training session trials followed one another without a break. As a rule eight trials were given in each session, though this was not invariable. The sessions were separated by an interval of at least 4 days. The criterion for successful training was eight consecutive turns towards the potent male.

During this part of the experiment the females received an average of 3.5 intromissions during each minute spent with the potent male, and one ejaculation every 2.7 min. The castrated males showed no sexual behaviour other than occasional desultory mounts. All eight females learned to choose the potent male to the criterion, in a mean of 32.2 trials (standard deviation 15.3). Using this criterion, a "criterion risk" (that is the risk of a criterion being reached, given random performance) of 5% is exceeded if more than thirty-one trials are run[4]. To ensure that the criterion had not been reached by chance, the position of the males was reversed for each female as soon as she reached the criterion, and she was then retrained to the same criterion in the same way. All eight animals relearned the task to criterion, in an average of 86.4 trials (s.d. 32.8). The learning curve for this part of the experiment is shown as Fig. 1. This curve illustrates the progressive learning shown by the females. It is clear that attainment of the criterion is the outcome of this gradual learning process, and not a chance effect. It should also be noted that the rats trained in this experiment showed a classic negative transfer, taking twice as long to learn the second as the first response.
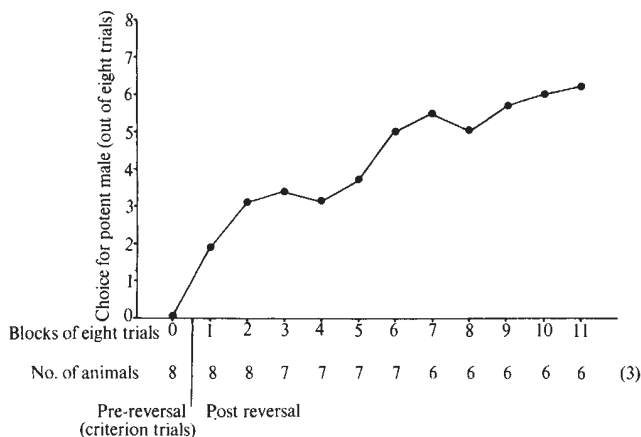

Blocks of eight trials   0 1 2 3 4 5 6 7 8 9 10 11

No. of animals   8 | 8 8 7 7 7 7 6 6 6 6 6   (3)

Pre-reversal | Post reversal
(criterion trials)

Fig. 1 Choice for a potent, as against an impotent, male by the female rat. This figure shows the course of learning when the position of the males is reversed following original training. The results from an animal are only included in the figure up as far as the end of the eight trials on which criterion was reached. By the eighty-eighth trial most of the animals had reached criterion, and the curve is therefore not continued beyond this trial.

When all the animals had reached criterion, the hormonal determinants of this learned approach to the male were examined. Six of the eight animals were run in the maze in the same way for a further period, in blocks of twelve trials given at weekly intervals. But interspersed among these "oestrous" blocks were blocks of trials similar in every way except that the females were not pretreated with hormones and hence were not sexually receptive. In all 204 "oestrous" trials and 108 "unreceptive" trials were run.

The absence of behavioural oestrus neither reduced the females' preference for the potent males nor increased the latency of the choice. During the 204 trials on which the females were sexually receptive, they chose the potent male on 73%, with an average latency of 4.4 s; on the 108 trials without hormone treatment they chose the potent male on 80% of the trials with an average latency of 2.6 s. On none of the "unreceptive" trials did they show any indications of lordosis. Altogether, then, these findings give no indication that oestrus

involves the stimulation of any behaviour more complex than the unlearned motor patterns characteristically associated with it.

Oestrus is associated with enhanced general activity[5], but seems to be independent of sexual receptivity. Progesterone, which synergizes with oestrogen to enhance sexual receptivity, does not increase such activity[6,7]; and differentiation as a normal male, which virtually eliminates female sexual responsiveness to oestrogens, does not prevent the greatly increased activity that results from ovarian implants[8]. The hyperactivity of oestrus, therefore, does not betoken an effort to seek out a male with which to mate because (1) it can be dissociated from sexual receptivity under several conditions and (2) approach behaviour directed to the male is found to be uninfluenced by ovarian hormones that suffice to produce sexual receptivity, when examined directly.

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Orientation-sensitive After-effects of Dichoptically Presented Colour and Form

McCOLLOUGH[1] discovered that if a grating pattern of (say) red vertical stripes is viewed alternately with one of green horizontal stripes for some minutes, an orientation-specific colour after-effect is observed when viewing a black-and-white test grating. White stripes in a given orientation appear tinted with the hue complementary to the hue presented at that orientation in the original stimulus. McCollough observed that if only one eye was exposed to the original sequence of stimuli, no after-effect was seen when the other eye was used to view the test grating. From this she concluded that the adaptation responsible for the after-effect must occur somewhere in the uniocular pathway before signals from left and right eyes are combined. She suggested as a possible explanation that orientation-sensitive channels in the uniocular nervous system ("edge-detectors") may be colour-coded, so that strong adaptation with bars of red light in one orientation leads to a "minus-red" after-response from the adapted channels to similarly oriented colourless bars. Harris and Gibson[2] have confirmed that the effect persists in conditions ruling out ordinary negative after-images, which Murch and Hirsch[3] have shown sufficient to induce it. Held and Shattuck[4] have demonstrated a corresponding after-effect of colour upon the perceived orientation of test bars.

In view of the reported absence of interocular transfer of this effect[1], the physiological locus of adaptation is of interest

as a clue to that of the presumed orientation-sensitive elements in the human visual system. Following a suggestion by Dr Stuart Butler of Birmingham (personal communication), we have investigated the after-effects of presenting information on colour and orientation separately to the two eyes, and have discovered a curious form of interaction between the two uniocular signals.

The subject sat in a darkened room and viewed with one eye a projection screen (2.15 metres away) on which orthogonal left-oblique and right-oblique black-and-white gratings (luminance 22 cd m^{-2} at centre of stripes) were presented alternately for equal periods of the order of 5–10 s, over a total period of 5 min. The patterns subtended 20° × 14° and had a spatial frequency of 2.2 cycles/degree at the observer's eye. (Oblique orientations were used to avoid any bias associated with horizontal and vertical.)
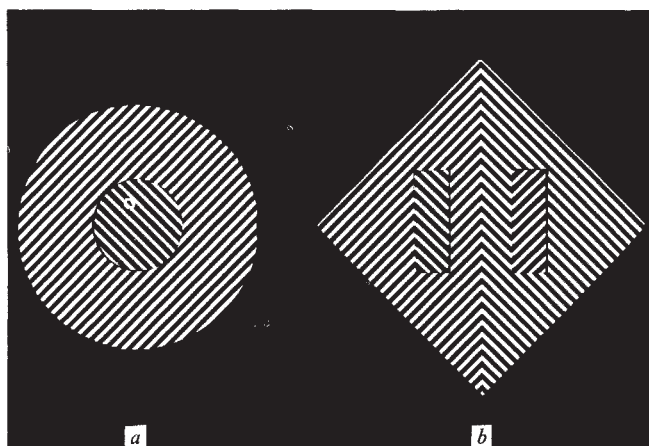

Fig. 1 Two of the test patterns used. The hue of the central patch(es) could be adjusted by the subject to match that of the background.

The subject's other eye was exposed to a uniformly illuminated diffusing screen whose colour changed from red to green as the striped patterns alternated. The visual subtense of the coloured field more than covered that of the striped patterns as viewed by the other eye. The luminances of red and green fields were matched at approximately 34 cd m^{-2}.

After 5 min of this dichoptic stimulation, subjects viewed a black-and-white test grating (2.2 cycles/degree) surrounded by an orthogonal black-and-white background grating of the same spatial frequency. Various shapes of test grating were used, the commonest being a disk subtending 4.5 degrees at the eye, at the centre of a circular background grating of 27 cd m^{-2} subtending 13.5 degrees (Fig. 1a). A later design which proved easier to use employed two oppositely oriented test patches side by side lying in oppositely oriented backgrounds (Fig. 1b). The two test orientations were always used alternately. As well as inviting verbal reports of perceived hue, we used a quantitative null-method of measuring the after-effect. The subject was provided with a (smooth-surfaced) knob by which the test patch could be made slightly red or green to neutralize its perceived hue. The luminance could be independently adjusted to match that of the background. The whole test field (patch plus background) could be rotated to give either orientation of the central test grating. As it turned out that many subjects had an initial bias whereby the test patch appeared greener or pinker than background according to slope even without prior stimulation, the measure adopted for the after-effect was the change in the bias

after adaptation. The bias itself was recorded as the difference between the readings for balance at the two orthogonal test orientations. We also verified that any after-effects of the faint colours imposed on the test patch during the matching process were too small to introduce a significant bias.

A detailed discussion of the results will be published elsewhere, but the most significant findings were as follows: (1) All subjects showed a significant orientation-sensitive colour after-effect of the dichoptic stimulation, most of them spontaneously reporting changes of hue from pink to green or vice-versa as the test grating was rotated through 90°. Subjects differed considerably in the precision with which they could reproduce a match, but in several cases there were significant signs of reversal of the after-effect after a few minutes, particularly in the eye that had received the coloured stimulus. (2) Quite unexpectedly, the initial after-effects in left (L) and right (R) eyes when tested singly were almost always in opposite directions. Table 1 shows a condensed summary of results obtained from nine subjects. As a check, all possible combinations of conditions were used (colours to L/R eye paired with patterns to R/L eye; each orientation paired with Red/Green; test field presented to L/R eye), though not all with every subject.

Table 1 Hues Seen when Viewing Black-and-White Test Grating with either Pattern-stimulated or Colour-stimulated Eye

	Subjects								
	V.M.	B.H.	S.J.	J.M.	E.M.	D.A.	R.M.	C.F.	D.M.
Hues seen with pattern-stimulated eye	S, S S, S	S	S, S S, ?	S, S	S, S	S, S S, ?	S, S S, S	S	S
Hues seen with colour-stimulated eye	C, C C, C	?	C, C C, C	C, ?	C, C	? ? ? ?	C, C C, C	C	C

S: Same as hue originally paired with similarly-oriented grating. C: Complementary to hue originally paired with similarly-oriented grating. ? : Inconclusive result.

After allowing for initial bias, there were no consistent exceptions to the following summary: (a) Seen through the eye that originally received (colourless) patterned stimulation, a black-and-white test grating has the hue originally associated with the same orientation. The measured strength of this effect was found to be variable, and at most roughly half that of the normal McCollough effect. (b) Seen through the eye that originally received coloured but non-patterned stimulation, the test grating has (more weakly) the complementary hue to that originally associated with its orientation.

One possible inference from the results is that some transfer of information between L and R eye channels may be taking place before the stage at which form and colour are associated[5]; but whereas orientational information seems to be transferred correctly, it looks as if colour transfer is antagonistic—that is, as if (say) red light in one eye gives rise to a signal of "minus-red" in the other channel.

An obvious physiological question raised by these results is whether any colour sensitive units at the geniculate or other early stages of the primate visual pathway show signs of complementary sensitivity to colour in the other eye. Inhibitory interaction between pattern-evoked signals from the two eyes has frequently been found in the cat lateral geniculate nucleate [6–8]. Alternatively, is there an efferent pathway whereby the neutral point of the red-green colour signalling system in both uniocular channels is centrally regulated?

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Diurnal Variations of Water in Developing Secondary Stem Tissues of Eucalypt Trees

Zahner[1] has stated that living cambial tissues must be under moderate to severe water stress almost daily during the growing season because of the great tensile forces which develop in the adjacent mature xylem. We have studied diurnal water variations within the developing tissues of tree stems.

Samples were obtained by removing strips of bark from the stems of E. regnans trees and immediately scraping the exposed xylem and phloem surfaces. Each tissue sample was placed in a tared glass tube which was stoppered, weighed and partially immersed in a mixture of dry ice and ethanol. The samples were freeze dried to constant weight, and the amounts of water and dry matter thus obtained. Sampling was done every 4 h during a 24 h period; eight or nine different trees were sampled at each sampling time and mean values were used to plot the graphs in Fig. 1. On the basis of the fresh sample weights, statistical analysis showed that: (1) for xylem, there are significant differences between times as compared with variation between trees within times; the average standard error of a mean is 1.0; (2) for phloem, the mean for 2400 h is significantly lower (1% level) than the mean of values at all other times, which do not differ significantly from each other; and (3) the difference between means for the two types of tissue is highly significant at 0400 h and at 2000 h, and not significant at other times; the average standard error of a difference between two means at a given time of day is 0.63.

On sampling days, meteorological data indicated that sunrise and sunset occurred at about 0510 h and 1900 h respectively. The days were partially cloudy, of high humidity (relative humidity > 65%) and of moderate temperature with little wind, so that transpiration would not have been excessive.

During daylight active transpiration begins with a resultant increase of tensile forces, chiefly in the outermost vessels. The operation of these forces withdraws water from the developing tissues, those cells nearest to the vessels being the most affected (for example, ref. 2). The effects of these forces is far-reaching: Wilson et al.[3] have shown that the water contents of leaves, stems and roots of herbaceous plants reach a minimum during the afternoon and attain a maximum during the night (see also refs. 4, 5). That is, the water stress would be greater in trees, for the developing stem tissues of the xylem than for those of the phloem. As a result of these conditions, the developing phloem tissues lose water at a slower rate (Fig. 1) than the developing xylary tissues (about 0500 h to 2000 h).

By comparison with the developing phloem tissues, the developing xylem tissues are still subject to a greater water stress at 2000 h. Hence between 2000 h and 2400 h the developing xylary tissues will rapidly withdraw water from the immediately adjacent developing phloem tissues until the water demand of the developing xylem tissues is moderated. Thereafter, all developing tissues will regain water as it becomes available, by way of the mature xylem vessels, from the root system of the tree. These indications support the deductions of Zahner[1] and other workers. The developing phloem tissues will regain their full complement of water at a later time than the developing xylem tissues because of their physical location within the bole of the tree.
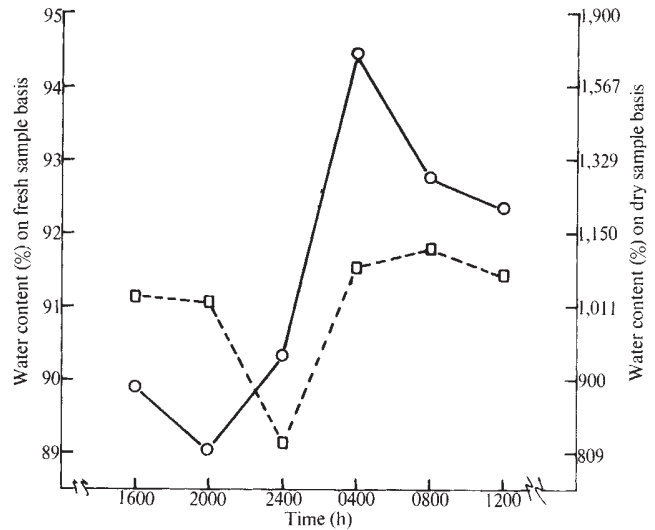

Fig. 1 Water content for developing tissues of Eucalyptus regnans tree stems. O——O, Developing xylem tissue; □ – – – □, developing phloem tissue.

If it is assumed that the dry matter, within the developing tissues of a tree stem, remains approximately constant in mass over a period of 24 h, then the samples of xylary tissues taken in the early morning contain about twice as much water as those collected during the late afternoon, early evening period (Fig. 1, right ordinate). These variations in water content imply that diurnal expansion and contraction of the developing cells take place, and may be of considerable physiological significance during the growth of developing secondary cells in a tree stem. Thus, changes in the concentrations of sugars and other soluble substances may be reflected in various interconversions between individual cytoplasmic materials, in the biosynthesis of cell-wall components and in other intra- or intercellular transformations (see also Zahner[1] and Kramer[6]).

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