Table 1 Response of apple maggot flies to ODP-marked hawthorn fruit before and after experience with ODP

Experiment	Treatment	*n*	% Rejection of ODP-marked fruit*	*n*	% Rejection of clean fruit after rejection of an ODP-marked fruit
1	No previous host or ODP experience	17	17.6 ($P \leq 0.001$)	5	40.0 (NS)
	Previous fruit and ODP experience	20	60	14	14.3
2*a*	Treatment *A* (naive)	29	13.8 ($P \leq 0.001$)	17	76.5 ($P \leq 0.001$)
	Treatment *B* (experienced)	28	64.3	20	10.0
2*b*	*A*	24	41.6 ($P \leq 0.08$)	17	41.2 ($P \leq 0.07$)
	B	27	66.7	21	14.3
3	*A*	16	75.0 (NS)	23	47.8 ($P \leq 0.02$)
	B	18	88.8	18	11.1
4	96-h ODP deprivation	16	62.5 (NS)	10	20.0 (NS)
	No ODP deprivation	16	56.3	9	22.2

* If a fly rejected ODP-marked fruit, we presented it with a clean fruit. If the fly also rejected the clean fruit we disqualified it from this analysis. NS, not significant.

information processing system, because flies may not encounter ODP-marked fruit in conditions of high fruit density, low fly population or when immature. However, once mature flies have oviposited in a single small hawthorn fruit (= native host fruit) they may gain, through tarsal contact with their own ODP trail, the pheromonal experience needed to activate the system.

We are carrying out further experiments to determine why naive apple maggot flies reject clean fruit more often after encountering ODP than do experienced flies.

We suggest that restricted learning of pheromone recognition may be more widespread than is believed. For example, Cammaerts-Tricot[7] and Le Moli and Passetti[8] suggested, but did not prove, that perception of pheromones by *Myrmica* and *Formica* ants, respectively, depends on experience, and Vinson *et al.*[9] demonstrated associative learning of kairomonal ovipositional cues by *Bracon mellitor*, a parasitic wasp. van Lenteren and Bakker[10] first demonstrated that *Pseudeucoila bochei*, a hymenopteran parasite of *Drosophila* larvae, must 'learn' to discriminate against parasitized hosts. Their results strongly suggest that the key component in the learning process is the marking pheromone deposited by *P. bochei* after oviposition. However, because the parasite marks its hosts internally, van Lenteren and Bakker were unable to demonstrate pheromonal contact. Our study parallels their pioneering work and provides the first unequivocal evidence for pheromone learning in insects.

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Behavioural and microspectrophotometric measurements of colour vision in monkeys

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Inherited abnormalities of colour vision are most commonly attributed to abnormalities of the photosensitive pigments in the cone cells of the retina[1,2]. Here, we describe direct microspectrophotometric measurements on the eyes of two squirrel monkeys whose colour vision had been shown to differ behaviourally. Our results are consistent with classical explanations of abnormal colour vision.

Some colour-deficient human observers are dichromats, which means that they are able to match any colour with a mixture of two primary lights, whereas the normal, trichromatic observer requires three variables. It is exactly two hundred years since von Gentilly[3–5] advanced the most natural explanation of this condition, that the dichromat lacks one of the three types of retinal receptor enjoyed by the normal trichromat. It is also one hundred years since Lord Rayleigh described[6] a different abnormality of colour vision, anomalous trichromacy. Like the normal, the anomalous observer requires three variables in colour matching, but in matching a mixture of red and green to a monochromatic yellow light (the 'Rayleigh match') he needs either more red (protanomalous) or less red (deuteranomalous) than the normal. This has been explained by supposing that the anomalous retina contains three types of photopigment but that the absorbance curve for one of them is displaced along the spectrum from its normal position[1,2,7–11]. Despite much work, the exact relationships between the various types of colour vision and retinal photopigments are far from settled. Two recent developments have led to the present report. First, it has been shown that among a population of squirrel monkeys (*Saimiri sciureus*) there occur clear variations in colour vision[12,13]. Second, the technique of microspectrophotometry[14–20], in which a narrow, monochromatic, measuring beam is passed through isolated photoreceptors, has advanced to a stage where it is possible to characterize the types of receptor within an individual primate retina and thus relate the results to earlier behavioural measurements on the same subject.

The squirrel monkeys examined in the present study were both adult females of the subtype exported through Iquitos, Peru[21]; they were drawn from a larger group trained on colour vision tests in Santa Barbara, California. The behavioural tests[12,13] were all conducted in a forced-choice discrimination apparatus in which the monkeys viewed three circular, transilluminated panels. They were taught to touch one of the three panels which was illuminated differently from the other two, in order to receive a 97-mg banana-flavoured food pellet. Which of

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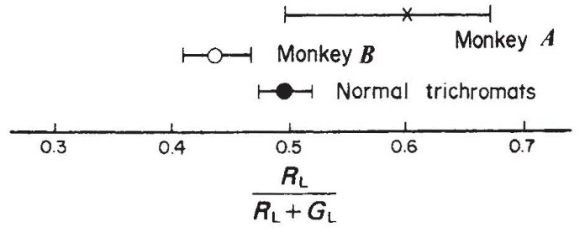

Fig. 1 Rayleigh match results from squirrel monkeys and humans. The match values are expressed as the ratio of the luminance of a red (624 nm) light (R_L) to the sum of the luminances of the red and green (536 nm) lights (R_L+G_L) needed in a mixture to match an equiluminant yellow (585 nm) light. The solid circles give the average values for 20 normal human trichromats, so categorized by their performances on the Farnsworth–Munsell 100-hue test. The horizontal line shows the total range of matches made by this sample of subjects. The results for the two monkeys were obtained from tests in which they were forced to discriminate between a red/green mixture and a yellow. Across repeated test sessions, 21 different mixture combinations were tested. The large symbols represent the midpoints of the range of mixtures over which they were unable to discriminate various red/green combinations from yellow; the horizontal bars enclose the mixture range over which their discrimination performances were not significantly different from chance (95% confidence level).

the three panels was positive (that is, differently illuminated) varied randomly from trial to trial.

Results from three tests of vision are reported. First, detection thresholds were measured for 540 and 640 nm monochromatic test lights superimposed on achromatic backgrounds (3 cd m^{-2}). One animal (*A*) was 1.27 log units less sensitive to the 640 nm light than to 540 nm, whereas the other (*B*) was much more sensitive to the long-wavelength light, showing a threshold difference of only 0.36 log units. Sensitivity variations of this magnitude are characteristic of this species[12].

Two further tests specifically examined colour vision. The first was a Rayleigh match assessing the relative proportions of mixed red (625 nm) and green (536 nm) light that the animal was unable to discriminate from a yellow (585 nm) (Fig. 1). Human subjects were tested in the same apparatus and the matches (mean and total range) obtained from 20 normal trichromats are shown in Fig. 1 for comparison. For the monkeys, the symbols represent the midpoints of the range over which they were unable to discriminate the red/green mixture from the yellow and the horizontal bars show the mixture range over which their discrimination was not significantly different from chance. It will be seen that monkey *B* required somewhat more green light in the mixture than any of the normal human trichromats whereas monkey *A* required much more red. Note also that the mixture range that could not reliably be discriminated from yellow was very much larger for subject *A*.

In another experiment we measured, at each of 10 spectral locations, how much the wavelength of a test light had to be shifted along the spectrum for the animal to discriminate a wavelength difference correctly. The abilities of the two monkeys to distinguish wavelengths were very similar for values from 450 to ~540 nm (Fig. 2). At longer wavelengths, monkey *B* continued to show relatively good discrimination, but *A*'s discrimination worsened strikingly.

If we categorize the animals in terms of human vision, then monkey *A* was a protan; we leave open the question of whether she was an extreme protanomal or a true dichromat. Monkey *B* requires significantly more green light in the Rayleigh match than the normal human trichromat, and we describe her as deuteranomalous, but she is less aberrant in this regard than the typical human deuteranomalous observer[1,2].

The behavioural results were not known to the microspectrophotometrists (J.K.B. and J.D.M.), nor the microspectrophotometric data to G.H.J., until the two sets of results had been handed to an independent third party.

The monkeys were flown to Britain, where microspectrophotometric measurements were made with a modified Liebman microspectrophotometer[16,22] under computer control. The preparation of tissue was as described for *Macaca fascicularis* by Bowmaker, Dartnall and Mollon[19]. Several samples were taken from each retina. The microspectrophotometer was programmed to step from 700 to 390 nm in 2-nm steps, taking wavelengths with even values, and to return taking the interleaved wavelengths. A total of 34 individual records were obtained from animal *A*, and 47 from *B*.

Figure 3 shows for each animal (1) the mean absorbance curve for each class of photoreceptor, excluding short-wave cones, which were too few to provide mean spectra, and (2) the distribution of peak sensitivities for all individual records. From animal *A* we recorded 2 violet-sensitive receptors (mean λ_{max} = 431.3 nm), 13 rods (mean λ_{max} = 496.4 nm, s.d. = 4.69) and 19 green-sensitive receptors (mean λ_{max} = 535.4 nm, s.d. = 3.45); the longest λ_{max} estimated for any cell of this animal was 542.5 nm. The mean and standard deviation for the P535 receptors closely resemble those for the middle-wavelength receptors of macaques[18-19]. Because animal *A* seems to have only one photopigment in the red–green range, its behavioural sensitivity at 640 nm relative to that at 540 nm should be directly predictable from the microspectrophotometric measurements. From the mean absorbance values at the two wavelengths we estimated log absorptance[19] for an axial beam, assuming an outer segment length of 30 μm and a pigment density of 0.015 μm^{-1} and assuming that absorption by the ocular media is identical at 540 and 640 nm. This calculation predicts a difference in log sensitivity of 1.23, very close to the obtained value of 1.27.

From monkey *B* we recorded one short-wave receptor (λ_{max} = 427 nm), 24 rods (mean λ_{max} = 501.7 nm, s.d. = 3.58), no receptors in the vicinity of 535 nm and a broad range of receptors with peak sensitivities between 546 and 577 nm. There is no overlap between the long-wavelength receptors from this animal and the P535 receptors from the protan, a highly significant difference (z = 5.63, Mann–Whitney U-test).

The long-wave receptors of animal *B*, taken as a whole, have a higher standard deviation (8.17 nm) than we should typically expect for a single class of photoreceptor in an individual primate; and *prima facie* they fall into two groups, with a gap in the distribution at 562 nm (Fig. 3*d*). The two groups have means of 552.2 nm (n = 16) and 568.2 nm (n = 9). The latter value can be compared with the mean of 567.0 nm obtained for the long-wavelength receptors of *Macaca fascicularis*[19]. Our confidence in the existence of more than one long-wavelength pigment in this animal is reinforced by the fact that the mean absorbance spectra for the two subgroups (Fig. 3*c*) show very similar absorbance at short wavelengths and seem to have a constant separation; we should not expect this to be the case if, say, the large variation in λ_{max} arose from variations in optical

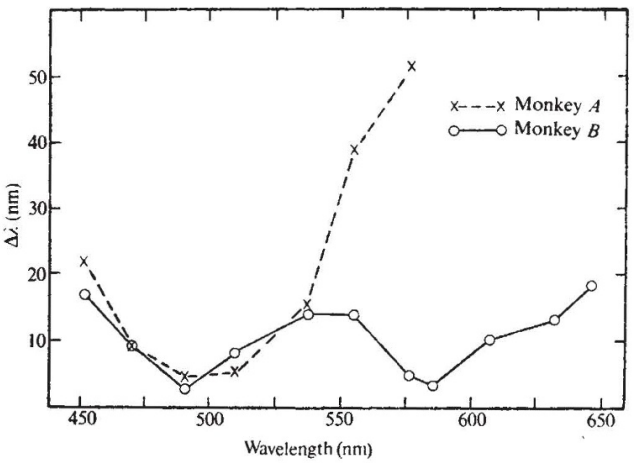

Fig. 2 Wavelength discrimination functions for two squirrel monkeys. The wavelength discrimination values (Δλ) indicate the magnitude of the wavelength change required at each spectral location to support discrimination between two equiluminant spectral lights at a criterial level of 70% correct. The values are averages for differences in both spectral directions except at 452 nm where the change could only be measured towards the longer wavelengths.

scattering or in the presence of photoproducts at short wavelengths, which would distort the absorbance spectrum.

As in macaques and man[19,20], the short-wave receptors seem to be rare in squirrel monkeys. In the case of the rods there is a 5-nm difference between animals in λ_{max}, a difference which is associated with a small difference in absorbance at short wavelengths; we do not know whether the latter difference reflects short-wave contaminants or a true difference in the absorbance spectrum.

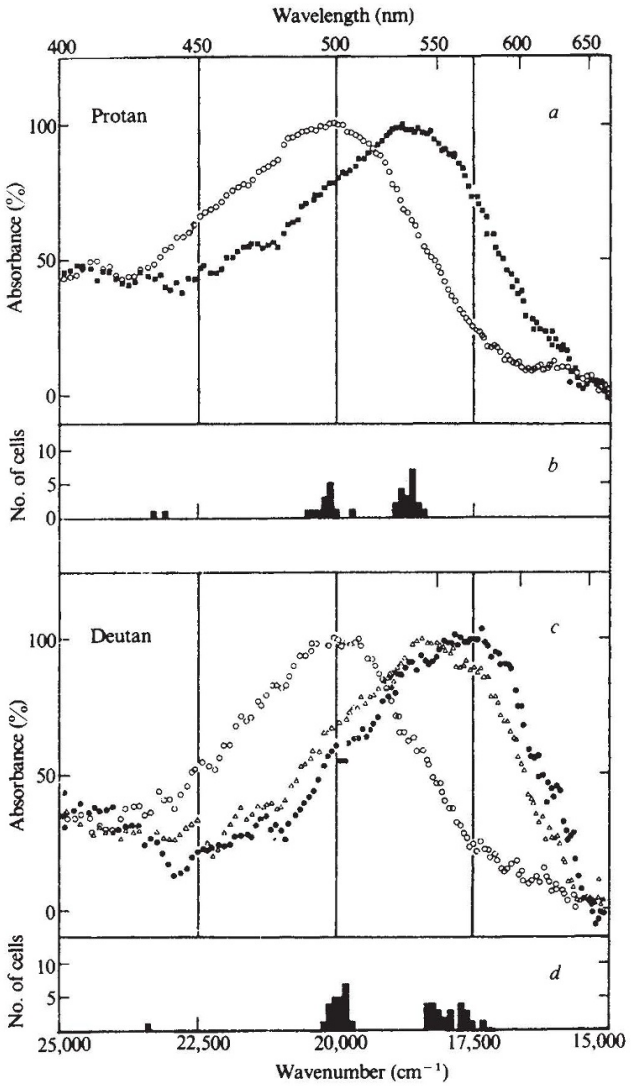

Fig. 3 *a, c*, Mean absorbance spectra for different classes of photoreceptor in two individual squirrel monkeys. Each datum point corresponds to the average of values obtained at two adjacent wavelengths, one value recorded in the descending scan (see text) and the other recorded in the ascending scan. The absorbance spectra for individual receptors were not normalized before averaging. The mean spectra have been normalized to have a maximum of 100%. *b, d*, Distribution of values of peak sensitivity of individual receptors from the protan (*b*) and deutan (*d*) animals. The bin size is 100 cm^{-1}. With the exception of the three short-wavelength receptors, values of peak sensitivity were derived as follows. The raw absorbance values for individual wavelengths were smoothed using an 11-nm running average. The approximate peak of this curve was estimated and each of 50 individual (smoothed) absorbance values on either side of the provisional peak was referred to an appropriate nomogram to estimate the wavenumber of peak sensitivity; this operation amounts to finding where the nomogram must be located on a wavenumber abscissa to yield the absorbance value under consideration. The mean of the many separate estimates for a given cell is the value entered in the histogram. This method resembles that described by Bowmaker *et al.*[19], except that the smoothing and subsequent analysis are carried out by the computer and more individual estimates are used. For the three short-wavelength records we estimated wavenumber of peak sensitivity directly from the 2-nm averages (see above) in the restricted range 400–475 nm, using the frog green-rod nomogram[22].

This first microspectrophotometric study of behaviourally different conspecifics is consistent with classical explanations of colour deficiency and anomaly. Within the limits of our sampling, the severely protan animal lacks entirely the long-wave receptors found in macaques[18,19]. The deuteranomalous animal lacks the P535 receptors found in the protan but probably has more than one type of receptor in the range 546–577 nm.

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Spatial summation and contrast sensitivity of X and Y cells in the lateral geniculate nucleus of the macaque

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Study of parallel processing in the visual pathway[1] of the cat has revealed several classes of retinal ganglion cells which are physiologically distinct and which project to various locations in the brain[2,3]. Two classes have been studied most extensively: X cells, which sum neural signals linearly over their receptive fields, and Y cells, in which the spatial summation is nonlinear[1,4]. In the cat's lateral geniculate nucleus (LGN) cells also can be classified as X or Y, a result of the parallel projection of retinal X and Y inputs to different geniculate neurones[5–9]. We report here our study of parallel signal processing in the LGN of the macaque monkey. We find that (1) monkey LGN cells can be classified as X or Y on the basis of spatial summation; (2) X-like cells are found in the four parvocellular and the two magnocellular laminae, whereas Y-like cells are found almost exclusively in the magnocellular laminae; and (3) the cells of the magnocellular laminae have high sensitivity and the parvocellular cells low sensitivity for homochromatic patterns. This implies that in macaque monkeys the magnocellular cells and their cortical projections may be the neural vehicle for contrast vision near threshold. The cells of the parvocellular laminae seem to be primarily concerned with wavelength discrimination and patterns of colour. As the human visual system is similar to that of the macaque in structure and behavioural performance, our findings are probably also applicable to man.

In macaque monkeys, as in man, the LGN is a highly organized, layered nucleus. There are four dorsal layers of small

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