pollination. This role of the stigma in actively regulating the breeding system may possibly apply to other bee-pollinated papilionaceous species.

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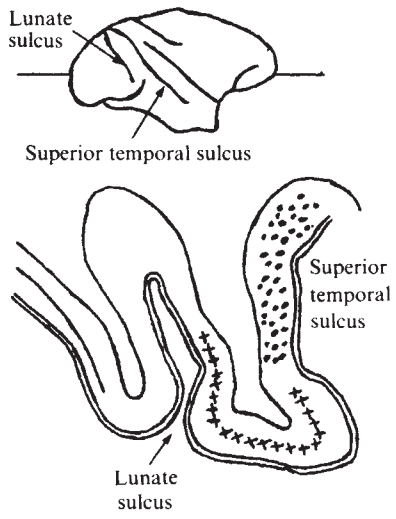


Fig. 1 The lower diagram shows a horizontal section of the brain of a rhesus monkey taken at the level indicated in the upper diagram to show regions of the prestriate cortex that are specialised for colour (marked by crosses) and motion (stippled) (adapted from Zeki[2]).

Does colour provide an input to human motion perception?

A PUZZLING feature of the visual system of primates is the occurrence of a multiplicity of separate 'maps' of the visual environment, each of which has its own independent set of afferent connections. Perhaps these maps represent an early stae in the analysis of visual information by the brain. Electrophysiological studies have shown that depth is analysed in V_2 (area 18) (ref. 1), that colour-coded cells occur mainly in V_4 and that motion in the visual field is analysed in the posterior bank of the superior temporal sulcus[2] (Fig. 1). We report here an experiment which suggests that colour and movement are handled separately in the visual system and that information defined by wavelength cannot be processed by the brain's motion-detecting mechanisms. This finding is consistent with Zeki's demonstration that "cells of the movement area are not concerned with colour"[2,3].

Stimuli used were based on Julesz' random-dot stereograms[4] (Fig. 2). The members of the pair of random-dot arrays are identical except that all the dots of a central square-shaped region are horizontally shifted to an equal extent in one display in relation to the other. On monocular inspection, only random dots are seen for either display, but when fused binocularly, the central shifted region stands out in depth from the rest of the dots, as a square having a sharp border; this may be described as an illusory contour, as it is not defined by the (irregular) dots of the displaced region.

Lu and Fender[5] found that when such a display is presented with coloured dots against a contrasting colour background, stereoscopic depth is lost when the dots and the background have equal luminance, although the dots are clearly seen by colour contrast at isoluminance.

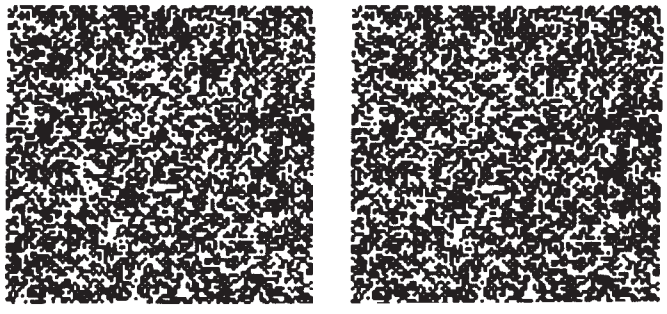
The use of random-dot stereograms has not been limited to stereoscopic experiments. In the present experiment, random-dot displays are not presented to give stereoscopic depth; they are optically superimposed, and are exposed alternately at a rate which gives apparent motion of the central displaced region, which then appears as a square oscillating horizontally[4,6]. The square has (very much as for stereoscopic presentation) a clearly defined illusory border. Neither the border nor the motion are visible without alternation of the pair of dot displays. The appearance of the border can be used as an independent and unambiguous criterion of motion perception[7].

We used these patterns to study the role of colour as an input to human motion perception. Each dot in the original pattern (Fig. 2) is defined by a stepwise change in intensity (that is, black dots on a white background). Our strategy was to convert these intensity gradients into gradients of 'pure' wavelength; that is, we replaced all black–white borders with red–green borders using an isoluminance projection system[8]. The intensity of the green areas was then varied continuously over a wide range so that at least at some setting the intensities of red and green must have been precisely matched.

Isoluminance, with exact registration of the colour areas to prevent brightness contours, was obtained by projecting a special colour transparency with combined epi and dia projection through a single lens[8]. Two light sources were independently controlled for intensity, the epi source, which illuminates the upper coloured (red) surface of the opaque regions of the transparency, and the dia source, which projects by means of a colour filter (green) through the transparent regions. The transparency may be photographically produced silk screen prints; or 3M colour-key contact imaging material (red opaque negative), as used here. The format was 60 mm^2.

An identical pair of these projectors allowed a Julesz pair of transparencies to be superimposed, and projected alternately with a pair of electrically synchronised rotating sector-disk shutters. 'Key-stoning' distortion was avoided by placing one projector behind and the other in front of a translucent screen.

Fig. 2 A Julesz random-dot stereogram (see text for explanation). The two patterns were optically superimposed and exposed alternately to produce apparent motion.



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The projected display was 37 cm^2 viewed from about 1 m, subtending 65°. The dot elements were 2 cm, subtending 3°, which was at least two orders above visual resolution at isoluminance. The screen luminance at isoluminance match was about 0.34 cd m^{-2}. Similar results were obtained at higher intensities (up to 34 cd m^{-2}).

Four volunteers were used and two of them were unaware of the purpose of the experiment. Each subject began by deliberately introducing a large brightness difference between the red and green areas. At a frequency of about 100; 50; 100 (stimulus duration 100 ms; interstimulus interval or ISI 50 ms), a square with well-defined edges could be seen oscillating back and forth horizontally. Using the luminance control knob the intensity of the green dots was then varied continuously over a wide range. The subject was asked to record what he saw as he rotated the knob.

As the green background luminance was gradually reduced from a high value to near isoluminance, all subjects reported disappearance of the square. The square then reappeared when the luminance of the green was reduced to a level below the 'isoluminance' point. The disappearance of the square was quite sudden, and reported spontaneously by all four subjects.

Table 1 Critical range of luminance of green dots for each of four subjects

Subject	Luminance range (cd m^{-2}) over which square was invisible	Luminance range (cd m^{-2}) at which motion was invisible
1	4.42	6.84
2	4.32	6.84
3	4.73	7.68
4	3.49	7.68

Each entry represents the mean value of four readings.

Table 1 shows the 'critical range' of intensities over which the square disappeared for each of the four subjects. For all subjects: (1) the square disappeared slightly earlier than motion and was completely invisible over a narrow range of about 58% which was fairly constant for each subject, (2) the luminance setting for motion disappearance was remarkably constant among subjects. At this setting, three of the subjects reported that they could still see a slight 'shimmering' but none of them could detect any motion.

Having found the critical range, we varied other parameters to see if the square could be restored. Increasing the frequency of alternation did not make any difference. On lowering the frequency to about half the original rate, some of the dot elements could be seen moving, but the direction of motion was ambiguous and the edge defining the square remained invisible. Neither the square nor unambiguous motion could be restored at any frequency. We also tried doubling or halving the size of dot elements and/or the spatial displacement of the inner square, but these proved equally ineffective.

It is important to note that at the setting at which motion disappeared, the individual dots could be discerned just as clearly as when luminance contrast was present. Conversely, even gross blurring of the pattern (by defocusing the projectors) did not destroy the square as long as brightness differences were preserved.

In a control situation we used light red–dark red dot patterns instead of red–green. The intensity of one of the reds was then varied continuously. All four subjects reported that the disappearance of the square (and of motion) coincided almost exactly with the actual disappearance of the dots at isoluminance. The critical range for the disappearance of the square and of motion was thus much narrower than that measured using red–green dots (Table 1). Thus, colour cues seem to have, if anything, a slightly detrimental effect on the perception of coherent apparent motion.

The disappearance of motion at isoluminance is exactly analogous to Lu and Fender's[5] discovery that stereopsis disappears at isoluminance in stationary random-dot stereograms. 'Classical' stereopsis, using monocularly visible line targets, apparently does not break down completely at isoluminance[9], and we now find that this is also true of apparent motion. If two simple line targets are alternated instead of random-dot patterns, motion does not disappear at isoluminance.

As in the case of stereopsis[9], random-dot targets may be processed differently from simple line targets. The former must involve cooperative interactions between large populations of cells tuned to either the same disparity[4,10,11] or even (in the case of motion detectors) the same direction and velocity. Our findings may imply that at isoluminance cooperative facilitation is not possible between colour contrast-sensitive motion detectors. Alternatively, the relevant motion detectors may be insensitive to wavelength, which is consistent with physiological evidence[3], and especially with the observation that monkey colour-opponent neurones give sustained responses whereas broad-band non-opponent neurones respond transiently[12–14].

Regardless of our interpretation, it is clear from our findings that colour and motion are handled separately by the human visual system and that colour provides only a weak 'cue', at best, to movement perception.

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Suppression of oestrogen-induced LH surges by social subordination in talapoin monkeys

IT is axiomatic that the social structure of a group of primates has a pervasive effect on each individual's behaviour. Thus, many monkeys form dominance hierarchies, based on the successful outcome of aggressive interactions, and the more subordinate animals show characteristic behavioural traits[1,2]. In particular, the social hierarchy has marked effects on reproductive behaviour, especially in talapoin monkeys , where sexual interactions tend to be the prerogative of the dominant males[3]. Subordinate male rhesus monkeys have limited access to sexually attractive females and produce fewer offspring[4], and in the few species that have been carefully examined, subordinate females, although apparently receiving sexual attention, are, nevertheless, less fertile than would be expected[5–7]. Recently, it has become clear that the dominance hierarchy affects not only behaviour but also hormone levels. Testosterone is higher in dominant males[8,9], cortisol and prolactin are raised in more subordinate animals[10]. We report here evidence that subordination can prevent the luteinising hormone (LH) surge which

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