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

We thank Gillian Toyne-Clarke and Dr D. Bond (the Plant
Breeding Institute, Cambridge) for seed material. C. P.
acknowledges financial support from Deutsche Forschungs-
gemeinschaft and P. Gates is in receipt of a SRC postgraduate
studentship.

Department of Botany,
University of Durham,
Durham, UK

C. PAUL
P. GATES
N. HARRIS
D. BOULTER

Received 30 May; accepted 21 July 1978.


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 affrent connections. Perhaps these maps represent an early
stage in the analysis of visual information by the brain. Electrophy-
siological 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 experi-
ment 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 demonstra-
tion that ‘cells of the movement area are not concerned with
colour’\(^2\).\(^3\).

Stimuli used were based on Julesz’s\(^4\) 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 in 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 and
diagonally. 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\(^6\). 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 trans-
parency 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 alter-
nately to produce apparent motion.
The projected display was 37 cm² 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>
<thead>
<tr>
<th>Subject</th>
<th>Luminance range (cd m⁻²) over which square was invisible</th>
<th>Luminance range (cd m⁻²) at which motion was invisible</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.42</td>
<td>6.84</td>
</tr>
<tr>
<td>2</td>
<td>4.32</td>
<td>6.84</td>
</tr>
<tr>
<td>3</td>
<td>4.73</td>
<td>7.68</td>
</tr>
<tr>
<td>4</td>
<td>3.49</td>
<td>7.68</td>
</tr>
</tbody>
</table>

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 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, 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, 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 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, and especially with the observation that monkey colour-opponent neurones give sustained responses whereas broad-band non-opponent neurones respond transiently.

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.

We thank Dr O. J. Braddick for providing some of the Julesz stereograms used for making the special transparencies for isoluminance projection.

V. S. RAMACHANDRAN* R. L. GREGORY

MRC Brain and Perception Laboratory, Department of Anatomy, The Medical School, University of Bristol, Bristol, UK

Received 5 May; accepted 18 July 1978.

* Present address: Kenneth Craik Laboratory, Department of Experimental Psychology, University of Cambridge, Cambridge, UK.


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. 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. Subordinate male rhesus monkeys have limited access to sexually attractive females and produce fewer offspring, 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. Recently, it has become clear that the dominance hierarchy affects not only behaviour but also hormone levels. Testosterone is higher in dominant males, cortisol and prolactin are raised in more subordinate animals. We report here evidence that subordination can prevent the luteinising hormone (LH) surge which