

TASTE BY TOUCH: SOME EXPERIMENTS WITH *OCTOPUS*

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INTRODUCTION

Any one who watches octopuses in aquaria or in the sea can observe that they find much of their food by touch. Travelling over the surface of the rocks among which it lives, or over the floor of its aquarium, an octopus continually picks up small objects and passes some of these under the interbrachial web to the mouth, discarding others. In the laboratory, octopuses have been shown to be sensitive to chemical stimuli applied to the suckers (Giersberg, 1926) and to discriminate by touch between live and dead shellfish, which presumably differ only in their chemical characteristics (Wells & Wells, 1956).

The present account is of training experiments made to confirm that octopuses can distinguish by touch between objects differing only in 'taste' and to gain some indication of the degree of sensitivity of this chemotactile sense.

MATERIAL AND METHODS

Octopus vulgaris Lamarck. from the bay of Naples were used, individuals of from 200-500 g. being kept in separate tanks, as described in Wells (1962). Twelve animals were trained; all were blinded by section of the optic nerves (Wells & Wells, 1957).

Test objects were 2.5×3 cm. Perspex cylinders, covered with 0.5 cm. thick porous paper (sold in Naples as dishwashing cloths) stuck on with Perspex cement.

The animals were trained to discriminate between two such objects, soaked in solutions (to be specified below) and presented one at a time by touching against any outstretched arm. The octopus was rewarded with a piece of fish if it passed one of these objects, 'the positive', to the mouth, and punished with an 8 volt a.c. shock if it did the same with the other. There were 40 trials per day, in two groups of 20 at approximately 5 min. intervals, each group systematized: + - + - + + - - + - + - - + + - + - + -. Groups of 20 trials were at least 6 hr. apart. A large number of tactile training experiments have been made under these conditions, and there has never been any indication that the animals can learn to recognize this (or any other) trials sequence (Wells, 1962).

Solutions of hydrochloric acid, sucrose and quinine sulphate were used to soak the test objects, which were returned to the solutions between trials. Common salt was also used to prepare solutions twice as saline as the normal Naples aquarium sea water (approximately 39 parts per thousand). Control 'tasteless' objects were soaked in sea water only.

The hydrochloric acid and quinine sulphate $[(\text{CO}_{20}\text{H}_{24}\text{N}_2\text{O}_2)_2 \cdot \text{H}_2\text{SO}_4 + 8\text{H}_2\text{O}]$ were 'Analar' grade and 'extra pure' respectively, the salt and sucrose commercial grade.

All were made up as solutions in sea water taken from the inflow to the octopus tanks. Hydrochloric acid, salt and quinine solutions were replaced by fresh solutions at irregular intervals, generally about once every 60 trials. Sucrose solutions were at first treated similarly, but were later made up afresh immediately before each group of 20 trials. The continual removal and replacement of the porous objects must have resulted in progressive dilution of the test solutions, which were in jars of approximately 1 l. capacity. This and the necessity to present the test objects under water make it certain that the animals were never actually exposed to solutions quite as strong as those that they were nominally receiving.

The circulating sea water remained at 26° C. ($\pm 2^\circ$) throughout the period of the experiments.

EXPERIMENTAL RESULTS

Preliminary experiments showed that octopuses can readily be trained to distinguish solutions of sugar and of acid, learning to discriminate between these within 40 trials, a rate comparable with that achieved in learning to discriminate between objects with gross differences in texture (Wells & Wells, 1957).

1. *Tests to determine the order of sensitivity to substances dissolved in sea water*

Twelve animals were then trained to distinguish between plain sea water and hydrochloric acid or sucrose or quinine in sea water. The initial solutions were made up at 0.02 N (HCl), and 7 % (sucrose), these strengths being ten times the figures given in Stevens (1951) as normally accepted for the absolute threshold of man's tongue to the same substances in distilled water. The quinine solution was made up relatively strong at 0.03 % (1000 times the human threshold).

The animals were trained to discriminate between plain sea water and successively more dilute solutions of the substances to be distinguished, each individual being transferred to training with a more dilute solution as soon as it had made a total of 10 errors or less in 40 trials (75 % or more correct responses in two successive groups). At each change, the test solution was diluted ten times. Test objects were washed for several hours in tapwater before transfer to more dilute solutions. Training was stopped when the animals had successfully learned to detect substances at concentrations 100 times as dilute as those said to be detectable by man in distilled water. This was more than 1000 times as dilute as I personally was able to taste in sea water. At this level the animals were still performing very consistently and there is no reason to believe that the threshold for the chemotactile sense of *Octopus* has been approached.

Details of the performance of the twelve octopuses are given in Table 1.

2. *Transfer tests*

At the end of this training period, all save one of the animals were used in experiments to determine whether all tastes are accepted as a collective alternative to 'no taste'. The animals were given groups of 20 trials in which alternate 'taste' trials were made using a chemical stimulus other than that which the animals had been specifically trained to take or reject. The results of these tests are summarized in Table 2; it would seem that, in general, 'taste' appears to be treated as an alternative to 'no taste' under these conditions, but the experiments are insufficient in number to be conclusive.

3. Training to distinguish equimolar solutions

Ten of the animals were then trained to distinguish between pairs of 0.2 mM solutions of hydrochloric acid, sucrose and quinine, starting in each case with the substance negative or positive in the dilution series experiment (§ 1, above) as negative or positive in the new series of tests.

The results are summarized in Table 3. It is quite clear that octopuses can distinguish between equimolar solutions of acid, sugar and quinine.

Table 1. *Number of errors made per group of 20 trials by individual octopuses trained to distinguish between plain sea water and sea water with the stated concentration of solute added*

On making a total of 10 errors or less within two groups of trials, training was continued with a solution 10 × as dilute as that already distinguished. There were 40 trials per day in two groups of 20 at an interval of not less than 6 hr.

Animal		Hydrochloric acid. 7% (= 2 M)										× 10 ⁻⁴				× 10 ⁻⁵			
		× 10 ⁻²					× 10 ⁻³												
J 63	Acid + ve	10	8	9	8	4	1	—	—	—	—	2	2†	4	—	2	3	—	—
J 79	Acid - ve	10	10	10	10	8	5	1	10	4	1	—	—	—	—	7	2	—	—
J 80*	Acid + ve	4	2	—	—	—	—	—	5	3	—	—	—	—	—	3	2	—	—
J 81	Acid - ve	7	5	2	—	—	—	—	10	9	6	2	—	—	—	3	3	—	—
J 82*	Acid - ve	10	10	6	6	3	—	—	10	10	10	4	4	—	—	8	4	1	—
		Quinine sulphate. 3% (= 0.04 M)																	
		× 10 ⁻²					× 10 ⁻³					× 10 ⁻⁴				× 10 ⁻⁵			
J 83	Quinine + ve	5	5	—	—	—	6	2	—	—	—	6	4	—	—	6	4	—	—
J 85	Quinine - ve	10	10	10	6	6	4	10	9	6	3	8	5	3	—	—	—	—	—
J 93	Quinine + ve	6	8	4	7	2	—	0	4	—	—	3	0	—	—	5	7	4	—
J 94	Quinine - ve	9	7	4	2	—	—	2	1	—	—	7	2	—	—	2	2	—	—
		Sucrose. 7% (= 0.2 M)																	
		× 1										× 10 ⁻¹				× 10 ⁻²			
J 50	Sucrose - ve	11	5†	10	8	10	8	5	9	3	7	2	3	4	0	—	—	—	—
J 52	Sucrose + ve	9	7†	10	10	7	9	3	6	—	—	4	3	4	4	—	—	—	—
J 78	Sucrose + ve	9	10†	10	10	10	2	2	—	—	—	2	0	2	(10	8	4	8)§	1

* J 80 and J 82 were used in a pilot experiment, learning to distinguish between an acid and a sugar solution; they had thus been pretrained to take or reject the acid-soaked object.

† J 63 should, of course, have been changed to training with a more dilute solution at this point.

‡ J 50, J 52, J 78: at this point it was realized that the sugar was fermenting between groups. Up to this point the animals might have been learning to distinguish alcohol, not sugar. Thereafter solutions were made afresh immediately before each group of trials.

§ J 78 rejected nearly every object presented during this period, but continued feeding.

4. Experiments with salt solutions

A final series of experiments was made with salt solutions. Eight of the animals were trained to distinguish between sea water and one or more of the following: sea water diluted to half strength with fresh (tap) water, fresh water, and sea water concentrated by adding 40 g. of commercial sodium chloride per litre. In all cases the animals were trained with plain sea water as the positive or negative stimulus as it had been in previous experiments with the same individual. The results of these experiments are summarized in Table 4. With one exception (an animal required to learn to accept an

Table 2. *Transfer tests*

After the training detailed in Table 1, some of the animals were used in further tests, under the same conditions but without rewards or punishments. In these tests, objects soaked in solutions other than those used in training were substituted at alternate 'taste' trials. Scores show the number of times each object was taken in a test group of 20 trials. To make the test scores for 'taste' and 'plain sea water' objects comparable, scores for 'tastes' in the tests have been doubled (indicated by an asterisk *).

	Animals trained with					
	Acid as positive		Acid as negative			Sucrose as positive
	J 63	J 80	J 79	J 81	J 82	
Last 20 trials of training						
Sea water + acid taken (7×10^{-5} %)	10	8	2	0	1	—
Sea water + sucrose taken (7×10^{-3} %)	—	—	—	—	—	10
Sea water alone	3	0	10	9	10	3
1st test						
Sea water + acid (7×10^{-5} %)	10*	10*	9*	0*	2*	8*
Sea water + quinine (3×10^{-3} %)	—	6*	—	0*	2*	—
Sea water + sucrose (7×10^{-2} %)	10*	—	10*	—	—	8*
Sea water alone	1	1	10	4	10	6
2nd test						
Sea water + acid	10*	5*	0*	—	—	10*
Sea water + quinine	—	2*	—	—	—	—
Sea water + sucrose	6*	—	10*	—	—	8*
Sea water alone	1	1	10	—	—	8
3rd test						
Sea water + acid	10*	—	0*	—	—	—
Sea water + quinine	—	—	—	—	—	—
Sea water + sucrose	8*	—	4*	—	—	—
Sea water alone	0	—	7	—	—	—
4th test						
Sea water + acid	10*	—	0*	—	—	—
Sea water + sugar	10*	—	2*	—	—	—
Sea water alone	1	—	10	—	—	—

Table 3. *Scores in training to distinguish between equimolar (0.2 mM) solutions*

Errors per 20 trials. Details of the previous experience of these animals are given in Tables 1 and 2. Successive experiments with the same animal read from left to right, (exceptions listed below) normally following without a break in training.

Animal	Previous training	HCl v. sucrose				HCl v. quinine				Sucrose v. quinine			
		8	7	10	0	3	1	(Acid + ve)		—	—	—	—
J 50	Sucrose - ve	8	7	10	0	3	1	(Acid + ve)	—	—	—	—	—
J 52	Sucrose + ve	2	0	—	—	—	—	—	4	6	—	—	—
J 63	Acid + ve	3	3	—	—	9	9	3	2	—	—	—	—
J 78	Sucrose + ve	5	3	—	—	—	—	—	—	7	3	—	—
J 79	Acid - ve	7	1	—	—	—	—	—	—	3	1	(Sucrose + ve)	—
J 80	Acid + ve	5	5	—	—	2	1*	—	—	—	—	—	—
J 82	Acid - ve	—	—	—	—	3	3	—	—	7	9	4	0†
J 83	Quinine + ve	—	—	—	—	8	7	7	4	10	10	4	6†
J 85	Quinine - ve	—	—	—	—	3	1	—	—	3	1	—	—
J 94	Quinine - ve	—	—	—	—	5	7	1	—	0	0†	—	—

* J 80 Acid v. quinine training precedes acid v. sucrose.

† Quinine positive.

‡ J 83, J 94 sucrose v. quinine training preceded acid v. quinine training. Training with J 83 on acid v. quinine was not completed.

Object soaked in concentrated sea water following previous training to reject an object soaked in sea water) the octopuses rapidly learned to distinguish between all of the pairs of solutions.

5. A note on the 'olfactory' organ

Octopus, like other coleoid cephalopods that have been examined, has a group of sensory cells located between the hind border of the eye and the edge of the mantle (Watkinson, 1909). In *Octopus vulgaris* the group lies in the angle between the edge of the mantle and the main part of the body, where it can be seen in life as a small (2 mm. diameter in an octopus of 500 g.) oval patch without chromatophores. Internally it is characterized by nerve cells with a cap of clear cytoplasm facing towards the exterior (Watkinson, 1909); similar cells are found in the suckers (Rossi & Graziadei, 1958). The organ is served by a nerve with a large number of very small fibres running to the 'olfactory lobe' on the optic stalk of the brain (Boycott & Young, 1956).

Table 4. *Training to distinguish between sea water and fresh water or sea water with fresh water (50:50) or sea water with 40 g./l. NaCl added*

Scores show the number of errors made per group of 20 trials. Previous experiments with these animals, see Tables 1-3.

Animal	Previous training	Sea water v. fresh water		Sea water v. sea water with fresh water		Sea water v. sea water with 40 g./l. NaCl added			
J 50	Sea water + ve	2	0	2	2	—	—	—	—
J 52	Sea water - ve	1	1	1	1	—	—	—	—
J 63	Sea water - ve	—	—	—	—	10	8	10	7
J 78	Sea water - ve	—	—	—	—	7	7	7	3
J 79	Sea water + ve	1	1	—	—	—	—	—	—
J 80	Sea water - ve	—	—	3	3	9	0	—	—
J 82	Sea water + ve	—	—	2	1	—	—	—	—
J 85	Sea water + ve	—	—	—	—	7	2	—	—

There is very little evidence that this is indeed an olfactory organ. Polimanti (1913) working with *Sepia* clamped in an aquarium by its shell, reported violent contractions of the mantle following releases of a variety of substances close to the olfactory organ. But he did not check whether the same reactions occurred after removal of the organ. Giersberg (1926) reported that excision made no difference to *Octopus*'s reactions to chemical stimuli, and I have recently confirmed this myself, the responses of blinded animals to sardine blood and indian ink (the former excites them to move around their tanks, the latter not) being quite unaltered by removal of the olfactory organs.

Their function, therefore, remains problematic. In view of the great chemical sensitivity of the arms, it is difficult to conceive of a behavioural test that will show conclusively whether or not the olfactory organ is chemosensitive, and so far a more direct electrophysiological approach has failed (Rowell, unpublished).

DISCUSSION

The experiments reported above were made to establish a method for studying the chemotactile sense of cephalopods. They were not made to establish absolute thresholds for chemosensitivity, and they do not, of course, prove that *Octopus* is capable of

qualitative discriminations between the various substances concerned. So far as the octopus is concerned, the 'tastes' of acid, quinine and sugar may all be alike, discriminations being based on quantitative differences in the degree to which each excites the sense organs concerned.

The method can be criticized on various grounds. It is arguable, for example, that the 'positive' object in each test becomes contaminated by the food rewards given when it is taken. This would be a serious objection were only one octopus trained at a time. But in the present series of tests, the animals were trained simultaneously, some individuals having as the 'positive' object cylinders also used as the 'negative' for others. Were contamination with food the cue used by the animals, some of them should have failed or at least have performed much more erratically than others; in fact performance was very consistent. Fresh objects were, in any case, introduced from time to time, and there was no evidence that these upset performance in any way. (This, incidentally, disposes of the possibility that the animals were by some means learning to recognize individual test objects from fine differences in their surface characteristics.) It can also be objected that presenting an object under water favours detection of substances with large, slowly diffusing molecules, ionized materials like hydrochloric acid becoming relatively rapidly lost as soon as the test object is dipped in the water. This will be a serious problem when an attempt is made to detect the limits of sensitivity to substances; in the present series it is unimportant as no attempt has been made to establish absolute thresholds. The same can be said of the method's lack of control of such environmental features as the pH and oxygen content of the circulating sea water which fluctuate with changes in temperature and the length of time since the recirculating water was exchanged for fresh sea water.

What the experiments show is that octopuses can be taught to distinguish between objects on a basis of their chemical differences alone, and that they are able to detect hydrochloric acid, sugar and quinine in astonishingly small quantities—less than 1 part in 10^7 in the case of quinine. The experiments with acid are perhaps particularly interesting, as the basis of discrimination must here be hydrogen ion concentration, it being most improbable that the animals are capable of detecting traces of chloride added to a solution that already approaches 4% sodium chloride. 0.02 mM HCl in sea water was readily recognized as different from plain sea water. The difference in pH to which the animals were presumably responding was not detectable using a Beckman 'Zeromatic' meter on solutions made up 24 hr. previously, although the animals responded appropriately.

Octopus quickly learns to recognize these very small chemical differences. It is clear that the taste of objects touched must be of the greatest importance in the life of the animal. Indeed, the chemotactile sense may well be of much greater importance than the more extensively studied mechanotactile sense of this animal (for references see Wells, 1962). It could, for example, constitute not only the basis on which *Octopus* recognizes its food, but also the means by which the animal finds its way about. Octopuses are solitary animals, and return to a 'home' in the rocks between expeditions, made mainly at night, presumably to seek food (Wells, 1962). They do not appear to learn to run mazes visually, and only succeed in detour experiments when able to maintain a constant orientation throughout (Wells, 1963). This makes the return of an octopus to its home somewhat puzzling since it seems that this cannot be

achieved on a basis of seeing objects and remembering which way to turn. But it could possibly be managed chemotactically, the animal learning to recognize something of the chemical geography of its territory, returning home perhaps along remembered taste trails or gradients. In the absence of any observations on the movements of octopuses in the sea (or even in large aquaria, with the 'home' out of sight), there is no evidence for or against this possibility. But the present account shows at least that the required sensitivity is there, and that the animals readily learn to recognize and react to chemical stimuli. The teachability of *Octopus* in this respect opens up a whole field of possibilities in the study of how marine animals find their way about.

SUMMARY

1. A method of teaching *Octopus* chemotactile discriminations is described.
2. The animals can be shown to be capable of distinguishing by touch between porous objects soaked in plain sea water and sea water with hydrochloric acid, sucrose or quinine sulphate added.
3. They can detect these substances in concentrations at least 100 times as dilute as the human tongue is capable of detecting them in distilled water.
4. They can be trained to distinguish between equimolar (0.2 mM) solutions of hydrochloric acid, sucrose and quinine.
5. They can also be trained to distinguish between sea water and fresh water or half-strength sea water or sea water with twice the usual quantity of salt.
6. The function of the 'olfactory organ' is discussed.
7. Chemotactile learning is discussed in relation to the means by which *Octopus* finds its way about the territory around its 'home'.

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