

## THE FUNCTION OF THE BRAIN OF *OCTOPUS* IN TACTILE DISCRIMINATION

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### INTRODUCTION

In a previous survey of the capabilities of the tactile nervous system of *Octopus* (Wells & Wells, 1956) evidence was presented suggesting that the brain correlates information from sense organs in the arms in a relatively simple manner. Animals trained to discriminate between objects differing only in their non-chemical surface characteristics could distinguish surfaces differing in degree of irregularity (e.g. by having a greater or lesser number of grooves cut into their otherwise smooth surfaces) but were unable to make discriminations dependent upon the recognition of the pattern or orientation of irregularities. It appears that octopuses do not make use of a projection of the sensory field or of any scanning mechanism in order to identify objects touched. It was suggested that these animals distinguish objects made of the same material on a basis of the proportion of mechanoreceptors stimulated in the sensory areas (the rims of the suckers) in contact, an object with a rough surface being recognized as distinct from one with a smooth surface because it stimulates a greater (or lesser) number of sensory endings, the arrangement of irregularities or the shape of the object being irrelevant. If this is correct, the ease with which it is possible to teach octopuses to discriminate between objects touched and the similarity of those objects in terms of the proportion of sensory endings that they excite should be closely correlated. The aim of the present series of experiments has been to test this correlation.

It was previously supposed (Wells & Wells, 1956) that the only way of obtaining a measure of the difficulty that an octopus has in distinguishing two objects was to count the number of trials that it took to learn to discriminate between them. This method is impractical because of the large number of experiments that it necessarily involves (see p. 134), and no attempt was made to compare the performances of individuals in this way. When further experiments were made, however, an alternative method of measuring the difficulty of discriminations was seen to be possible. It was observed that under any given set of training conditions octopuses, after an initial rapid improvement in performance, settle down to making a more or less constant proportion of errors to trials, and continue to err at this rate irrespective of the duration of training (but see p. 138). This proportion of errors is related to the

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similarity of the objects that they are required to distinguish, and provides a means of measuring and comparing the difficulty of different discriminations independent of the rates of learning of the experimental animals.

#### MATERIAL

*Octopus vulgaris* Lamarck of between 250 and 1000 g. caught in the Bay of Naples were used; methods of catching and keeping these octopuses have been described by Boycott (1954). The temperature of the sea water circulating through the tanks in which the experimental animals were kept varied from 16° C. (spring and late autumn) to 23° C. (summer), the water being heated in winter to about 18° C., because at temperatures below 13° C. *Octopus* ceases to feed regularly.

Animals were trained after section of the optic nerves as described in Wells & Wells (1956). The experiments quoted are from animals trained in 1954, 1955 and 1956. Animals used in 1954 are identified by a number preceded by the prefix A (e.g. A173), those in 1955 by B, and those during 1956 by C. Experiments made with the A (1954) series of animals have been reported in a previous paper.

#### EXPERIMENTAL METHOD

##### A. Training method

The method used to train blind octopuses to discriminate between objects, and the movements they make in accepting or rejecting objects touched, have been described fully elsewhere (Wells & Wells, 1956). Briefly, each experiment consisted of a number of trials at each of which one or other of a pair of objects was presented to an animal, which was rewarded with a small crab or piece of sardine for passing the 'positive' object to the mouth, and given a small (6-9 V. a.c.) electric shock if it responded in the same way to the 'negative' object. There were eight trials per day, at intervals of not less than 1 hr., the objects being presented in an order that repeated itself every 8 days. As a control against initial preferences for one or other of the objects and the possibility of contamination of the positive object by food, each group of animals was divided and one-half trained to react negatively to the object positive for the other.

During these experiments animals grew very rapidly, often increasing in weight by as much as 50% during 3 weeks of training. The results with occasional animals that ceased to feed regularly and lost weight were discarded.

##### B. Objects used in the tests

A series of Perspex cylinders each 2.5 × 3.0 cm. long was used, and into all but one of them (which remained smooth) deep grooves 1 mm. wide were cut. The frequency, arrangement and orientation of the grooves relative to the length of the cylinders was varied (Fig. 1), and the pattern on the sides of the cylinders was as far as possible continued on their end surfaces, except for P2, which had ungrooved ends. It will be noted that the proportion of groove to flat surface was independent of the arrangement and orientation of the grooves. In Fig. 1 this proportion is

expressed as a percentage for each object so that the similarity of any two objects can be expressed in terms of the difference between two percentages. This assumes that the pattern and orientation of the grooves is irrelevant and that *Octopus* cannot make use of these attributes in distinguishing between the members of this series of objects. This assumption is based on experiments already reported elsewhere, showing that octopuses find it difficult or impossible to distinguish between P1 (which has grooves running along the length of the cylinder) and P2 (grooved circumferentially) or P6 (a pattern of squares). In the present analysis we shall show that the proportion of errors to trials made when octopuses are trained to distinguish these objects is consistent with the view that they cannot distinguish them other than by the proportion of grooves.

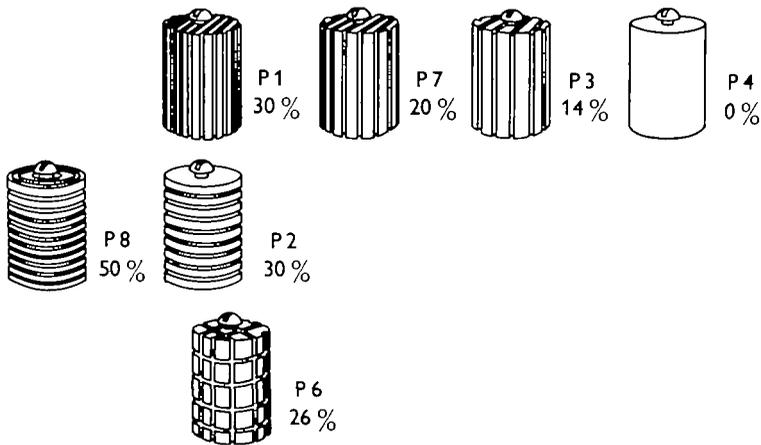


Fig. 1. The objects used in the tests. The series is arranged so that there is a decreasing proportion of grooved to flat surface from left to right. This proportion is indicated as a percentage for each object. The top row contains objects that differ only in the frequency of vertical grooves cut into them. P2 differs from P1 only in the orientation of the grooves cut into it. P6 has very nearly the same proportion of groove as P1, but the grooves are arranged to form a pattern of squares. Octopuses apparently find P1, P2 and P6 difficult or impossible to distinguish, but can be taught to discriminate between the members of the top row (and between P8 and P4) relatively easily.

### EXPERIMENTAL RESULTS

When blind octopuses in good condition are trained in the manner already described, they at first pass all the objects, positive and negative, to the mouth. Training thus consists for the most part of teaching the animals not to respond positively to the negative object, whilst retaining their positive responses to the positive object. Animals given shocks for taking the negative object learn either to withdraw the arms from contact with such objects (presented whenever possible to extended arms) or, more usually, to thrust such objects away. Responses to the positive object do not alter in nature, but increase in speed, the time taken to examine and pass this object under the web to the mouth commonly falling from about 15 sec. to less than 5 during the first twenty or thirty trials of training in simple discriminations.

There is considerable variation in the behaviour of individual octopuses during the first forty or fifty trials of training. Most animals react as described above, examining each object presented to them by feeling it over with the suckers for 5 or 10 sec., and react in a predominantly positive manner throughout training, making errors mainly by taking the negative object. A minority, after receipt of several electric shocks, become temporarily almost wholly negative in their reactions, snatching their arms away from objects touched without examining them. Such animals naturally take longer to learn to distinguish the objects in the test, although they eventually reach a condition in which their behaviour is in all respects like that

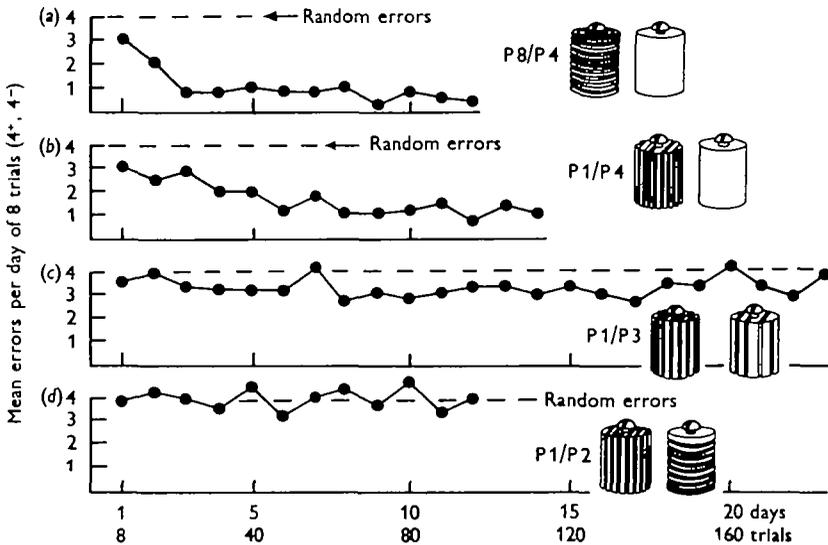


Fig. 2. A summary of the errors made in the course of four series of training experiments in each of which six (or twelve in the case of P8/P4) octopuses were trained to distinguish between two Perspex cylinders. The four series are arranged in order of difficulty for *Octopus*, P8/P4 being the easiest discrimination for them and P1/P2 the most difficult.

of the initially more 'positive' animals. As a result of these differences in reaction to the training conditions, tending to produce a considerable scatter in the number of trials required to train animals to a given criterion, the 'number of trials to criterion' cannot be used as a means of comparing the difficulty that *Octopus* has in distinguishing the test objects under these conditions unless a very large number of experiments be made.

In Fig. 2a the result of training a number of octopuses to distinguish between the grooved cylinder P8 and the grooveless P4 is plotted. Evidently this is rather an easy discrimination for *Octopus* to make, and in these experiments the initial improvement in performance was rapid, so that by the end of the first day (= 8 trials, 4 positive, 4 negative) of training, typical animals made substantially less than random errors and on the third day (i.e. after only sixteen trials) better than 85% correct responses to the test objects. This rate of improvement was not maintained,

however, and from the third day onwards the daily proportion of errors to trials remained more or less constant. In similar experiments it was found that the proportion of errors made was not further reduced by increasing the voltage of the electric shocks given as punishment, despite the fact that the majority of errors were due to the animals taking the negative objects. While decreasing the voltage eventually increased the proportion of errors because the animals tended to ignore the shocks altogether, increasing them from 9 V. upwards was without effect until shocks of the order of 12–15 V. were given, at which level animals commonly became entirely negative in their reactions to the test objects, so that the proportion of total errors rose sharply, due to the animals refusing the positive objects as well as the negatives. Nor was the proportion of errors noticeably altered by variations, within wide limits, in the size or quality of the rewards given (e.g. crabs instead of fish).

It could, on the other hand, be reduced considerably by increasing the frequency of the trials. In the present series of experiments octopuses trained to distinguish P 1 from P 4 tended to settle down to making errors at a rate of about one per day of eight trials (Fig. 2*b*). In experiments to be reported in a later account octopuses were trained to discriminate between the same objects at a rate of forty trials per day; under these conditions the proportion of errors to trials dropped to about half that made under the 'eight trials per day' conditions, typical animals making about one mistake in thirteen trials as against one in eight. We have chosen to compare the performance of octopuses under training at a rate of eight trials per day because it was convenient to do experiments this way and not because there is any particular virtue in this rate of training.

Fig. 2 shows the results of training octopuses to make discriminations between the members of four different pairs of Perspex objects. These discriminations range from P 4/P 8, which octopuses can readily be trained to distinguish, to P 1/P 2, which they evidently cannot distinguish at all. It can be seen that in all cases there was very little, if any, improvement in performance after the first forty or fifty trials, the proportion of errors made thereafter remaining approximately constant even though training was continued in some cases for as many as two hundred further trials.

The proportion of errors made during any period after the first forty or fifty trials can therefore be used as a measure of the difficulty of the discrimination concerned and to predict how many errors will be made if training is continued. The ratio of errors to trials in such a period thus approximates closely to the probability of error at any one trial during that period, and the term 'probability of error' will be used here to refer to the figure so obtained, although strictly no prediction of probability can be made in training experiments unless it can be demonstrated that the animals concerned have reached a steady state.

Defined thus the probability of an individual animal erring in any given trial during the last 5 days of the P 4/P 8 series of experiments was 0.075 (a total of thirty-six errors was made by twelve animals in these forty trials). During the same period (days 8–12) of the experiments with P 4/P 1 the probability of error was 0.165,

with  $P_1/P_3$  0.39 and with  $P_1/P_2$  0.505. It must be stressed that these figures for 'probability of error' are not directly comparable with the 'indices of correct differential response' used by Boycott & Young (1957) as a measure of the relative difficulty of visual discriminations, since the latter are based upon the errors made throughout the course of experiments including the initial period of rapid improvement.

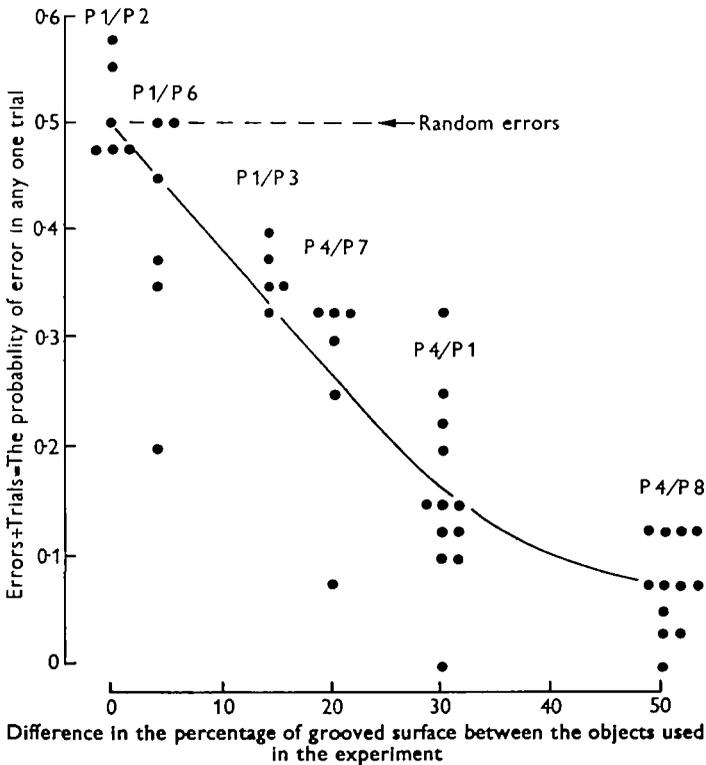


Fig. 3. Results of forty-eight training experiments, showing the relation between errors made and the similarity of objects to be discriminated. Each point shows the probability of error by one animal trained to make a stated discrimination (indicated  $P_1/P_2$ , etc.). In each case this figure is derived from the forty trials during days 8-12 of the experiment. The probabilities of error by these animals during the last forty trials of the same experiments, the length of which differed considerably, are listed in Table 1. For details of the objects used see Fig. 1.

The relation between the proportion of errors that forty-eight octopuses made in six different discriminations, and the difference between the test objects concerned expressed as the percentage of grooved surface (see description of the objects used on page 133), is plotted in Fig. 3. For this figure the proportion errors/trials was in all possible cases measured from the forty trials on days 8-12 of training (i.e. from the 56th to the 96th trial). The selection of this particular period was determined by the  $P_8/P_4$  experiments, which ended after 12 days. Table 1 shows the total errors made during this period by each individual octopus, together with the total errors made by the same animal during the *last* forty trials of its training. It can be seen

Table 1

Discrimination	Animal	Errors in 40 trials on days 8-12 of exp.	Errors in last 40 trials	Probability of error in last 40 trials	Total length of exp. in trials at 8 per day	Previous exps.	
P8/P4	C23	5	5	0.125	96	P1/P3	
	C26	5	5	0.125	96	P1/P2	
	C27	0	0	0.0	96	P1/P3	
	C28	3	3	0.075	96	P1/P2	
	C34	5	5	0.125	88	P1/P2	
	C96	1	1	0.025	96	—	
	C113	3	3	0.075	96	—	
	C114	1	1	0.025	96	—	
	C124	3	3	0.075	96	—	
	C127	5	5	0.125	96	—	
	C132	2	2	0.05	96	—	
	C135	3	3	0.075	96	—	
	P1/P4	A127	10	10	0.25	72	—
		A133	6	6	0.15	72	—
A135		4	4	0.1	72	—	
A159*		13	13	0.325	112	P1/P3	
A166*		8	10	0.25	112	P1/P6, P3/P5	
A173*		4	4	0.1	112	P1/P6	
A185*		6	5	0.125	128	P1/P6	
A186*		5	4	0.1	112	P1/P6	
A194		9	9	0.225	72	P1/P2	
B10*		0	0	0.0	120	—	
B42		5	5	0.125	96	—	
B43		6	6	0.15	88	—	
P7/P4		B178	3†	2	0.05	184	—
		B180	13†	4	0.1	184	—
	B181	10†	10	0.25	184	—	
	B183	13†	15	0.375	136	—	
	B186	13†	15	0.375	144	—	
	B187	12†	10	0.25	144	—	
P1/P3	A159	15	17	0.425	240	—	
	A168	22	23	0.575	240	—	
	C4	13	18	0.45	192	—	
	C5	14	14	0.35	192	—	
	C23	16	16	0.4	192	—	
	C27	14	17	0.425	192	—	
P1/P6	A158	15	20	0.5	184	P3/P5	
	A160	8	8	0.2	88	P3/P5	
	A166	18	21	0.525	160	P3/P5	
	A173	20	19	0.475	192	—	
	A185	20	19	0.475	192	—	
	A186	14	17	0.425	192	—	
P1/P2	A194	23	18	0.45	160	—	
	A203	20	20	0.5	88	—	
	C26	22	21	0.525	144	—	
	C28	19	20	0.5	144	—	
	C29	19	19	0.475	104	—	
	C30	19	19	0.475	144	—	
P1/P5	A145	5	5	0.125	56	—	
P3/P5	A145	6	8	0.2	144	P1/P5	
	A158	12	11	0.275	144	—	
	A160	11	11	0.275	144	—	
	A166	15	19	0.475	144	—	

\* Animals used for plotting Fig. 2b.

† From days 12 to 16, experiments done in winter and heating broke down during days 8 to 12.

In experiments lasting less than 12 days (=96 trials) figures given in the 'Errors on days 8-12' column are from the last forty trials in each case.

that continuation of training after the first fifty trials (up to 200 trials in the case of difficult discriminations such as P<sub>1</sub>/P<sub>6</sub> or P<sub>1</sub>/P<sub>3</sub>) rarely led to any further improvement in performance. In fact training under these conditions appears to increase rather than decrease the probability of error when continued for more than 100 or so trials. Of twelve animals trained to discriminate P<sub>1</sub> from P<sub>6</sub> or P<sub>1</sub> from P<sub>3</sub>, seven made a higher proportion of errors in the last forty trials of training after an average of 144 trials, than in the forty trials on days 8–12 after only fifty-six trials; of the remaining five, three made exactly the same proportion of errors and only two showed a slight improvement in performance.

Why long continuation of training should lead to an increase in the proportion of errors made is obscure. It is possible that the octopuses become accustomed to receiving electric shocks; it is also possible that the rewards, remaining the same size throughout the experiment, become inadequate as the animals grow bigger and presumably hungrier, although it is unlikely that they were fed to anything approaching repletion at any time during these experiments. A similar tendency for the total errors to increase when training is long continued can be traced in visual discrimination experiments (Sutherland, 1957).

The spread of results obtained when a number of octopuses are trained to make the same discrimination is due to individual variation and is not an artifact produced by defects in the experimental method. It can be seen in Table 1 that with few exceptions animals making a relatively small number of errors in one discrimination performed correspondingly well in the next, and vice versa. The wide individual differences in ability, particularly evident in the case of very difficult discriminations such as P<sub>1</sub>/P<sub>6</sub>, are presumably due to using animals from a wild population. *Octopus* is a solitary animal, each individual living, so far as is known, in a rather restricted territory around its home, so that, in addition to the genetical source of variation, it is likely that the behaviour of animals will differ widely due to their individual experiences in the sea before capture.

#### *Results with another Perspex object*

In the original series there was an object P<sub>5</sub>. This was like the others in size and shape, but the grooves cut into it were 2 mm. instead of 1 mm. wide. P<sub>5</sub> had eleven such vertical grooves and therefore a proportion of grooved to flat surface similar to P<sub>1</sub> (P<sub>5</sub> 28%, P<sub>1</sub> 30%). In the case of the objects other than P<sub>5</sub> the percentage of grooved surface can be taken as a measure of the proportion of the surface of the applied suckers *not* in contact with the object. In the case of P<sub>5</sub> this measurement was seen to be meaningless when it was observed that the rims to the suckers of most of the experimental animals were flexible enough to touch the bottom of the wide grooves on this object.

In so far as the proportion of the area of the suckers in contact was concerned, P<sub>5</sub> therefore more closely resembled P<sub>4</sub>, which was entirely smooth, than it did any of the other objects. This is reflected in the experimental results. An animal (A145) trained to discriminate between P<sub>1</sub> and P<sub>5</sub>, which on a basis of groove proportion

should have been almost impossible for it, made a proportion of errors comparable with that made by other animals in distinguishing P<sub>1</sub> from P<sub>4</sub> (five errors in forty trials against an average of 6.3 errors made by animals in P<sub>1</sub>/P<sub>4</sub> discriminations). When the same animal and three others were trained to discriminate between P<sub>3</sub> and P<sub>5</sub> the average number of errors made was eleven. Although no P<sub>3</sub>/P<sub>4</sub> experiments were made, the average number of errors in P<sub>4</sub>/P<sub>7</sub> discriminations (P<sub>7</sub> being the object most like P<sub>3</sub> in the present series) was 10.6; one would expect the proportion of errors in P<sub>3</sub>/P<sub>4</sub> experiments to be slightly higher than this because P<sub>3</sub> is more like P<sub>4</sub> than is P<sub>7</sub> (its surface being 16% grooves against P<sub>7</sub>'s 20%). When this is taken into account it can be seen that the figure of eleven for the P<sub>3</sub>/P<sub>5</sub> experiments is reasonable if P<sub>5</sub>  $\equiv$  P<sub>4</sub> or nearly so.

Whilst these results confirm the view that the experimental octopuses were distinguishing the objects on a basis of the proportion of the sucker surface in contact with them, they have not been included in the summary in Fig. 3 because of the impossibility of calculating the correct proportion of groove (untouchable) to smooth (touchable) surface on P<sub>5</sub>.

#### DISCUSSION

It is relatively easy to teach octopuses to distinguish between Perspex cylinders that differ in having a greater or lesser number of grooves cut into them, but difficult or impossible to teach them to make discriminations dependent upon the recognition of the arrangement of these grooves relative to one another or to the shape of the cylinders. The proportion of errors made in discriminating between any two such cylinders is closely related to the difference in percentage of groove on their surfaces, the probability of error and the groove percentage difference being related almost linearly over the range 0-30% (Fig. 3). This is equally true of discriminations such as P<sub>1</sub>/P<sub>3</sub>, P<sub>1</sub>/P<sub>4</sub>, in which the objects differ only in the frequency of grooves cut into them and of others (P<sub>1</sub>/P<sub>2</sub>, P<sub>1</sub>/P<sub>6</sub>) where the objects are also potentially separable using different criteria. Evidently octopuses do not make use of cues such as the orientation or pattern of irregularities in distinguishing these cylinders. The groove percentage difference can therefore be taken as a measure of the similarity of these objects to *Octopus*, and used to predict the proportion of errors that will be made in further discriminations of this type.

That *Octopus* does not make use of the arrangement of surface irregularities relative to each other or to the shape of objects can probably be attributed to the extreme mobility of its suckers. It seems probable that the brain of *Octopus* is not capable of integrating proprioceptive information about the relative position of its individual suckers with tactile information from the sense organs on these in sufficient detail to permit the recognition of patterns of irregularity on surfaces touched (Wells & Wells, 1956).

The tactile system of *Octopus* does nevertheless permit it to recognize quite small differences in the percentage of irregularities on surfaces touched, and this is seen to be explicable when the structure of the relevant parts of the sensory nervous system in the arms is examined. The sensory endings in the suckers are of at least two types.

Of these it seems likely that the fusiform endings, which are found throughout the skin and are most common in the rims of the suckers, are the mechanoreceptors concerned in distinguishing objects touched. Alexandrowicz (1927) has described such endings in detail from the cornea and orbital membrane of the eye of *Sepia* where they probably act as receptors recording distortions of the eyeball produced by pressure changes arising from accommodation or sudden movement (Alexandrowicz, 1928). He also found similar endings in the skin of the arms of *Sepia*, and we have ourselves found a great many endings of similar appearance in the suckers of *Octopus*. There are several thousand such receptors in each sucker, distributed more or less irregularly but particularly in the rims of the suckers which are more

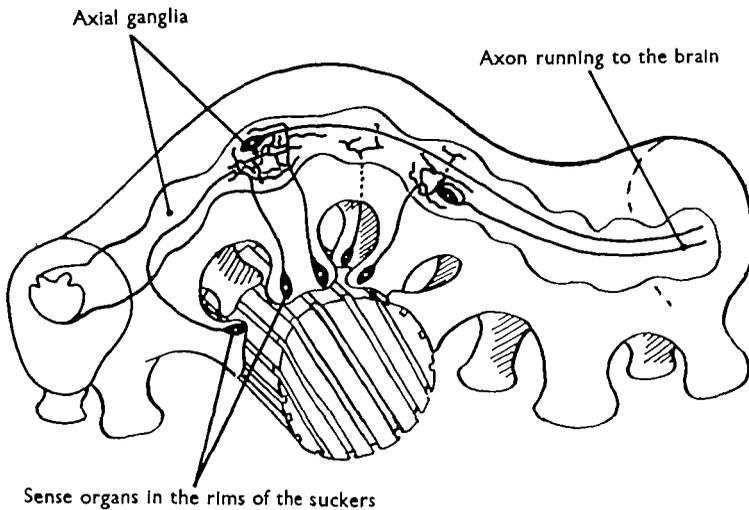


Fig. 4. Diagram of part of an arm of an octopus touching one of the test objects (P1). Only sensory nerves are shown. The existence of pathways from the sense organs passing through the axial ganglia, and of long axons from the axial ganglia to the brain is inferred from physiological data and degeneration experiments respectively (see text).

sensitive to mechanical stimulation than any other part of the arms (Ten Cate, 1928). These endings have nerves running from them that join with the sensory nerves described by Guérin (1908) as coming from areas in and around the rims of the suckers. Each sucker is represented by a ganglionic swelling in the axial nerve cord above it, and the sensory nerves from the receptors in the suckers run directly into that ganglion where they ramify in the central white matter of the nerve cord. Physiological evidence (von Uexküll, 1894) suggests that some pass into the neighbouring two or three ganglia but for no greater distance along the arms.

In the axial ganglia there are nerve-cell bodies that have processes running along the arms towards the brain. Section of an arm at a point about half-way along its length produces degenerating fibres among the nerves entering the brain from the arms, so that at least some of these processes run directly into the brain. The situation is summarized in Fig. 4.

Such a system would have the properties already described provided that the brain is capable of frequency analysis and the individual mechanoreceptors discharge or alter a resting rate of discharge when stimulated. Whether the sense organs discharge when in contact with a surface (the grooves in the test objects representing areas in which they are not excited) or when distorted (by bulging of the rims of the suckers into the grooves) is irrelevant. In either case the number of nerve impulses arriving in the ganglion over a sucker will be a reflexion of the degree of irregularity of the surface of any object touched by that sucker.

One effect of any increase or decrease in the number of nerve impulses arriving in an axial ganglion will be to change the general level of excitation and therefore the state of the individual cell bodies within that ganglion. As has already been pointed out, a number of these cell bodies have axons running directly to the brain. The frequency of nerve impulses along these axons is presumably related to the state of excitation within the ganglia in which they arise and thus represents the information from many individual sense organs in a summarized form.

The brain of *Octopus* must therefore be capable of setting in motion reactions whose nature (acceptance or rejection) is dependent upon quantitative differences in the sum of nerve impulses reaching it as a result of contact with objects encountered by the arms. There is no need to suppose that it can gain additional information about such objects by simultaneous or successive comparisons of the inputs from different nerve fibres as would be necessarily involved, for example, in the recognition of patterns of irregularity.

#### SUMMARY

The results of fifty-three experiments in which octopuses were trained to make tactile discriminations between the members of pairs of Perspex cylinders are reported. Grooves cut into these otherwise smooth cylinders varied in number and arrangement. The proportion of errors made in distinguishing such objects depends upon the difference between the proportions of groove on the objects concerned, and is not affected by the pattern or orientation of the grooves. It has thus been possible to measure the similarity to *Octopus* of the objects used and to predict the errors that will be made in any such discrimination.

When these results are considered in the light of the known nervous arrangements in the arms, it is possible to present a hypothesis about the mode of action of the peripheral tactile sensory system and the function of the brain. It is necessary to suppose that the latter distinguishes frequencies of nerve impulses in the sensory nerves from the arms; it is not necessary to postulate any projection of the sensory field or scanning mechanism involving the use of proprioceptive information.

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