EVIDENCE THAT *OCTOPUS* IS COLOUR BLIND

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SUMMARY

1. Six octopuses were trained on a series of visual discrimination tasks where the discriminanda were presented simultaneously, and where different tasks alternated in a single training session.

2. All the octopuses could make discriminations based on brightness and orientation over the same period of time.

3. Over a period in which all octopuses discriminated a black from a white vertical rectangle none discriminated a yellow vertical rectangle from a grey (of matching brightness).

4. Over a period in which all octopuses discriminated a vertical from a horizontal grey rectangle none discriminated a violet vertical rectangle from a matching grey.

5. The behaviour of the octopuses was qualitatively different in the hue versus grey situations, their attacks being considerably slower and less certain.

6. These results, which agree with previous behavioural findings and a variety of morphological, physiological and biochemical evidence, make it increasingly probable that *Octopus vulgaris* is colour blind.

INTRODUCTION

In an earlier paper, evidence was presented that in a training situation octopuses do not discriminate between different hues, though they readily discriminate between different brightnesses (Messenger, Wilson & Hedge, 1973). These experiments are open to certain objections however, perhaps the most serious of which is that the animals were trained by a successive presentation method, when it has been established that simultaneous presentation is a more effective training method for *Octopus* with a difficult discrimination (Sutherland, Mackintosh & Mackintosh, 1963).

Accordingly we designed a short experiment that required octopuses to discriminate a yellow from a grey rectangle, and a violet from a grey rectangle, when the rectangles were presented simultaneously. Yellow and violet were chosen because they had not been tested previously (Messenger *et al.* 1973); and grey was chosen as the other discriminandum because there is still no evidence as to whether octopuses can discriminate a hue from a grey of matching brightness.

Table 1. *Plan of experiment*

Stage	Task I (simultaneous presentation)		Task II (simultaneous presentation)
1	black +ve/white −ve (*brightness*)	alternating with	yellow +ve/grey −ve (*hue 1*)
2	black +ve/white −ve (*brightness*)	alternating with	vertical +ve/horizontal −ve (*orientation*)
3	violet +ve/grey −ve (*hue 2*)	alternating with	vertical +ve/horizontal −ve (*orientation*)
4	black +ve/white −ve (*brightness*)	alternating with	vertical +ve/horizontal −ve (*orientation*)

The octopuses were trained in a novel way to provide a control for discrimination performance throughout training; during each session they were trained on two different discrimination tasks, a trial on Task I alternating with a trial in Task II (Table 1). In this situation, octopuses did not make discriminations on the basis of hue during periods in which they were discriminating on the basis of brightness, or of orientation.

The important implications of these findings for colour camouflage, at which octopuses are adept, are considered elsewhere (Messenger, 1974; Packard & Hochberg, 1977; Froesch & Messenger, 1977).

MATERIALS AND METHODS

Subjects were experimentally naïve *Octopus vulgaris* from the Bay of Naples, kept separately in running sea water in tanks measuring 100 × 60 cm with water to a depth of 40 cm. There was a recessed 'home' at the centre rear of the tank from which they could view figures introduced at the front of the tank against a pale creamy-white screen. This had a central perpendicular piece, projecting 20 cm towards the octopus, that partitioned the front of the tank into equal right and left areas, so that when a pair of figures was introduced the octopus could only attack and grasp one figure at a time. The animals were first trained for two days to stay in the home, by gently pushing with a clear Perspex rod and, if need be, by 'chasing' with outspread hands; once in the home they were fed a crab and left alone. (It is essential that the animals be in the home at the start of each trial and it was sometimes necessary during the experiment to chase animals back home at the beginning of the training session.) The animals were then trained for one other day to swim down and attack a single grey square (side 32 mm) presented on alternate sides for six trials; attacks were rewarded by about 1 g sardine. The animals were coaxed or chased back into the home after each trial. We commenced with eight animals but one stopped attacking on the second training session and another escaped from its tank after the third session, reducing the group size to six.

Figures. The figures were 10 × 2 cm rectangles, shaken up and down by hand three times per second. In the brightness and the hue tasks the rectangles were vertically orientated. For the brightness discrimination black and white Perspex rectangles were used; for the hue discrimination, papers from the Color Aid Co. range (Messr

Langford & Hill Ltd, Warwick Street, London, W1) were stuck onto Perspex rectangles and varnished with clear polyurethane. To select the papers a dark-adapted human observer matched a series of yellows, violets and greys in dim light. The closest matches were between; Color Aid 'yellow hue' (λ_{max} 580 nm*) and Color Aid 'grey 1' (50% reflectance†) and Color Aid 'violet hue' (λ_{max} 400 nm*) and Color Aid 'grey 8' (5% reflectance†) and these pairs were used in stage 1 and 3 of the experiment respectively (Table 1). For the orientation task the animals were shown rectangles of grey Perspex (intermediate in brightness to Color Aid grey 1 and 8) oriented vertically or horizontally.

Pre-training. For three sessions, each of 8 trials, the animals were shown a single black (4 trials) or a single yellow rectangle (4 trials). Yellow and black were presented in random order and each was shown twice on the left and twice on the right. Attacks were rewarded by 1 g sardine so that at the end of pre-training each animal had been fed 12 times for attacking the black vertical and 12 times for attacking the yellow vertical. Later in the experiment we interpolated 12 pre-training trials with a single violet vertical.

Training. The two figures of Task I were presented simultaneously and the octopus allowed to make a response. An attack on the positive figure was followed immediately by food reward and the attack scored 'correct'. An attack on the negative figure was not rewarded; after 10 s the figure was removed from the octopus, which was lured back to its home. The attack was scored as 'incorrect' but the figures were shown again to the octopus and the procedure repeated until the animal had made the correct choice, which brought a food reward. This is the 'correction training' of Sutherland & Muntz (1959): it sometimes necessitated as many as eight re-presentations. The two figures of Task II were then shown simultaneously and when the octopus attacked, it was either given the food reward, or correction training. Tasks I and II alternated but the position of the positive figure was varied from side to side in a semi-random sequence; in any case correction training eliminates side preference (*ibid*). During each training session of 16 trials, 8 trials on Task I alternated with 8 trials on Task II. It is emphasized that no shocks were administered for an incorrect attack and that there was no time limit for making a correct attack.

Because of this correction training the interval between trials varied somewhat: it was usually about 10 min but there was always at least a half-hour break after the middle (eighth) trial so that it is appropriate to plot the results by half-sessions (Fig. 1).

RESULTS

These are set out in Fig. 1 and need little amplification. Even by the end of the first half-session there is a striking difference between the behaviour exhibited to the two tasks. In the brightness discrimination the new, white figure is largely ignored as the animals continue to attack the black figure that has been previously associated with a food reward. In the hue discrimination the effect of pre-training is not apparent: the yellow figure is attacked at about the same level as the grey figure that the animals have never seen before. This difference continues over the three sessions and in

* By reflectance spectrophotometry (Unicam Sp 735).
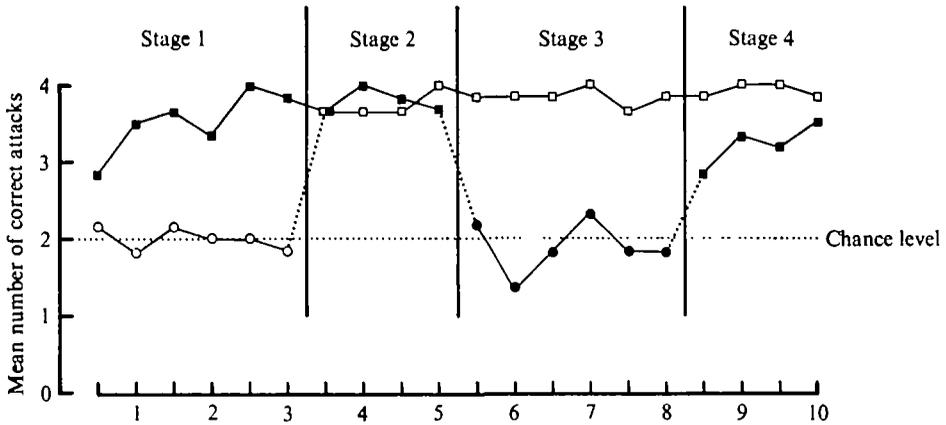† According to Color Aid specification.

Fig. 1. Results of training octopuses on two alternating tasks during the four stages of the experiment; scores are plotted for each half-session. Performance on the hue/grey discriminations hover around the chance level. ■, black/white vertical rectangles; ●, violet/grey vertical rectangles; □ horizontal/vertical rectangles (grey); ○, yellow/grey vertical rectangles.

each of them performance on the hue task remains at chance level while performance on the brightness task is significantly better than chance ($P < $ 0·001, Mann–Whitney U-test).

By the third session the animals were attacking very slowly during the hue task and showing signs of becoming 'disturbed' (see Discussion). Accordingly, for two sessions, without any pre-training, we substituted the very easy orientation discrimination for the hue discrimination to discover whether octopuses can in fact show discrimination to two simultaneous tasks alternately presented. Obviously they can do so and, as Fig. 1 makes clear, the introduction of this new task (orientation) does not interfere with performance on the other task (brightness).

We then interpolated 12 pre-training trials with a violet rectangle prior to stage 3 of the experiment when, alternating with the vertical/horizontal discrimination, we presented the second hue task: violet versus grey. The octopuses continued to discriminate vertical from horizontal at a highly significant level ($P < $ 0·001, Mann–Whitney U-test) but at once began to score randomly on the hue task and continued to do so over six half-sessions. The data were very 'noisy', however, as might be expected with such a small group (Fig. 1): on the second half-session the group actually attacked the negative (grey) figure significantly more than the positive ($P < $ 0·05, Mann–Whitney U-test) and the score hovers below chance. Over all trials, however, no single individual ever made significantly more attacks on the negative figure; nor did any animal make significantly more attacks on the positive figure *despite having been pre-trained to attack it*.

During this stage of the experiment there were striking qualitative differences in the behaviour of the animals on the two tasks. Attacks were swift and sure with the verticals and horizontals but increasingly slower and uncertain with the violet and grey shapes: the octopus might start towards one and then turn to the other shape before reverting to the first choice, or perhaps stopping and retreating to the home. Indeed it became extremely difficult to elicit attacks with these shapes. In the eighth

ession only eight out of 48 attacks on vertical or horizontal shapes took longer than 5 s to complete, whereas all 48 attacks on grey or violet took longer than 5 s. Some animals took up to a minute before attacking and some had to have the figures removed and re-presented before they would attack. Moreover, the skin often showed the mottled pattern that is associated with a 'conflict' situation (Packard, 1963) when the violet and grey shapes were presented (see Discussion).

Finally we reintroduced the brightness discrimination for two sessions without further pre-training, to ensure that the animals had not lost the ability to discriminate two tasks at the same time. Although performance was at first lower than it had been in stage 1, it was still significantly better than chance both on the first half-session ($P < 0.05$, Mann–Whitney U-test) and overall ($P < 0.001$). (The lower initial score may have arisen because the black figure was only slightly darker than the violet and grey figures that had elicited conflict behaviour during the previous stage of the experiment.)

DISCUSSION

The most important observation brought out by these experiments is that the subjects did not discriminate on the basis of hue *at the very time that they did make discriminations on the basis of brightness* (sessions 1–3). The design of the experiment effectively rules out the possibility that the octopuses were sick, satiated or simply incapable of making visual discriminations during the particular 3 h period when they did not discriminate yellow from grey. The simultaneous method is especially powerful because it does not lower the level of attack. Thus all the animals attacked on every trial but over the first three sessions the 144 attacks that the whole group made on the hue task were shared equally between the yellow (72) and the grey figure (72) while over the same three sessions the 144 attacks on the brightness task were shared in the ratio 127 black to 17 white.

A similar state of affairs can be seen when we examine performance on orientation and hue (sessions 6–8); the 144 attacks on the hue task were shared in the ratio 68 violet to 76 grey while over the same three sessions the 144 attacks on the horizontal task were shared in the ratio of 138 vertical to 6 horizontal. We must be cautious here, however, because the positive figure of the orientation pair (the vertical) is a strongly preferred figure, given the vertical direction of motion, and it can be argued that we are merely allowing the octopuses to express that preference (Sutherland & Muntz, 1959)*. Even if individually acquired experience played only a small part in determining the octopuses' behaviour, however, the fact remains that they discriminated these figures and did so at a time when they were not discriminating violet from grey. The important qualitative differences in behaviour at this stage of the experiment speaks even more eloquently for the indiscriminability of the violet and grey rectangles. It is difficult to imagine the animals attacking more slowly or changing course in mid-attack unless the figures looked identical and the octopuses could not learn to 'attach' the food reward to one particular figure. Nevertheless it is curious that they behaved like this even though they were not being punished for making a

* The vertical was made positive because it is difficult to reverse this preference without administering shocks, which we were unwilling to do since it depresses the level of attack (Sutherland & Muntz, 1959).

wrong choice. It is difficult to believe that the correction procedure is aversive in itself. Perhaps the conditions of the experiment, with the alternating tasks, foster the development of a 'wait-for-a-certainty' strategy. If so, the rapidity with which it is developed is another example of the remarkable plasticity of these animals' behaviour.

One possible criticism of these experiments (apart from the unavoidable small numbers) is that the animals were never trained for more than 24 trials: but future experimenters with unlimited time at their disposal should recall the important finding of Sutherland & Muntz (1959) that in a simultaneous training situation learning is virtually complete after only 10 pre-training trials on the positive shape. Our results with the brightness discrimination bear this out fully and suggest that increasing the number of trials would not improve scores.

The demonstration for the first time that, in a discrimination learning situation, octopuses confuse hues with greys of equal brightness (to a human observer using rod vision) is important presumptive evidence for colour blindness (Autrum & Thomas, 1973). Obviously one could go on indefinitely trying to demonstrate whether octopuses are colour blind, comparing a whole range of different greys and hues, using very large groups of animals and perhaps developing more subtle training methods (see for example Sutherland, et al. 1963). Ideally, too, one would use lights instead of paints; one recent investigator has made a start in this direction, although unfortunately he examined one individual only (Roffe, 1975). The brief experiment reported here, however, suggests that much further expenditure of time and effort would be unprofitable. These results support our earlier behavioural findings (Messenger et al. 1973) and those of Roffe (1975) and are in agreement with a body of morphological (e.g. Cohen, 1973), biochemical (e.g. Hara & Hara, 1972) and physiological (e.g. Hamasaki, 1968 a, b) data from a variety of cephalopods. Taken together, these make it increasingly less likely that octopuses have colour vision.

REFERENCES

AUTRUM, H. & THOMAS, I. (1973). Comparative physiology of colour vision in animals. In *Central Processing of Visual Information* (ed. R. Jung) (*Hbk. Sens. Physiol.* VII/3, 661–92).

COHEN, A. (1973). An ultrastructural analysis of the photoreceptors of the squid and their synaptic connections. *J. comp. Neurol.* **147**, 351–426.

FROESCH, D. & MESSENGER, J. B. (1977). On leucophores and the chromatic unit of *Octopus vulgaris*. (in preparation).

HAMASAKI, D. I. (1968a). The electroretinogram of the intact anesthetized octopus. *Vision Res.* **8**, 247–58.

HAMASAKI, D. I. (1968b), The ERG-determined spectral sensitivity of the octopus. *Vision Res.* **8**, 1013–21.

HARA, T. & HARA, R. (1972). Cephalopod retinochrome. In *Photochemistry of Vision* (ed. H. J. A. Dartnall) (*Hbk. Sens. Physiol.* VII/1, 720–46).

MESSENGER, J. B. (1974). Reflecting elements in cephalopod skin and their importance for camouflage. *J. Zool., Lond.* **174**, 387–95.

MESSENGER, J. B., WILSON, A. P. & HEDGE, A. (1973). Some evidence for colour-blindness in *Octopus*. *J. exp. Biol.* **59**, 77–94.

PACKARD, A. (1963). The behaviour of *Octopus vulgaris*. *Bull. Inst. océanogr. Monaco*, no. spéc. 35–49.

PACKARD, A. & HOCHBERG, F. G. (1977). Skin patterning in *Octopus* and other genera. *Symp. zool. Soc. Lond.* **38**, 191–231.

ROFFE, T. (1975). Spectral perception in *Octopus*: a behavioural study. *Vision Res.* **15**, 353–6.

SUTHERLAND, N. S., MACKINTOSH, N. J. & MACKINTOSH, J. (1963). Simultaneous discrimination training of *Octopus* and transfer of discrimination along a continuum. *J. comp. Physiol. Psychol.* **56**, 150–6.

SUTHERLAND, N. S. & MUNTZ, W. R. A. (1959). Simultaneous discrimination training and preferred directions of motion in visual discrimination of shape in *Octopus vulgaris* Lamarck. *Pubbl. Staz. zool. Napoli* **31**, 109–26.