[52] Vlahakis, G., Heston, W. E., and Smith, G. H., *Science*, **170**, 185 (1970).
[53] Bentvelzen, P., Daams, J. H., Hageman, P., and Calafat, J., *Proc. US Nat. Acad. Sci.*, **67**, 377 (1970).
[54] Bittner, J. J., *Cancer Res.*, **2**, 710 (1943).
[55] Heston, W. E., Hall, W. T., Vlahakis, G., Charney, J., and Moore, D. H., *J. Nat. Cancer Inst.*, **45**, 937 (1970).
[56] Murray, J. A., *Sci. Rep. Invest. Imp. Cancer Res. Fund.*, **4**, 114 (1911).
[57] Andervont, H. B., and Dunn, T. B., *J. Nat. Cancer Inst.*, **28**, 1153 (1962).
[58] Hall, W. T., and Feller, W. F., *J. Nat. Cancer Inst.*, **39**, 1155 (1967).
[59] Penrose, L. S., MacKenzie, H. J., and Karn, M. N., *Brit. J. Cancer*, **2**, 168 (1948).
[60] Smithers, D. W., Rigby-Jones, P., Galton, D. A. G., and Payne, P. M., *Brit. J. Radiol.*, Suppl. No. 4 (1952).
[61] Anderson, V. E., Goodman, H. O., and Reed, S. C., *Variables Related to Human Breast Cancer* (University of Minnesota Press, 1958).
[62] Papadrianos, E., Haagensen, D. C., and Cooley, E., *Annals of Surgery*, **165**, 10 (1967).
[63] Clemmesen, J., *Acta Pathol. Microbiol. Scand.*, **266** (1965).
[64] Lacassagne, A., *CR Acad. Sci.*, **195**, 630 (1932).
[65] Bonser, G. M., Dossett, J. A., and Jull, J. W., *Human and Experimental Breast Cancer* (Thomas, Springfield, Illinois, 1961).
[66] Charney, J., and Moore, D. H., *Nature*, **229**, 624 (1971).
[67] Nowinski, R. C., Old, L. J., Moore, D. H., Geering, G., and Boyse, E. A., *Virology*, **31**, 1 (1967).
[68] Sibal, L. R., Feller, W. F., Fink, M. A., Kahler, B. E., and Hall, W. T., *Science*, **164**, 76 (1969).
[69] Temin, H. M., and Mizutani, S., *Nature*, **226**, 1211 (1970).
[70] Baltimore, D., *Nature*, **226**, 1209 (1970).
[71] Spiegelman, S., Burny, A., Das, M. R., Keydar, J., Schlom, J., Travnicek, M., and Watson, K., *Nature*, **227**, 563 (1970).
[72] Came, P. E., and Moore, D. H., *Proc. Soc. Exp. Biol. Med.* (in the press).

Colour and Brightness Preferences in Monkeys

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A method has been developed for testing the preferences of monkeys for simple visual stimuli. Preliminary results for colour and brightness have already been obtained.

THE basis of people's everyday decisions is usually "aesthetic" preference. Clothes are chosen for their colour; a bar of soap is chosen for its smell; the route of a journey is chosen for the scenery along the road. Very little is known, however, about these preferences—the stimuli that are preferred cannot be specified in any detail; it is not known how far they depend on genetic, developmental and cultural factors; almost nothing is known about their evolutionary history and little about what biological advantage they bring.

With these general questions in mind, I have investigated the preferences of male rhesus monkeys (*Macaca mulatta*). It is of theoretical importance to know whether any comparable phenomena occur with lower primates. If they do, there will be the practical advantage of being able to study some of the central questions I have listed in an experimental animal, which can be subjected to environmental and physiological control. I have begun by looking at preferences for simple visual stimuli, and wish to describe a method and some preliminary findings.

In studies of "sensory reinforcement" such as those of Butler[1], sensory stimuli have been made the primary goal of the animal's behaviour. I have chosen, instead, to study what happens when the stimuli are made incidental to behaviour which already has an independent goal. I have given a monkey a free choice of alternative behavioural routes to obtain food, each of which is equally efficient but involves exposure to different visual stimuli: to the extent that the monkey chooses one route rather than another, he shows a preference for the associated stimuli.

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A monkey was put in a testing chamber where visual stimuli could be back-projected on one of the walls. The chamber contained a single response key and the monkey was rewarded with food for holding down this key for a cumulative period of 100 s, independently of his detailed pattern. The key controlled the presentation of the visual stimuli and the programme ran as follows. In any particular session there would be two alternative stimuli, say X and Y, which would be produced alternately by successive holds on the key. When the monkey pressed the key first he might get X, which would stay on as long as the hold was maintained; when he released the key and pressed again he would then get Y, which, likewise, would stay on as long as the hold was maintained; the next press would produce X, the next Y, and so on. To exercise a preference the monkey had simply to hold the key down when he preferred the current stimulus and release and press again when he did not.

The testing chamber (Fig. 1) was a small rectangular box, $80 \times 65 \times 45$ cm, painted black inside. At one end of the chamber, covering the wall, was a ground glass screen, 45×45 cm, on which the alternative stimuli were projected from either of two projectors. The stimuli could be varied by changing the slides in the projectors. Bars across the chamber confined the monkey to a relatively small compartment at the opposite end to the screen so that he sat facing the screen at a convenient visual distance from it, about 40 cm. In front of him was a sloping dashboard bearing the response key and

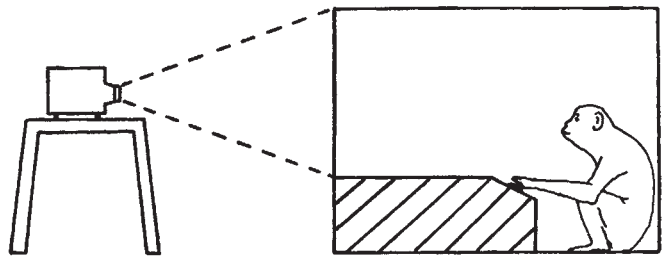

Fig. 1 Testing chamber.

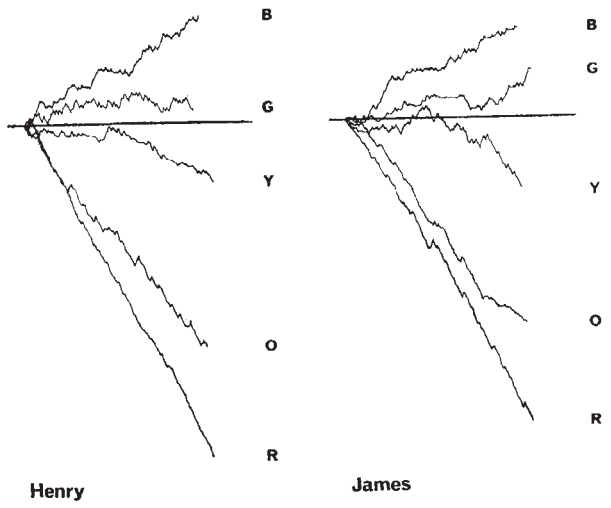

Fig. 2 Sample records from tests for colour preference. The test stimuli were homogeneous coloured fields of equal subjective brightness, paired in each case with a standard white field of the same subjective brightness. The lines show how the monkey divided his time between the test and the standard stimuli: the recording pen moved upwards at 75° when the test stimulus was on and downwards at 75° when the standard comparison stimulus was on, so that upward slopes represent positive preference and downward slopes negative preference relative to the standard. B, blue; G, green; Y, yellow; O, orange; R, red.

below that was a pellet tray. In the roof was a small pea-bulb which served as a dim houselight during time-out periods. When the monkey first entered the chamber the houselight was on and the response key was inoperative. After a short while the houselight went out and the response key became effective. The monkey was then free to press the key as he chose, alternating between the two stimuli and holding either as long as he wished, although with the constraint that neither was to stay on longer than 10 s or else it was automatically terminated and he had to release and press again (in practice this limit was very rarely reached). When he had clocked up 100 s of total response, the houselight came on again and the key was inoperative for the next 50 s during which time five banana pellets were delivered to the tray. The houselight then went out, the key became effective and the programme was recycled. At the end of ten such cycles (1,000 s of total response), the houselight came on finally and the sequence was terminated. In the course of the experiment measurements were made of the total number of alternations between the two stimuli and the total time spent in the presence of each. The monkey's performance was also displayed on a pen recorder which showed from moment to moment how he divided his time between the two stimuli: the recording pen moved upwards at an angle of 75 degrees when one stimulus was on and downwards at an angle of 75 degrees when the other was on, so that the overall slope indicated the preference.

The principal results obtained so far concern colour and brightness preferences. The stimuli here were homogeneous fields of light filling the whole screen, with brightness and colour determined by filters in the projectors. For the brightness study the fields were white and ranged in brightness in eleven steps from 0.1 to 1.7 log foot-lamberts. For the colour study the fields were coloured red, orange, yellow, green and blue (Kodak Wratten filter numbers 25, 22, 12, 58 and 38A, respectively) and were adjusted in subjective brightness with an SEI photometer to 0.9 log foot-lamberts for the human eye, which has a sensitivity curve almost identical to that of the rhesus monkey[2]. So that all measurements of preference should be directly comparable, a white field of 0.9 log foot-lamberts was used as a standard stimulus with which to pair each other stimulus to measure the relative preference.

Four monkeys, all adolescent males imported from India about one year previously, took part in this experiment. Outside the testing sessions they were housed in pairs in cages in the home colony and were fed on a diet of chow which was freely available. One pair, Henry and James, had more extensive testing than the others, and the results for these two will be given in detail. They were tested 6 days a week, twice a day, for colour preference in the morning and for brightness preference in the afternoon. The different levels of brightness and the different colours were tested in a random order which was the same for both monkeys. The set of brightness stimuli was run through twice consecutively and the set of colour stimuli three times, that is, for each level of brightness two measurements were made separated by about 2 weeks, and for each colour three measurements separated by about 1 week.

About 15 days' training with irrelevant stimuli was given to familiarize the monkeys with the contingencies of the testing situation. With this preliminary experience the pattern of performance settled down and became very constant. The monkeys responded usually without interruption and completed the 1,000 s of stimulus presentation in about 1,300 s (not counting time-out periods). During this time they alternated rapidly between the two stimuli, on average about 400 times. The number of alternations was higher overall for the brightness tests than for the colour tests (means of 439 and 354, respectively: $P < 0.01$ on a t test), but otherwise it had little relationship either to the nature of the stimuli or, surprisingly, to the degree of preference shown: an increase in preference could mean either an increase in the time for which the preferred stimulus was held on or a decrease in the time for which the non-preferred stimulus was held on, and the sum of these periods—the time for two alternations—need not, and did not, vary systematically. The preferences tended to be quite stable from the beginning to the end of a session; there were no marked swings, and the monkeys showed little sign of losing interest in the stimuli even when the sessions were extended to twice their usual length. Rapid alternation in combination with a basically stable preference led to almost linear performance records.

Figs. 2 and 3 show for Henry and James some sample records from individual sessions, and Fig. 4 shows the mean

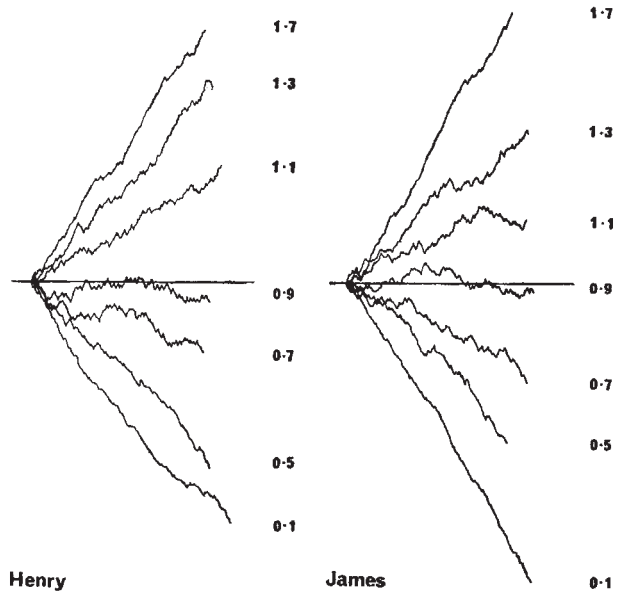

Fig. 3 Sample records from tests for brightness preference. The test stimuli were homogeneous white fields of different brightness. The numbers give the brightness of the test stimuli in log foot-lamberts.

preferences for each test stimulus in terms of the amount of time per 1,000 s session spent with that stimulus as opposed to the standard stimulus. Table 1 gives the results of three-way analyses of variance on the preference and alternation scores.

Table 1 Results of Three Way Analyses of Variance

A Preference scores

Source of variation	Degrees of freedom	Variance ratio
(i)		
Brightness levels	10, 10	509*
Repeated measurements	1, 10	3.13
Monkeys	1, 10	0.00
(ii)		
Colours	4, 8	112*
Repeated measurements	2, 8	0.45
Monkeys	1, 8	0.02

B Alternations

Source of variation	Degrees of freedom	Variance ratio
(i)		
Brightness levels	10, 10	0.77
Repeated measurements	1, 10	1.05
Monkeys	1, 10	1.03
(ii)		
Colours	4, 8	0.51
Repeated measurements	2, 8	0.87
Monkeys	1, 8	2.79

* Significant at 0.1% level; no other results were significant at 5% level.

Both monkeys had strong preferences related to both brightness and colour. These preferences were not, as might have been expected in a two-choice situation, all or none, but were finely graded. The brightness preferences were monotonically related to brightness over the range used, and, more surprisingly, the colour preferences were monotonically related to wavelength. Repeated measurements were highly consistent, and there was remarkably little variation even between the two monkeys.

The other pair of monkeys, who were actually rather younger than Henry and James, showed similar strong and reliable

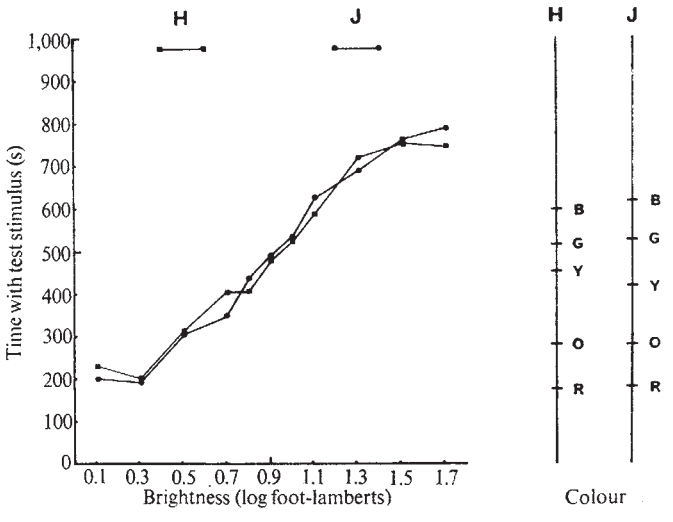

Fig. 4 Mean preferences on the brightness and colour tests, averaged over two sessions for brightness and three sessions for colour. The ordinate gives the amount of time per 1,000 s session spent with the test stimulus as opposed to the standard stimulus.

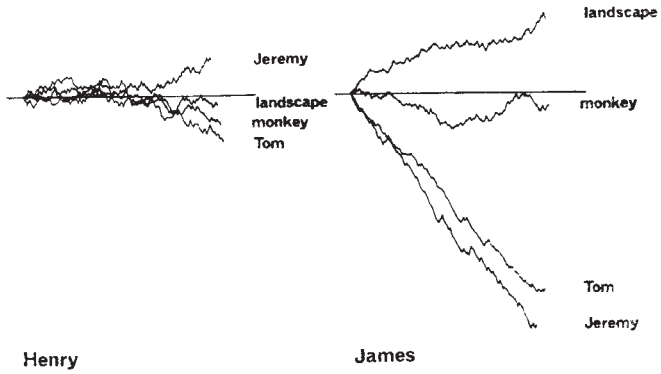

Fig. 5 Sample records from tests for picture preference. The test stimuli were coloured photographs of equal subjective brightness to the standard stimulus. Jeremy, the laboratory photographer; Tom, the animal cleaner; monkey, a frightened monkey in a cage; landscape, a mountain in Connemara.

preferences. Their preferences were quantitatively close to those of Henry and James in the case of brightness, but were smaller in the case of colour, although the same rank order of colours obtained.

To follow up the striking similarity in the behaviour of the different monkeys, I made additional tests with other kinds of stimuli. It was found, predictably, that with more complex and meaningful stimuli this similarity no longer held. Fig. 5 shows sample records from sessions where the stimuli were "pictures" instead of homogeneous fields. The pictures were coloured photographs of people, animals and outdoor scenes, adjusted in overall brightness (when defocused) to 0.9 log foot-lamberts; as before, each was compared with the standard white field. With these stimuli the preferences of individual monkeys diverged. Henry, for example, was relatively indifferent to a picture of Tom, the cleaner, whereas James apparently disliked it; of the other monkeys, one strongly liked the same picture, whereas the other disliked it as much as James.

These results as a whole show the method to be an effective way of demonstrating and measuring visual preferences. The specific findings raise many points for further exploration. (1) To what extent, if at all, are the demonstrated preferences peculiar to this testing method? In particular, what is the significance of using primary reinforcement to maintain the key pressing behaviour? Would the results have been the same had some other reward than food been used or had it been practicable to use no reward at all? (2) What are the formal characteristics of the preferences? For example, if stimulus *A* is preferred to *B*, and *B* is preferred to *C*, does it follow that *A* is preferred to *C*? Or, if stimulus *D* is strongly preferred to *E* and only weakly preferred to *F*, does it follow that *F* is preferred to *E*? (3) What is the origin of the preferences? Can the similarity in the brightness and colour preferences of different monkeys be taken to mean that these preferences are species-specific and independent of individual experience, or could it be that these monkeys happened to have had the same experience at some critical period in their early life? (4) How far are the preferences a function of a particular set of environmental and bodily conditions? How would they be affected, for example, by changes in ambient temperature, changes in time of day, or changes in motivational state? (5) What is the adaptive value of the preferences? In so far as they are innate, what significance do they have for a monkey in the wild?

This work was financed by the Medical Research Council. I thank Professor L. Weiskrantz for his interest.

Received December 1, 1970.

[1] Butler, R. A., *Behavior of Nonhuman Primates* (edit. by Schrier, A. M., Harlow, H. F., and Stollnitz, F.), chap. 13 (Academic Press, New York and London, 1965).
[2] De Valois, R. L., and Jacobs, G. H., *Science*, **162**, 533 (1968).