensitive and the other is colour-sensitive. Fast movement is signalled via a single motion pathway that is contrast-invariant and not colour blind.**

We measured the perceived velocity of grating patterns of low spatial frequency as a function of contrast for slow (1 deg $s^{-1}$) and moderate velocities (8 deg $s^{-1}$). Gratings were either modulated in luminance or modulated along a red/green line in the isoluminant plane[4]. The slope of the function relating log-contrast to relative speed is invariant under multiplicative transformations of the contrast scale, and therefore allows a meaningful comparison between luminance and colour. Experienced

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psychophysical observers judged which of two spatially separated patterns moved faster. Figure 1*a* shows the difference in perceived velocity of five luminance gratings when compared with one of three standard luminance gratings. For the slowly moving standard, the lower-contrast gratings require a higher velocity to match the perceived speed of the higher-contrast gratings; this is consistent with previous reports[10,11]. The slope of the function that relates perceived speed to contrast is the same across all standard contrasts, as indicated by the best-fitting regression lines in Fig. 1*a*.

When isoluminant red/green gratings are used as both the comparison and standard, the effect of contrast on perceived velocity is dramatically different from the results with luminance targets (Fig. 1*b*, triangles) under otherwise identical conditions. The dependence of perceived velocity on colour contrast is much stronger than for luminance contrast (Fig. 1*b*, squares compared with triangles). Similar results were obtained for isoluminant yellow/blue S-cone-isolating targets. The range of contrasts used for the isoluminant red/green gratings in our experiment went from the highest contrast we could attain with our monitor (corresponding to 10% and 24% cone contrast in the long- and middle-wavelength sensitive cones, respectively) down to 1 log unit below this. The luminance contrasts were selected to bracket the value of luminance contrast that produced a velocity match to the mid-point of the isoluminant contrasts. We have confirmed that there is little effect of spatial frequency; the same slope is seen for both square-wave and sinewave gratings.

Figure 1*c* shows the results for a series of experiments in which the speed of the standard grating target was 8 deg s$^{-1}$, otherwise the conditions were identical to those for the 1 deg s$^{-1}$ experiments. There is a small but consistent increase in perceived speed with decreasing contrast for achromatic gratings (Fig. 1*c*, squares), confirming a previous report[10]. However, it is clear that, unlike the low-velocity data in Fig. 1b, at higher velocities the chromatically modulated targets behave exactly like the achromatic target.

To summarize the results across subjects, we have determined the relative slope for all the conditions. The results for four subjects are shown in Fig. 2, where there are three distinct clusters of slopes—one set of negative slopes (fast L and C conditions) associated with fast-moving targets, a second set of positive but shallow slopes (slow L) associated with the slow-moving luminance targets and a third group of steeper slopes (slow C) that are associated with the slow-moving chromatic targets.

For targets moving at moderate speeds, we show definitely that red/green isoluminant stimuli, which isolate the red/green colour opponent mechanism, are effective in producing a veridical percept of motion (Fig. 1*c*). Therefore, for these targets either the opponent colour system contributes effectively to

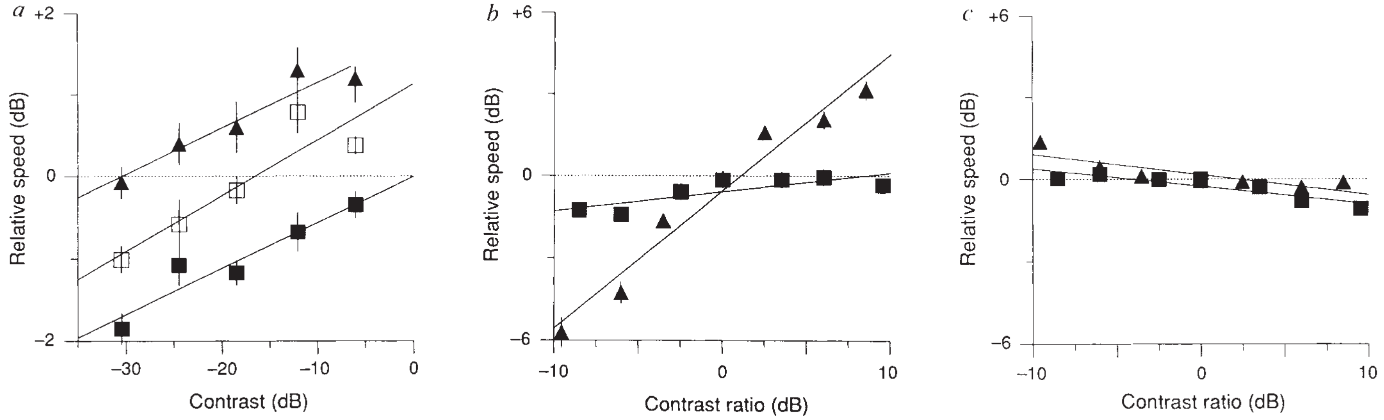

FIG. 1 The relationship between perceived velocity and contrast for different combinations of achromatic and chromatic sinewave gratings. All the data are for a single observer (mh); the slopes of each set of data for four observers are shown in Fig. 2. *a*, Each data set shows the difference in perceived velocity for five comparison gratings, each of different contrast, when compared with a single standard grating of 3, 12 or 50% contrast—triangles, open squares and closed squares, respectively. Contrast on the *x*-axis is given in decibels, 20 times the $\log_{10}$ of contrast. Relative speed (equal to velocity of standard pattern/velocity of comparison pattern at the match) is plotted on the *y*-axis. A positive value indicates that the actual velocity of the comparison was lower than the velocity 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 the standard when the perceived velocities were equal. For this experiment both the standard and comparison were vertically oriented achromatic gratings with a spatial frequency of 1 cycle deg$^{-1}$. The speed of the standard was constant at 1 deg s$^{-1}$. To measure the thresholds, a spatial two-alternative forced-choice procedure was used to drive a staircase which adjusted the velocity of the comparison stimulus. The observer was instructed to fixate a small central square for the duration of the trial, which was 2 s. The next stimulus was presented immediately after the subject responded; no feedback was given. Stimuli were generated by a True-Vision Vista video controller and displayed on a Barco colour monitor (CCID 7351B), 28 × 21 deg. The general methods of stimulus generation, calibration and control have recently been fully described elsewhere[19]. Twelve pairs of turns on the staircase were found for each condition; each condition was repeated six times. The same procedure was used throughout all the experiments. Subjects were seated 71 cm from a display monitor, positioned using a chin rest. They viewed binocularly with natural pupils. All subjects were optimally corrected to better than 20/20 and had normal colour vision. In a set of trials, there was a standard and a number of comparison stimuli, between 5 and 7. For a single trial, the standard was presented in either the upper or lower window (window size, 21° × 7°) and one of the comparisons was presented in the other window. The standard and the test drifted horizontally, in opposite directions. *b*, The standard and comparison gratings were either luminance/luminance (squares) or isoluminant/isoluminant (triangles). Otherwise, the conditions and experimental procedure are the same as described for *a* except for the contrast of the standards which are given below. In this graph and in *c*, contrast is expressed as the ratio of the contrast of the comparison to the contrast of the standard. Note that the relative velocity scale has been changed in this graph to accommodate the much greater slope of the isoluminant condition. *c*, Data for a faster velocity, 8 deg s$^{-1}$. The scale on the ordinate is the same as in *b*; note in particular that isoluminant gain (triangles) is much lower at the high velocity and indistinguishable from the luminance condition (squares). The contrast of luminance standard in *b* and *c* was 4%; the contrast of the isoluminant standard was 30% of the maximum attainable modulation. The contrasts were chosen to be approximately at equal multiples of detection threshold. Detection thresholds are −24 dB and −28 dB on the *x*-axis in *b* for luminance and colour, respectively. In *c*, the thresholds are −29 dB and −21 dB. The dotted lines in *a*, *b* and *c* show the prediction if velocity perception was contrast-independent.

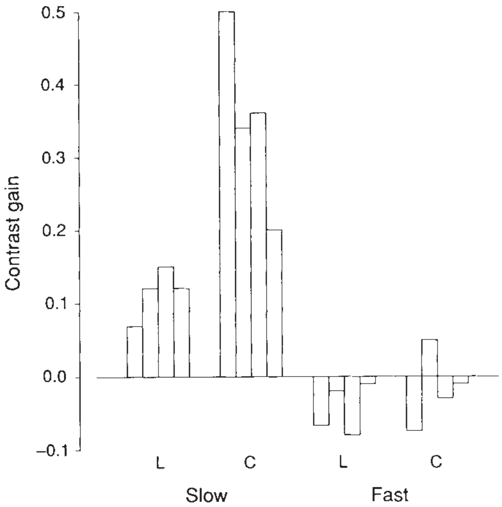

FIG. 2 The effect of contrast on the relative velocity of the comparison targets when compared with the standard target is given by the slope (contrast gain) of the regression lines in Fig. 1. This figure shows the contrast gain for four subjects in each of the four conditions. Slow and fast refer to the velocity of the standard targets, 1 deg s$^{-1}$ and 8 deg s$^{-1}$, respectively. L and C refer to the two stimulus types, luminance and red/green isoluminant, respectively. For all four observers there is a substantially higher gain for the slow isoluminant stimulus. In a separate series of experiments, we measured both detection and identification threshold contours[20] of 1 cycle deg$^{-1}$ drifting gratings for a range of temporal frequencies ranging from 1 to 16 cycles s$^{-1}$ for a full range of directions in colour space which included points densely spaced around the isoluminant point. The isoluminant points were derived from these experiments.

motion perception or the luminance mechanism is sensitive to pure modulations in chromaticity. Whichever is correct, motion perception of moderate to fast movement is invariant to changes in contrast and chromaticity, such that the motion system is not blind to coloured targets.

The perception of slow movement is not invariant to changes in contrast and chromaticity. At low speeds there are two mechanisms for signalling the direction and velocity of moving targets. One is based on the well documented achromatic, directionally selective channel which is low pass in temporal frequency selectivity[12,13]. The characteristics of the chromatically selective mechanism are not well known. One possibility is that the chromatic stimulus produces a response in the luminance mechanism. Origins of this signal could be chromatic aberration, variation in individual cells' isoluminant point or nonlinearities in the cells' response to contrast. These possibilities are ruled out by our findings. If the chromatic signal was operating by stimulating the neurons in the luminance pathway, it would be expected that the slope of the velocity-matching function for both red/green and yellow/blue targets would be identical to that of the luminance targets. This is clearly not the case.

Spatio-temporal energy filters are the basic building blocks for most current models of motion perception[14-17]. The response of these filters confounds temporal frequency and contrast. To extract a correct velocity, most models of motion perception take the relative output of an array of these filters. Our results show that contrast invariance holds at moderate to high temporal frequencies, but that there are significant deviations from these models' predictions at low temporal frequencies.

We conclude that motion processing at moderate and fast speeds is independent of colour and proceeds via the established motion pathway which includes the extrastriate motion area MT. The neural mechanisms responsible for perceiving slowly moving targets are unclear. There is some evidence for the involvement of the parvocellular pathway[18]. Our results indicate that at least two separate neural pathways are needed. ☐

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# Oscillation and noise determine signal transduction in shark multimodal sensory cells

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**OSCILLATING membrane potentials that generate rhythmic impulse patterns are considered to be of particular significance for neuronal information processing[1-4]. In contrast, noise is usually seen as a disturbance which limits the accuracy of information transfer[5-8]. We show here, however, that noise in combination with intrinsic oscillations can provide neurons with particular encoding properties, a discovery we made when recording from single electrosensory afferents of a fish. The temporal sequence of the impulse trains indicates oscillations that operate near the spike-triggering threshold. The oscillation frequency determines the basic rhythm of impulse generation, but whether or not an impulse is actually triggered essentially depends on superimposed noise. The probability of impulse generation can be altered considerably by minor modifications of oscillation baseline and amplitude, which may underlie the exquisite sensitivity of these receptors to thermal and electrical stimuli. Additionally, thermal, but not electrical, stimuli alter the oscillation frequency, allowing dual sensory messages to be conveyed in a single spike train. These findings demonstrate novel properties of sensory transduction which may be relevant for neuronal signalling in general.**

Oscillating spike generation in sensory afferents is primarily indicated by a rhythmic grouping of impulses called 'bursts'[9-12]. However, there is a different type of impulse pattern (Fig. 1) which also implies oscillating transduction processes but which, additionally, has an essential noise component[11-15]. The oscillation does not trigger groups of impulses but merely initiates single spikes, with occasionally no impulse at all (Fig. 1*a*). Despite the seemingly irregular impulse trains, the interval histograms show distinct modes (Fig. 1*b*): the interspike intervals

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