VISUAL DISCRIMINATION OF DISTANCE BY OCTOPUSES

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Summary

If two stimuli are presented to an octopus simultaneously, but at different distances from the animal, the nearer of the two is usually attacked. This preference was used to test the ability of octopuses to discriminate distance. White discs, 37 mm in diameter, were used as stimuli, and two parameters were varied: the distance of the farther stimulus from the animal (D), and the difference between the distances of the farther and nearer stimulus (d). Animals chose the nearer stimulus on 70 % of occasions under the most difficult conditions used, where D was 370 mm and d was 50 mm. This percentage increased as D decreased or d increased. Further tests showed that varying the size of the discs, or using white vertical or horizontal rectangles instead of discs as stimuli, did not affect performance.

The most likely cue being used by the animals to discriminate distances is accommodation. If this is the case octopuses can detect blurring of points on the retinal image comparable in size to a single retinal receptor, and lens displacements of around $10\,\mu$m.

Introduction

Despite the importance for most animals of the ability to judge distances, comparative work in this area is sparse (see Collett & Harkness, 1982, for a review). The present paper reports the results of experiments on distance discrimination in octopuses. It is known that octopuses are able to judge distances reasonably well. Boycott & Young (1956) showed that octopuses could readily discriminate squares of different sizes, and that the discrimination was not affected when the smaller square was presented closer to the animals, at a distance such that it subtended the same visual angle as the larger one. Maldonado (1964) found that when octopuses attacked crabs, the attack was made to the correct distance even if the lights were turned off after the attack had been launched. This shows that the distance must have been correctly estimated beforehand. In Maldonado's experiments, however, the crab was always presented at the same distance, and it would be possible for the animals to have learned the correct strength with which to launch the attack by trial and error without needing to estimate the distance visually.

During a recent study on visual acuity in *Octopus australis* and *O. pallidus* (Muntz & Gwyther, 1988), in which a simultaneous discrimination situation was used, it became apparent that, other things being equal, the animals attacked the closer of two stimuli more frequently than the farther one. This preference was used in the present experiments to determine the accuracy of depth discrimination at different distances.

Materials and methods

Four male *O. pallidus* and two male *O. australis*, weighing 75–230 g, were used. They were caught in traps in Port Phillip Bay, and kept in individual black plastic tanks with transparent lids, measuring 80 cm × 20 cm × 40 cm in depth, on an open seawater circulation, in the Marine Science Laboratory, Queenscliff. A pottery home was provided at the centre of the tank. The water temperature rose from 14·5 to 19·5 °C during the course of experiments.

The stimuli were made of white Perspex, 3 mm in thickness. They were presented on the end of transparent Perspex rods 6 mm in diameter, and moved vertically by hand at given distances from the animal. Distance was controlled using a transparent Perspex tube, located by notches across the top of the tank. Vertical slots cut in the tube formed guides for the Perspex rods, controlling both the direction of movement of the stimuli and their distance from the animal (Fig. 1). In this way the stimuli could be presented 370, 320, 270, 220 or 170 mm from the centre of the tank, at either end.

During the first part of the study two circular 37 mm diameter discs were presented at varying distances on each trial, one at each end of the tank, and the animals rewarded with a small piece of prawn for attacking the nearer stimulus, thus reinforcing their natural preference. 581 trials were given, distributed between conditions as shown in Table 1.

In the second part of the experiment the stimuli were always presented at 370 and 270 mm from the centre of the tank, one at each end, and stimulus size was varied to test whether visual angle was being used as a cue to distance. For example, at a distance of 370 mm the 37 mm discs used subtend 0·1 rad at the centre of the tank, whereas at 270 mm they subtend 0·137 rad, and it could be that the animals were responding on the basis of this difference. Tests were therefore carried out using the 37 mm disc at 270 mm and a 50 mm disc at 370 mm, which both subtend the same angle at the tank centre. Rewards continued to be given for attacks on the closer stimulus.

Octopuses have an interocular distance of 30–60 mm, depending on their size, and were not always located exactly at the tank centre. After about 3 days of using the 50 and 37 mm discs, trials were therefore introduced in which 55 and 45 mm discs at 370 mm were paired with the 37 mm disc at 270 mm, so that visual angle could not be a consistent cue to distance. No reinforcements were given on these test trials, performance being maintained by also giving rewarded trials with the 50 and 37 mm discs on each day. The discrimination of distance was also tested
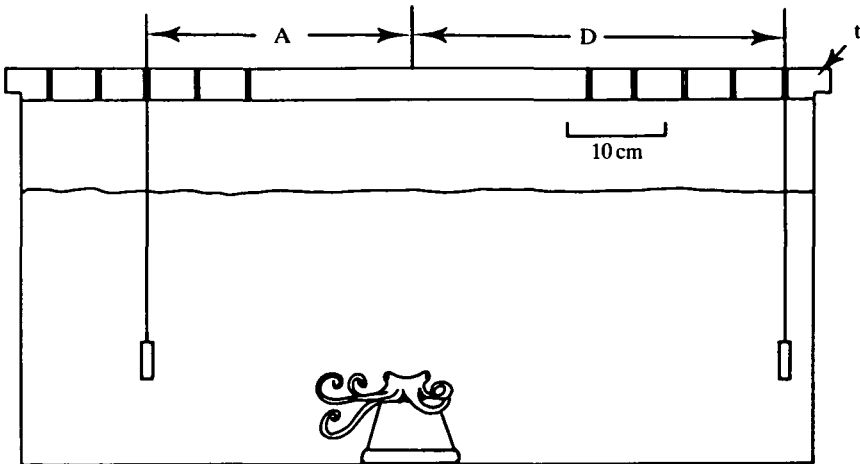
Fig. 1. Elevation of the experimental situation. The stimuli are positioned by vertical slots cut in the transparent Perspex tube, t. The distance to the farther stimulus is D. In the text, d refers to the difference in the distances of the two stimuli, D–A.

with pairs of vertical and horizontal rectangles, 55 mm × 11 mm, presented at 370 and 270 mm, attacks to the closer stimulus being rewarded. 921 trials were given in all with these various stimuli, distributed as shown in Fig. 3.

During the first part of the experiment, with the two 37 mm discs, three *O. pallidus* and two *O. australis* were used. Octopus no. 1 (*O. australis*) stopped attacking consistently after the first part of the experiment and a new animal (no. 6, *O. pallidus*) was used. During the tests using horizontal and vertical rectangles animal no. 4 (*O. pallidus*) also stopped behaving consistently and its results were discarded.

As in Muntz & Gwyther (1988), the number of reinforcements an animal would accept varied markedly among animals and from day to day, and, as a consequence, the number of trials that could be given also varied. In all parts of the experiment the end of the tank at which the nearer stimulus was presented was varied randomly.

Results

Distance judgement with the 37 mm discs

All possible pairings of distance were used with each animal. For most animals 10 trials were given on each pairing: however, there were some departures from this, particularly in the early stages of the experiment when procedures were to some degree still being developed. The results are shown in Table 1 and Fig. 2. For a given difference in the distance of the two stimuli (d) performance improved when the stimuli were presented close to the animal, and similarly for a given distance (D) of the farther stimulus from the animal performance improved as d increased. Applying Ferguson's (1971) monotonic trend test for correlated

Table 1. *Responses of octopuses to the 37 mm discs presented at different distances*

	D			
d	370	320	270	220
50	0·70 (70)	0·69 (66)	0·75 (64)	0·88 (50)
100	0·67 (52)	0·81 (64)	0·89 (55)	
150	0·78 (50)	0·78 (58)		
200	0·85 (52)			

d refers to the difference in the distance of the two stimuli in mm, and D refers to the distance of the farther stimulus in mm.

The entries show the mean probability of attacking the nearer stimulus, and in brackets the total number of trials given on each distance combination.
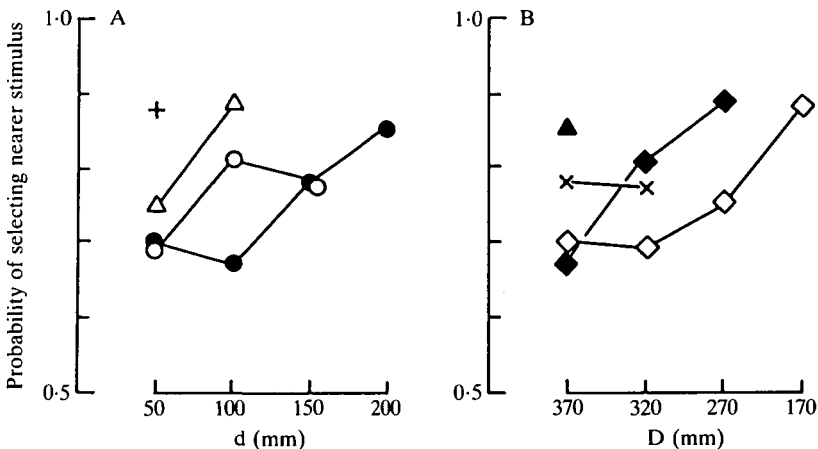

Fig. 2. Probability of selecting the nearer stimulus under the various combinations of d and D. (A) Effect of d for given values of D. D = 370 mm (●); D = 320 mm (○); D = 270 mm (△); D = 220 mm (+). (B) Effect of D for given values of d. d = 50 mm (◇); d = 100 mm (◆); d = 150 mm (×); d = 200 mm (▲).

samples to the data obtained with individual animals for D when d = 50 mm, and to the data for d when D = 370 mm, showed that both trends were significant at the 5 % level. The results were also analysed separately for the two species: only small and insignificant differences were found.

Distance judgement with other stimuli

The results obtained with these different stimuli are shown in Fig. 3. Except with the 45 mm and 37 mm discs, the stimuli used did not affect performance. With the 45 mm and 37 mm discs, performance was worse, but applying Friedman's two-way analysis of variance (Siegel, 1956) to the data for octopuses 2, 3, 5 and 6 (the four animals that completed all the tests in this part of the experiment) showed
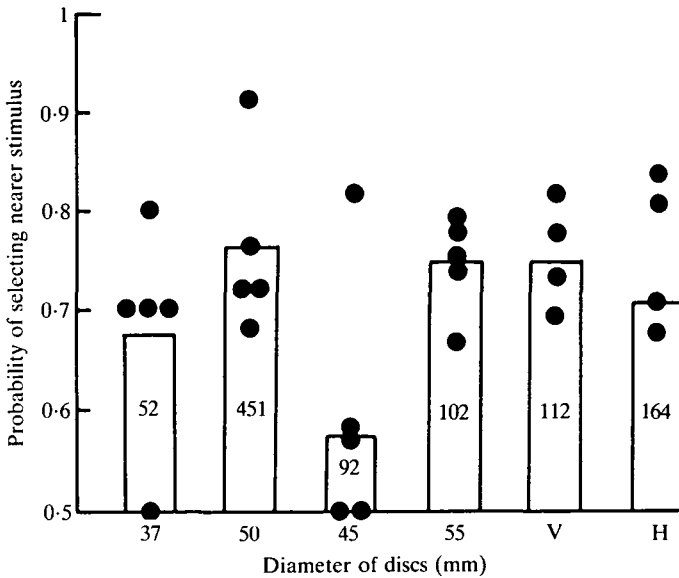
Fig. 3. Probability of selecting the nearer stimulus with the different stimulus pairs used in the second part of the experiment. The results for d = 100 mm and D = 370 mm from the first part of the experiment are also shown for comparison (left-hand bar). The bars show the mean scores, the filled circles show scores for the individual animals, and the figures within each bar show the total number of trials given with each stimulus combination. On the horizontal axis the figures show the diameter, in mm, of the different white discs used, paired in each case with a 37 mm disc; V, the results with vertical rectangles; H, the results with horizontal rectangles.

that this effect was not significant ($\chi_r^2 = 3.8$, df 4). The single specimen of *O. australis* used in this part of the experiment did not differ in performance from the specimens of *O. pallidus*.

Discussion

The results show that, under the conditions used, octopuses can discriminate distances with considerable accuracy. It is assumed that the animals were using visual cues to do this. The only alternative would be the detection of mechanical vibrations from the movement of the stimuli. Octopuses are, however, probably comparatively insensitive to vibrations (Williamson, 1988) and, in the dark do not respond to moving stimuli, such as those used here.

The stimuli were presented at opposite ends of the tank, thus requiring the animals to compare information received separately through the two eyes. There are a number of means by which such monocular judgements of distance could be achieved (Collett & Harkness, 1982). In the present context the most likely are motion parallax through movements of the animal itself, relative stimulus size in terms of visual angle, and accommodation.

Wells (1966) observed that *O. vulgaris* often moves its head up and down several times before launching an attack, and suggested that this might reflect ranging by parallax. Such behaviour was not, however, observed by us in *O. australis* or *O. pallidus*, and on many occasions the attacks were launched without any discernible preliminary movements. There may, of course, have been some fine eye movements too small to be observed (see J. Y. Lettvin, cited in Young, 1971), but it is very unlikely that such small movements would produce motion parallax large enough to account for the accuracy of discrimination observed. Before an attack was initiated, animals also frequently showed increased ventilatory movements which resulted in some movement of the eyes but, from observation, these movements were negligible in the plane perpendicular to the line from the stimulus to the animal. Motion parallax does not therefore appear to be involved in the present case.

Size can be another monocular cue to distance, although for it to be useful the absolute size of the object must be known. Although it is possible that the animals learnt the size of the stimuli during the first part of the present experiments, the data given above show that this cue was not being used to estimate distance. In theory the animals could also have used the size of the Perspex rod as a cue to distance. This seems unlikely because attacks were always made to the stimuli and never to the rods which, seen by reflected light against the black ends of the tank, were inconspicuous compared with the stimuli. [It has been suggested that if the Perspex rod acted as a polarizer it might be conspicuous to octopuses, although barely visible to the human observer, since octopuses can detect polarized light (e.g. Moody & Parriss, 1961). The rods were, however, made of unplasticized Perspex which is isotropic (Hendry, 1948), and viewing the rods in the experimen-
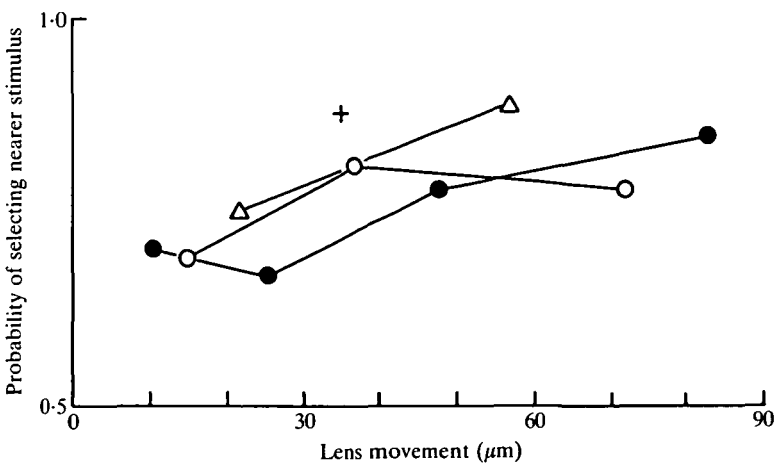

Fig. 4. Calculated lens movements necessary to focus on each of the two stimuli under the various distance combinations used in the first part of the experiment. The lines join the points for equal values of D. Symbols as in Fig. 2A.

tal situation through a polarizing filter revealed no detectable optical activity.] Similarly, the point at which the Perspex rods break the water surface could have been used as a cue unaffected by stimulus size. This is also unlikely, because cues distant from the locus of response are poorly discriminated by animals (Sutherland, 1962).

The most likely cue being used is accommodation. Although accommodation is, at best, a weak cue to distance for humans (Campbell & Westheimer, 1959), it is the main cue in chameleons (Harkness, 1977) and probably amphibians (Ingle, 1976). Accommodation in cephalopods is not fully understood (Alexandrowicz, 1927) but, since the lens is spherical and rigid, it must involve movement of the lens backwards or forwards with respect to the retina. Monitoring the distance of the lens from the retina could thus give an estimate of object distance.

To calculate the lens movements necessary for accommodation under different conditions the focal length of the lens must be known. Cephalopod lenses show considerable chromatic aberration, and they also show astigmatism and other variations in focal length depending on the point of entry and obliquity of the beam (Sivak, 1982; Sroczyński & Muntz, 1985, 1987). Measurements on Australian octopuses have not yet been carried out and, for simplicity, a value of 2·5 times the lens radius, approximating to Matthiessen's ratio (Pumphrey, 1961), was assumed here: we also assumed a lens radius of 2 mm, giving a focal length of 5 mm.

Using these values we calculated the movement of the lens relative to the retina needed to alter focus from the far to the near stimulus under the various conditions of these experiments. Strictly, such movements alter the distance of both the object and the image planes from the centre of the lens, but since the lens movements were very small compared with the distance of the stimulus from the animal, for simplicity the former was ignored. The results of these calculations are shown in Fig. 4. If accommodation were the only factor affecting performance, all the points should have fallen on the same line. This is clearly not the case and, for a given lens movement, performance is better when the stimuli are closer to the animal. However, many other factors will have contributed to the animals' performance in these experiments: in particular, the animals' preference for attacking closer stimuli need not be linearly related to distance, as would be required for all the points in Fig. 4 to fall on the same line. At all events, Fig. 4 shows that if accommodation is the relevant cue, lens displacements of 10–20 μm can be detected.

To accommodate it is necessary to detect that the image is out of focus, and this can only be done if the blurring of the details of the image exceeds the resolving capacity of the retinal mosaic (Collett & Harkness, 1982), which is directly related to the size of the retinal receptors. Given the above assumed dimensions for the lens, we calculated the blur circle on the retina resulting from a point source located 320 mm from the eye when the eye is focused at 370 mm, corresponding to the *most difficult discrimination used: its diameter is* 4·29 μm. This is comparable to the maximal width of an octopus retinal cell across its two rhabdomeres, which appears from electron micrographs of tangential sections to be about 5·4 μm in

O. vulgaris (V. C. Barber, cited in Young, 1971) and 4 µm in *O. bimaculatus* (?) (R. Nishioka, cited in Eakin, 1972).

To maximize the effects of misfocus the system should have a poor depth of field, which can be achieved by a wide aperture. In the above it was assumed that the full width of the lens was used. The octopus has a pupil in the form of a horizontal rectangle, and so although this will be true along the horizontal axis of the lens, in the vertical plane the effective aperture is much smaller. The shape of the pupil and the probable astigmatism of the lens could also cause the importance of vertical and horizontal contours to differ (Heidermanns, 1928; Sroczyńsky & Muntz, 1985). However, experiments with vertical and horizontal rectangles failed to reveal any such effects.

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