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Methods

Modelling the SAS of phytoplankton

We counted and measured phytoplanktonic cells by using a video-interactive, microscopyimage analysis system that permits the discrimination and elimination of detritus and other non-living particles. Individual linear measurements were transformed into estimations of cell volume through numerical computation, and these were then distributed along an octave (log_2) scale of cell volume. Finally, a regression mode 1 was applied to the log-transformed values of cell abundance (y axis, cells per ml) and cell volume (x axis, μ m³). The resulting key parameter is the slope (b) of the regression model:

 $\log[\text{cell abundance (cells per ml)}] = a - b \log[\text{cell volume }(\mu \text{m}^3)]$

A general account of methods for the analysis of the size structure of planktonic communities can be found in ref. 10.

Computation of vertical velocity

In the framework of the Quasi-Geostrophic (QG) approximation, the vertical component of the velocity field (w) can be estimated from a diagnostic equation known as the Omega equation²⁶. This equation can be solved in a three-dimensional domain provided that (1) the QG vertical forcing is know at every point of the domair; and (2) boundary conditions are specified. The vertical forcing term can be computed by finite differences from hydrographic data alone (for example, from density and/or dynamic height data), which must have been previously interpolated from stations to a regular grid. Regarding boundary conditions, we assumed w = 0 at the bottom and surface, and Neumann conditions at the lateral boundaries²⁷. Several tests show that the sensitivity of vertical velocity fields to lateral boundaries restricts to the few outermost grid points, with no significant influence on the results obtained in the inner domain.

Received 6 September 2000; accepted 3 January 2001.

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Acknowledgements

This work was supported by the MAST III programme of the European Commision and the CICYT-CYTMAR programme (Spain). We thank M. Emelianov for translating the Russian work of H. J. Semina. We also thank the officers, technicians and crew of *BIO Hesperides* for their help during the OMEGA cruise.

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Ecological importance of trichromatic vision to primates

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Trichromatic colour vision, characterized by three retinal photopigments tuned to peak wavelengths of ~430 nm, ~535 nm and \sim 562 nm (refs 1, 2), has evolved convergently in catarrhine primates and one genus of New World monkey, the howlers (genus Alouatta)³. This uniform capacity to discriminate redgreen colours, which is not found in other mammals, has been proposed as advantageous for the long-range detection of either ripe fruits^{4,5} or young leaves⁶ (which frequently flush red in the tropics⁷) against a background of mature foliage^{8,9}. Here we show that four trichromatic primate species in Kibale Forest, Uganda, eat leaves that are colour discriminated only by red-greenness, a colour axis correlated with high protein levels and low toughness. Despite their divergent digestive systems, these primates have no significant interspecific differences in leaf colour selection. In contrast, eaten fruits were generally discriminated from mature leaves on both red-green and yellow-blue channels and also by their luminance, with a significant difference between chimpanzees and monkeys in fruit colour choice. Our results implicate leaf consumption, a critical food resource when fruit is scarce¹⁰, as having unique value in maintaining trichromacy in catarrhines.

In Kibale National Park, Uganda, leaves eaten by trichromatic chimpanzees (*Pan troglodytes*), black-and-white colobus (*Colobus guereza*), red colobus (*Piliocolobus badius*) and red-tailed monkeys (*Cercopithecus ascanius*) could be discriminated from mature leaves in colour only by the red–green channel (Fig. 1a). Consumed leaves, which included some leaves of mature status, had a higher average luminance, but the red–green colour channel was a far better discriminant (Fig. 1b), primarily because many young red leaves were dark. There were no significant differences overall between primate species in the colours of leaves eaten (Duncan's multiple range test, P > 0.05), and the red–greenness of the leaves was highly positively correlated with the ratio of protein content to toughness (Spearman's test, R = 0.58, P < 0.001). This ratio was consistently higher in leaves consumed by each primate than in mature foliage (Fig. 2).

In contrast, eaten fruits were distinguishable on both the redgreen and yellow-blue colour channels (Fig. 3), as well as luminance (Duncan's multiple range test, P < 0.001 for each case). Fruits selected by monkeys were more yellow than mature foliage (P < 0.03), whereas those eaten by chimpanzees were significantly more yellow than those eaten by monkeys (Duncan's multiple range

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test, P < 0.001), principally because these were fully ripe when chimpanzees ate them.

Many catarrhine primates and howler monkeys eat leaves at critical periods when fruits are unavailable, preferring 'young' leaves where possible¹¹. Our results support the value of trichromacy to a foraging catarrhine because the yellow-blue channel shared with dichromats fails to detect young leaves. Leaf age, however, is probably not a cue in itself; the link that we show between nutritional reward and leaf colour, the latter being more reliable than leaf size at detecting developmental state⁶ and salient at greater distance, offers a clear selective advantage. Although the colour of young leaves in temperate regions is nearly always green, a substantial proportion of those in tropical floras are red: 50-62% in the Old World and 18-36% in the New World^{7,12}. Redness results partly from 'delayed greening' where plants postpone chloroplast function until full leaf expansion^{7,13}. The anthocyanin pigments responsible for reddening may prevent photoinhibition, defend against fungi or deter invertebrate herbivores7,13.

Regardless of function, the nutritional gain to a primate perceiving a red–green transition in leaves, to which a dichromat would be blind, lies in the ingestion of protein during developmental stages before mechanical toughening. The ratio of protein content to fibre (or protein to toughness, as toughness is the dominant sensory attribute of cell-wall fibre to which it is nonlinearly related¹⁴) is an important measure of leaf quality for primates¹⁵. As primate folivory is far less costly to plant fitness than that by invertebrates¹⁶, primates probably exert insufficient selective pressure for plants to modify leaf characteristics such as colour.

It is also unlikely that trichromatic primates influence fruit colour because there is no clear suite of fruit characteristics associated with them^{17–19}. This is partly a reflection of their competition against many other frugivores, like birds and bats, which are known to confer successful seed dispersal^{17,19}. It has been suggested that plants that seem to target primates as seed-dispersers produce large fruits with characteristic colours (such as yellow, orange or brown), a thick peel, single large seeds and acid-sweet flesh^{20,21}. If this hypothesis were true, however, it would not explain why the external properties of fruits seem to be consistent throughout the tropics, even where primates are principally dichromatic, as in the New World, or absent, as in New Guinea¹⁸.

A further weakness in suggesting co-adaptation between trichromacy and fruit colour is that one whole group of trichromatic primates, the colobine subfamily of Old World monkeys, are seed



Figure 1 Distribution of leaf colours eaten by the four primates (red squares) in relation to the domain of mature foliage (outlined in green). **a**, Eaten leaves are distinguished on the horizontal L/(L+M) 'red–green' axis (F = 78.1, P < 0.001), where increasing redness lies to the right side, but not on the vertical S/(L+M) 'yellow–blue' axis (F = 0.347, P = 0.556). **b**, Differences in red–greenness are far greater than differences in luminance (plotted as a proportion of reflectance from a compacted barium-sulphate powder standard), as shown by the variance ratio for the latter (F = 13.27, P < 0.001). Some mature leaves were eaten, but others simply had a mature colour, differing in other physico-chemical properties. The proportion of feeding time spent consuming

destroyers, frequently consuming unripe fruits expressly for their immature seeds²². In addition, cercopithecines, the other subfamily of Old World monkeys, often select unripe fruits in Kibale, offering them a competitive advantage over apes although, very often, this is to the detriment of the seeds they process²³. Finally, the contention that primate trichromacy evolved to detect pre-existing fruit colours also seems implausible because, despite a high degree of frugivory and similar fruit colours to the Old World tropics¹⁸, most neotropical primates are basically dichromatic.

The fruit-feeding hypothesis for trichromacy in higher primates is unconvincing. In this study, fruits selected by sympatric primates not only differed significantly in colour, but also the yellow–blue channel, common to all dichromatic mammals, could distinguish



Figure 2 Protein (in %BSA equivalents) to toughness (in J m⁻²) ratios of leaves eaten by the primates compared with those of mature leaves present on the same trees (Duncan's multiple range test, P < 0.001). Protein alone was higher in eaten leaves, whereas toughness was lower. Use of a ratio follows analogous previous use¹⁵. Tannins interfere with protein uptake, but their levels in leaves in this study were relatively low, which is well known in Kibale³⁰. Plots show medians; boxes enclose 50% of data; bars show ranges. A higher protein : toughness ratio reflects greater ease in opening leaf cells to release more nutritious cellular contents. There was no difference in the red–greenness of leaves between primates.



non-mature leaves was 61.6, 66.7, 32.4 and 4.4% for *Piliocolobus badius, Colobus guereza, Cercopithecus ascanius* and *Pan troglodytes*, respectively. Leaf eating by chimpanzees is low at Kanyawara owing to frequent consumption of terrestrial herbaceous vegetation. Elsewhere, leaf consumption by chimpanzees is much more common²⁹. Consumption of mature leaves (that is, of the background itself) was sporadic: 3.8% in *P. badius*, 14.8% in *C. guereza*, 1.5% in *C. ascanius*, and 1.0% in *P. troglodytes*. In some key plant species, leaf flushing was year-round, but there were two re-leafing peaks that seemed to coincide with the onset of the wet season.

many fruits from leaves (Fig. 3). This would explain why dichromatic tropical mammalian frugivores, such as all New World primates except *Alouatta*, can find fruits of the same colour range with no apparent difficulty¹⁹. Indeed, howler monkeys are sluggish primates in comparison with sympatric New World monkeys, such as spider monkeys that feed on the same general range of fruit species, and are rarely likely to be first into fruiting trees.

We thus argue that our results support the value of trichromacy to a primate foraging for leaves. In all four species studied, the overall uniformity of leaf colour choice matches the uniformity in their photopigment tuning. This is despite the two colobine species, with ruminant stomachs, having diets of differing plant composition in comparison with those of the simple-stomached red-tail monkey and chimpanzee. The potential nutritional reward in detecting the red–green transition would thus be valuable to all these primates regardless of digestive physiology (Fig. 2). To an individual dichromatic primate, a young red leaf might appear dark and mature and thus tough and unpalatable⁶.

Selection pressures that maintain trichromacy in primates are clearly indicated by the near absence of individual variation outside Homo sapiens (such as the genus Macaca, where < 0.1%of individuals have been found to be dichromatic²⁴). Because leafing and fruiting are distinct alternating events both in Kibale and elsewhere in Africa¹⁰, the regular biannual reliance of catarrhine primates on young leaf matter may account for the selective pressures resulting in uniform trichromacy, regardless of whether these primates are effective seed-dispersing frugivores or not. Few diurnal tropical mammals feed on a generalized range of leaves in the manner of higher primates. Of New World primates, only Alouatta spp. and Brachyteles arachnoides (whose retinal cone pigments have not been examined) feed on leaves to any great extent. The contrast between this and the dependence of most catarrhines on leaves, either as a critical resource when there is a fruit dearth or as in colobines as a staple, has been explained by differing inter-continental patterns of leaf phenology¹⁰.

Competition for ripe fruit attracts many other frugivores that signal its availability. Although the red–green colour channel can help a group to identify such fruits at long range⁸, the yellow–blue channel can often do this too⁹. Furthermore, many closer-range preingestive cues, including smell and texture, reinforce visual indications. In contrast, finding palatable leaves is, on any leaf patch with leaves of differing states, more purely an individual task for which the value of the red–green channel is very clear. Its sensitivity is paramount in that very small colour changes in leaves reflect a large change in their quality (Figs 1 and 2). We believe that full trichro-



Figure 3 Histograms of colour distributions on the S/(L+M) 'yellow-blue' axis of eaten leaves and fruits in comparison with mature leaves. **a**, The distributions of eaten fruits and mature leaves overlap, but mainly the peak of the fruit distribution lies significantly to the left (F = 12.7, P < 0.001), reflecting the more yellow hue of many fruits. **b**, There is no difference on the yellow-blue channel between the distribution of eaten leaves and mature foliage (F = 0.347, P = 0.556).

matic vision evolved originally for leaf foraging in higher primates. Its independent evolution in folivorous howler monkeys in the neotropics, where proposed fruiting/re-leafing synchrony¹⁰ and a possible lower incidence of red leaves may have decreased the overall importance of trichromacy to most primate species, supports this contention.

Methods

Animals and study area

Studies were carried out at the Makerere University Biological Field Station (Kanyawara) in Kibale National Park, Uganda (0° 13′ to 0° 41′ N; 30° 19′ to 30° to 32′ E). The site is moist evergreen rainforest²⁵. The primates were observed for 1,170 h between January and October 1999. Focal animal techniques with several observers were used to maximize data. New focal animals were selected every 10 min. We collected a total of 386 h of feeding observations on these primates, in which time they ate parts of 118 plant species.

Food samples

Specimens of all observable food items were systematically collected and analysed for colour, chemical content and toughness. All foods were processed fresh with the aid of a field kit designed to assess physico-chemical food characteristics³⁶. Food samples were either those dropped by primates or, if not, vacated trees were climbed to collect food items with fresh bite marks. Full physicochemical characteristics were obtained for 350 eaten leaves, 164 mature leaves and 110 eaten fruits, which formed the dataset analysed here.

Physico-chemical methods

An Ocean Optics S2000 spectrometer was connected to, and powered by, a laptop PC through a DAQCard1200 PCMCIA card. Illumination was provided by an Ocean Optics LS-1 12-volt 3100 K tungsten halogen lamp giving adequate light between 350 and 700 nm. For colour recording, small (~3 mm×3 mm) food samples were placed in a purpose-built chamber with both light conduction and transmission to the spectrometer via 200–400 μ m Ocean Optics patch fibre optic cables equipped with lenses. The food reflectance spectra were decoded into potential excitations of short (S), medium (M) and long (L) wavelength retinal cone pigments, following which the two colour channels of primate trichromatic vision were constructed^{5,27}: yellow-blue, S/(L+M); and red-green, L/(L+M). For protein analysis (spectrophotometry), cables were connected to an Ocean Optics cuvette holder for 1-cm quartz cuvettes. Results for the Coomassie blue (Coomassie brilliant blue G-250; Sigma) test for protein were expressed as a percentage of bovine serum albumin (%BSA) equivalents. Radial diffusion assays were run for tannins, results being expressed as percentage quebracho equivalents. We measured toughness with a portable universal testing machine²⁸. Data were analysed by analysis of variance after logarithmic transformation of the variables (except yellow-blue signals, which were normally distributed; Fig. 3).

Received 7 September; accepted 22 December 2000.

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Acknowledgements

We thank D. Osorio for help with colour registration; E. Ting, P. Y. Cheng, I. C. Bruce, R. T. Corlett, L. Ramsden, N. Yamashita and A. Walker for comments, P. Kagoro, B. Balyeganira and M. Musana for field assistance in Uganda; J. Magnay, R. W. Wrangham and C. A. Chapman for logistic support in Uganda; and the Ugandan National Council for Science and Technology, Ugandan Wildlife Authority and Makerere University Biological Field Station for permission to work at Kibale. Supported by Research Grants Council of Hong Kong, National Geographic Society, Sigma Xi, Explorer's Club and Croucher Foundation of Hong Kong.

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Suppressing unwanted memories by executive control

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Freud proposed that unwanted memories can be forgotten by pushing them into the unconscious, a process called repression¹. The existence of repression has remained controversial for more than a century, in part because of its strong coupling with trauma, and the ethical and practical difficulties of studying such processes in controlled experiments. However, behavioural and neurobiological research on memory and attention shows that people have executive control processes directed at minimizing perceptual distraction^{2,3}, overcoming interference during short and long-term memory tasks³⁻⁷ and stopping strong habitual responses to stimuli⁸⁻¹³. Here we show that these mechanisms can be recruited to prevent unwanted declarative memories from entering awareness, and that this cognitive act has enduring consequences for the rejected memories. When people encounter cues that remind them of an unwanted memory and they consistently try to prevent awareness of it, the later recall of the rejected memory becomes more difficult. The forgetting increases with the number of times the memory is avoided, resists incentives for accurate recall and is caused by processes that suppress the memory itself. These results show that executive control processes not uniquely tied to trauma may provide a viable model for repression.

Executive control processes studied in behavioural^{6,9,14} and neurobiological^{2,4,10–13,15–17} research on cognition may provide a mechanism for the voluntary form of repression (suppression)

proposed by Freud¹. To test this hypothesis, we adapted the go/ no-go paradigm used to study executive control over motor actions in primates¹⁸ and humans^{15–17} for use in a memory retrieval task. First, we trained subjects on 40 unrelated word pairs (for example, ordeal-roach) so that they could recall the right-hand member of each pair when provided with the left-hand member. Next, subjects performed a critical task requiring them to exert executive control over the retrieval process. On each trial of this think/no-think task, a cue from one of the pairs appeared on the computer screen. Depending on which cue appeared, subjects were told either to recall and say (think about) the associated response word (respond pairs), or not to think about the response (suppression pairs). For the latter pairs, we emphasized that subjects should not allow the associated memory to enter consciousness at all. If subjects accidentally responded to a suppression pair, they heard a beep signalling an error. To increase the need to recruit inhibitory control mechanisms, we required subjects to fixate on the cue word for the entire time (4s) that it appeared on the screen, discouraging perceptual avoidance and generating a constant threat that the associated memory might intrude into consciousness. Thus, suppression trials required the stopping of both a prepotent motor



Figure 1 Final recall for respond and suppression items as a function of the number of repetitions for the same-probe (SP) and independent-probe (IP) tests. **a**, **b**, Experiment 1; **c**, **d**, experiment 2; **e**, **f**, experiment 3; **g**, averaged across experiments. Note the negative slope for recall of the suppressed item, indicating increasing inhibition. Inhibition (0 vs 16 suppressions) was significant (P < 0.01) in all experiments, and did not interact with type of test cue (F < 1 in all cases; analysis of variance). Inhibition was significant (P < 0.05) in every SP and IP test for every experiment (**a**–**f**).