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SHORT COMMUNICATION

THE VISUAL ACUITY OF OCTOPUSES FOR GRATINGS OF DIFFERENT ORIENTATIONS

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A recent study has shown that the minimum separable angle of visual acuity of *Octopus pallidus* and *O. australis* lies between 4·4′ and 9·7′ when vertical and horizontal gratings are used as test objects (Muntz & Gwyther, 1988). In view of other observations – the horizontal rectangular shape of octopus pupils, the pronounced astigmatism of the lens of *Eledone cirrhosa* (Sroczyński & Muntz, 1985), the difficulty that *O. vulgaris* has in discriminating between oblique rectangles (Sutherland, 1957), and the vertically and horizontally arranged rectilinear organization of both retina and neurones in the optic lobe of *O. vulgaris* (Young, 1960) – it seemed worthwhile testing the effect of grating orientation on visual acuity in more detail, and in particular extending the measurements to include oblique gratings oriented at 45° with respect to gravity.

The animals were trained to discriminate gratings of different orientations from uniform grey stimuli, using the conditional simultaneous discrimination procedure described by Muntz & Gwyther (1988). The two stimuli to be discriminated were presented stationary at the two ends of the tank, and a moving 3·7 cm diameter disc shown in front of each of them. Attacks were rewarded when made to the disc presented in conjunction with a grating. Two minor modifications were made to the previous procedure. First, it was found unnecessary to use electric shock as punishment, with the result that the level of attack improved, especially with the more difficult discriminations. Second, circular backgrounds (grating or grey) of diameter 13·0 cm were employed instead of square ones, so that the overall appearance of the gratings was not altered by their orientation. Gratings with stripes subtending 52·9′, 15·4′, 7·1′ and 5·3′ at the centre of the tank were used, in all cases paired with the uniform grey stimulus.

The subjects were three male *O. pallidus*. They were initially trained using the 52·9′ grating alone. About five rewarded trials were needed before the animal learnt to attack with little or no hesitation. Discrimination between this grating and the grey stimulus was then introduced, and was learnt after two or three unrewarded attacks towards the grey stimulus. Only the results of trials following this training period are included in the data. In this part of the experiment only the three larger gratings were used, and during each experimental session, gratings of

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Table 1. *Results for gratings with stripes subtending 7·1′ at the centre of the tank*

	Vertical			Horizontal			Oblique		
Animal	1	2	Sum	1	2	Sum	1	2	Sum
1	8/11	18/24	26/35	6/11	15/25	21/36	8/10	16/23	24/33
2	7/10	12/17	19/27	4/10	12/22	16/32	10/14	17/27	27/41
3	9/11	16/21	25/32	5/10	11/20	16/30	9/14	16/25	25/39

Entries show the number of correct responses out of the total number of trials given for the first (1) and second (2) series of trials, and their sum.

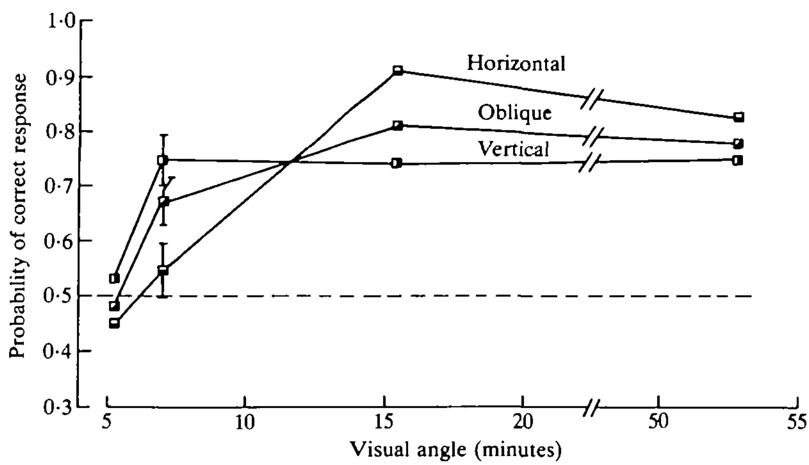

Fig. 1. Probability of correct response with gratings of different orientations and stripe widths. The abscissa gives the visual angle subtended at the centre of the tank by a single stripe. The two sets of results for the 7·1′ grating have been averaged, and the bars show the standard errors ($\sqrt{pq/N}$) for the scores at this visual angle. Standard errors for the other gratings varied between 0·062 and 0·089.

two of the three sizes in all three orientations were presented in random order. This phase of the experiment was continued until each animal had received between 10 and 16 (mean 11·4) trials with each stripe width at each orientation.

The results are shown in Fig. 1 and Table 1. With the 7·1′ gratings, performance of all three animals was worse for the horizontal gratings than for the vertical and oblique gratings, and did not exceed chance levels. For the 15·4′ and 52·9′ gratings, although the mean scores for the three orientations fell in the same order in each case, this order was not consistent between individuals.

A second series of trials was given using only the 7·1′ gratings, until each animal had received between 17 and 25 (mean 22·7) trials on each of the three orientations. The results for the 7·1′ grating from both series of tests are shown in Table 1. In their total scores, all three animals performed best with the vertical grating and worst with the horizontal grating: on a Friedman two-way analysis by ranks for correlated samples this effect of orientation is significant at the 5 % level.

χ^2-tests were carried out to test further the significance of the findings at 7·1′. No individual (nor the group as a whole) showed any significant difference between the two series of tests carried out at this visual angle, and there was no significant difference between animals. It was therefore reasonable to pool the results over animals and over the two series of tests. For the pooled results, the different scores on the three orientations yielded a χ^2 value of 9·50 which, with 2 d.f., is highly significant ($P < 0.01$). Comparing the different orientations with each other in pairs yields χ^2 values significant at better than the 1 % level for vertical against horizontal (8·66) and vertical against oblique (7·92), but the difference between horizontal and oblique (1·28) did not reach significance (1 d.f. in all cases).

Finally, each animal was given 10 tests at each orientation with stripes subtending 5·3′. The animals were not able to discriminate this width of stripe from grey (Fig. 1).

Fig. 1 suggests that there may be an interaction between stripe width and orientation, with vertical gratings most readily discriminated at the narrower widths, and horizontal gratings at the two wider widths. However, χ^2-tests on the data for the two larger gratings showed no significant effects for animals, orientation or stripe width. Also, using the GLIM statistical computer package revealed no significant interaction between orientation, stripe width and performance, either with the original data or with the data pooled for the two narrower and the two wider gratings.

Overall the results are in good agreement with the data of Muntz & Gwyther (1988) in giving an estimate for the minimum separable angle of between 8′ and 5′. In that experiment performance for horizontal gratings opposed to grey was also worse than for vertical gratings when 9·7′ and 15·4′ gratings were tested, although the effect was not significant with the statistical tests used. Sutherland (1963) found that when *O. vulgaris* was trained to discriminate narrow stripes from slightly wider stripes, performance was better with vertical stripes than with horizontal ones (with broader stripes the effect disappeared or reversed), and Sutherland (1961) and Mackintosh *et al.* (1963) have shown that in visual discriminations between rectangles differences in horizontal dimensions are more readily learnt than differences in vertical dimensions. Both these findings are in accord with the present results, in that they could be explained if vertical contours are better resolved than horizontal ones.

The reason for the poorer performance with horizontal gratings is unclear, although the eye of the octopus has a number of optical characteristics that will have a differential effect on the quality of the retinal image for different orientations of contour, and which may be contributing to the effect. For example, the pupil has a horizontal rectangular shape, and photographs of three animals taken in the experimental tanks gave estimates for the vertical extent of the pupil of 0·87 mm, 1·31 mm and 1·18 mm, and for the horizontal extent of 4·99 mm, 5·93 mm and 5·92 mm. This pupil shape means that diffraction will have a greater effect on horizontal than vertical contours, although even with the former the spatial cut-off will be at considerably smaller visual angles than the finest gratings the animals are able to discriminate. The lens of the octopus *Eledone cirrhosa* also shows both chromatic aberration and astigmatism (Sroczyński & Muntz, 1985), and it is probable that the lenses of *O. pallidus* are similar. Chromatic aberration would act in the opposite direction to diffraction, affecting vertical contours more than horizontal ones (Heidermanns, 1928), and the effects of astigmatism would depend on how the eye was focused. Finally, although the rectilinear organization of the retina means that receptor packing is the same along the horizontal and vertical axes, central nervous factors could obviously also be involved.

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