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CHANGES IN TEXTURAL PREFERENCES IN *OCTOPUS* AFTER LESIONS

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INTRODUCTION

Octopuses with their optic nerves cut can readily be trained to discriminate between rough and smooth spheres or cylinders, and this textural discrimination has been used repeatedly as a basis for determining the effect of brain lesions on touch learning (for references see Wells, 1965). Recent work on split-brain octopuses with extensive lesions to the inferior frontal system has, however, brought to light a hitherto unsuspected complication to the interpretation of these experiments; octopuses with very large lesions to the touch-learning system 'prefer' rough objects to smooth. They will learn to discriminate between rough and smooth when rough is the positive object (that is, the one for which food is given in training experiments) after lesions that stop them learning to make the same discrimination when smooth is positive (Wells & Young, 1965).

The experiments reported here were made to study this preference effect. They show that octopuses with very large lesions to the inferior frontal system do indeed prefer rough to smooth objects but further, more surprisingly, that animals without central lesions have a measurable preference in the opposite direction for smooth rather than rough. This had not previously been detected.

MATERIAL AND METHODS

Octopus vulgaris Lamarck from the Bay of Naples was used. Animals in the size range 200–500 g. were presented with rough and smooth Perspex balls 2½ cm. in diameter. The objects were always presented one at a time to the right-hand side of the octopus and wherever possible to the second arm from the front on that side. The capacity for discrimination was tested in two sets of experiments—extinction and training. (1) In the extinction experiments there were no rewards and no punishments. Each animal was given half a sardine after each session. Tests were made in groups of 16, 8 with each object. The objects were presented one at a time, alternating, at intervals of about 5 min. There were two groups of trials per day, about 6 hr. apart. At each trial the animal was scored as having made a 'positive' response if it grasped the Perspex ball and bent the arm to pass it under the interbrachial web towards the mouth. It was scored as making a 'negative' response if it pushed the object away or merely dropped it after examination with the suckers. Tests continued for 5 days, 160 trials, 80 with each object. (2) For the training experiments (pp. 408 et seq.) the animals were rewarded for taking the 'positive' object by giving them a small piece of fish immediately after removing the object. They were punished for taking the 'negative' object, by touching them with a probe giving a 9 V. a.c. shock, again immediately following removal of the object. Trials were otherwise arranged exactly as in the extinction experiments.

In all the octopuses used the optic nerves had previously been cut. 'Normal' animals had no other operation. In the rest the supraoesophageal brains were either split by a vertical longitudinal cut and/or parts were removed from the central supraoesophageal mass, at the same time as they were blinded. Animals were kept for a few days after operation, until they were feeding regularly, before being presented with the test objects.

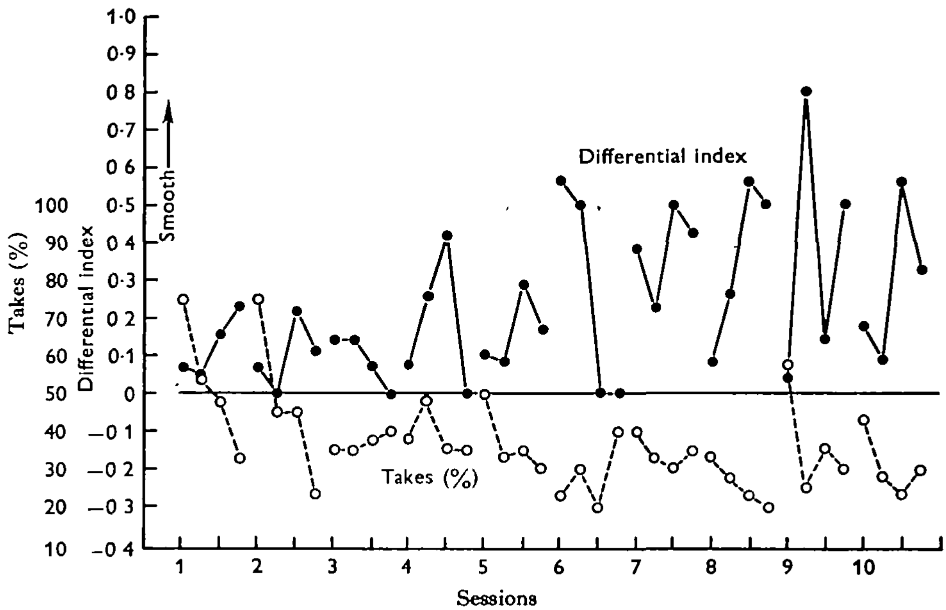

Fig. 1. An extinction experiment with ten normal animals (optic nerves cut but no central lesions). The results of these unrewarded tests are plotted in terms of the proportion of takes to trials (open circles), and an index of differential responses calculated as takes of smooth (x) less takes of rough (y) divided by total takes, $(x-y)/(x+y)$ (filled circles). This gives a measure of the animal's preference for one object compared with the other, a positive index indicating smooth preference. Each point plotted represents a mean of forty tests; that is, the peformance of ten animals with two presentations of each of the two objects to each animal.

RESULTS

1. *Extinction experiments*

1.1. *Normal animals*

Ten animals were given 160 tests (ten sessions); six of them were given a further 160 tests (Table 1). Some of the animals were tested beginning with a presentation of the smooth object at each session, and some with a presentation of the rough. The two treatments made no detectable difference to the proportion of takes of each object and the results have been pooled.

Figure 1 shows the progress of the experiment over the first ten sessions. The animals began by taking rather more than half of all the objects presented at the first session, with a marked decline in the number of takes during the session. The second session repeated this pattern, with a slightly smaller total number of takes, and the animals thereafter settled down to taking about one in three of all objects presented, less at the end than the beginning of each session. Over the whole 160 trials 36 % of all objects presented were taken. The six octopuses that were tested for a total of 320 trials were still taking about 28 % of all objects presented at the end of the experiment.

Figure 1 also summarizes the preferences of the animals used in this extinction experiment. These octopuses consistently took more smooth than rough spheres from the start of the experiment. In Fig. 1 this preference is shown in terms of an index, calculated as takes of the smooth object, x, less takes of the rough, y, divided by the total number of takes [$i = (x-y)/(x+y)$]. While the pattern of preference did not change consistently during the individual sessions, the animals became somewhat more likely to take the smooth in the later sessions. By the end of the experiment the octopuses were taking about twice as many smooth as rough spheres. In the first 160 trials all save one of the individuals took more smooth than rough objects (Table 1). The exceptional animal took smooth objects at 46 % of its 60 takes. In general the animals that took most objects showed the greatest preference for the smooth sphere (Fig. 6).

Table 1. *Extinction in normal animals*

	1st 160 trials Smooth first			2nd 160 trials Rough first		
Animal	Takes Smooth	Takes rough	% 'correct' (smooth +)	Takes smooth	Takes rough	% 'correct' (smooth +)
351	66	42	65	57	20	73
352	28	15	58	18	6	58
353	13	10	52	7	14	46
356	67	35	70	34	11	64
357	23	14	56	19	11	55
474	27	33	46	43	26	61
206	30	20	56	178	88	59 5
	Rough first					
209	53	41	58			
216	34	16	61	% take 27·7		
217	12	3	56			
	353	229	57·8			

% take (smooth and rough) 36·4 %

Ten blinded octopuses with no other lesion. Takes of smooth and rough spheres in 80 trials with each. No rewards.

For six of the animals, after the 160 trials in which the smooth sphere was given first at each session there were a further 160 trials with the rough given first.

The fourth column shows the results calculated as percentage of 'correct' responses, taking smooth as the object to be taken, rough to be rejected. This method of calculating takes account both of the total and differential take.

In the second 160 trials, with the rough sphere given first at each session, all the animals save one again preferred the smooth. The exceptional individual was not the same animal that had shown a rough preference before (Table 1). There is thus evidently some fluctuation in the preference in each individual, as well as variation between individuals, but the greater tendency to take smooth is marked.

1.2 Extinction in animals with the vertical lobes removed

Eight animals were tested. These octopuses, as a group, took a higher proportion of the objects presented than the normal octopuses (60 % as against 38 %), but they were considerably more variable and included individuals taking more and individuals taking fewer objects than any of the normals (Table 2 and Fig. 6). The extent of the lesions in individual animals is summarized in Table 2. To judge from this rather small sample there seems to be no constant relationship between the extent of lesions made and the proportion of takes. The number of takes declined throughout most of the sessions, although it generally began and remained at a higher level than in the normal animals (Fig. 2). The mechanism responsible for extinction is therefore not confined to the vertical lobe (see Young, 1965).

Table 2. *Extinction without vertical lobes*

Animal	Smooth	Rough	% correct (smooth +)	Vertical lobe % removal	Damage to other lobes: msf	lsf	sv	db
OHS	55	44	57	90	0	0	1	1
OGT	56	48	55	87	0	0	1	1
OHU	79	76	52	100	1	1	2	2
OHV	76	57	62	100	0	0	2	2
OZE	60	56	53	80	0	0	2	2
OZC	39	47	45	92	0	0	0	0
OZD	17	24	46	100	0	0	2	2
OLN	15	14	51	100	3	2	2	1
	397	366	52·4					

% take (rough & smooth together) 59·6 %.

Octopuses blinded and vertical lobes removed. Takes of smooth and rough spheres in 80 trials with each. No rewards. Damage is given separately for median and lateral superior frontal (msf and lsf,) subvertical (sv) and dorsal basal lobes (db). 3 = complete removal, 2 some damage, 1 slight damage, 0 no damage.

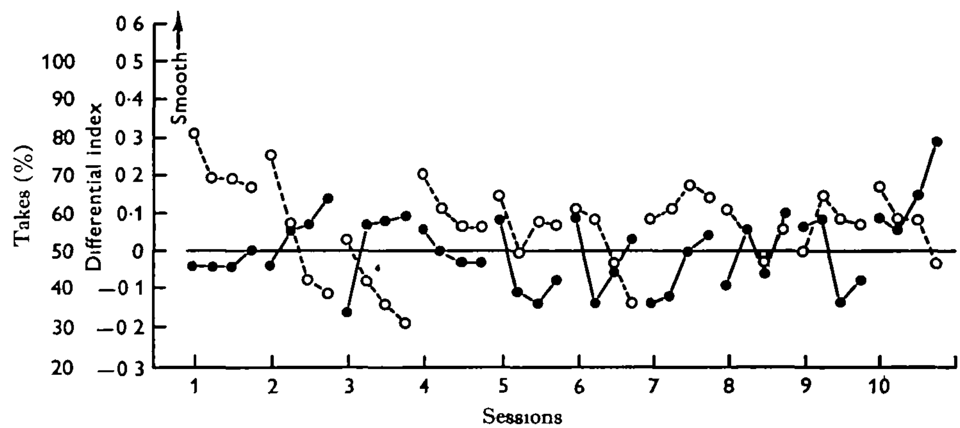

Fig. 2. An extinction experiment with eight octopuses with the vertical lobes removed, plotted as Fig. 2. Compared with normal octopuses the animals took at a higher proportion of trials, and showed a lesser preference for smooth. ●, Differential index; ○, % takes per trial.

The animals with the vertical lobes removed, again considered as a group, took slightly more rough than smooth objects during the first session. In later sessions the level oscillated irregularly at about 50 % for each sphere. There was no consistent pattern of change of preference within the sessions. The preference for smooth is definitely less marked (53 %) than in normal animals (58 %). Individual animals varied considerably in preference, as in their proportion of takes (Table 2). Two of them took rough more often than smooth, and the remaining six showed varying degrees of preference for smooth. Again, as with the normal octopuses, taking more objects was found to correlate with an increased preference for smooth (Fig. 6).

Table 3. *Extinction in half-brain octopuses*

Animal	Takes smooth	Takes rough	% correct (smooth +)	Sub-frontal	Post-bucc.	Vert. lobes remaining on R
OIC	23	19	53	0	0	3
OID	27	44	39	2	2	1½
OIE	52	33	62	1	0	3
OLX	7	7	50	1	0	1
OLY	25	34	44	0	0	3
OZF	36	48	43	1	1	1
OKQ	2	10	45	1	0	2½
OIP	26	37	43	1	0	2½
OLF	21	15	54	0	0	3
OIQ	22	26	48	1	1	2½
OKR	5	3	51	0	0	3
OKS	18	17	51	1	0	2½
	264	293	48·5			

% take trials (rough and smooth together) = 29·0 %.

Twelve octopuses blinded and with supraoesophageal lobes split. Takes of smooth and rough spheres in 80 trials with each. No reward. The damage to subfrontal and posterior buccal lobes on the right-hand side (the one tested) is shown. 3 = complete removal, 2 some damage, 1 slight damage, 0 no damage. The vertical lobe is subdivided into 5 longitudinal segments; the last column shows the number of segments remaining on the right (tested) side of the brain.

1.3. *Extinction in half brains*

Twelve animals were tested (as usual on the right side only) after longitudinal division of the supraoesophageal brain (Table 3). These half-brain animals, like normal octopuses, began by taking the majority of the objects presented. As with the unoperated animals, the proportion of takes fell steadily throughout the first two sessions, and thereafter settled down (Fig. 3). The steady level of takes was, however, lower than in normals, so that in the fourth session and subsequently until the end of the experiment these octopuses took only about one in four of the objects presented. The overall proportion of takes was 29·0 %, compared with 36·4 % by normal and 59·6 % by octopuses with the vertical lobe removed. Once again there was considerable individual variation; two of the animals took less than 10 % of all objects presented. The tendency to take does not correlate with the degree of damage to the right-hand (tested) side of the brain, which varied somewhat depending on the precise position of the central cut (Table 3).

Considering the group as a whole, the split-brain octopuses took the rough object more often than the smooth. The overall score was 48·5 % takes of smooth. The preference was erratic, varied a great deal within sessions and from one session to the next and did not obviously correlate with the proportion of takes, which remained more or less constant from one session to the next after the first three sessions of the experiment (Fig. 3). Individual preference did not follow the pattern of 'more takes—more preference for smooth' found in animals without brain lesions (Fig. 6). There was much variation in preference between individuals. Six showed distinct preferences for rough and the remainder were almost neutral, only one reaching a 62 % smooth preference (Table 3).

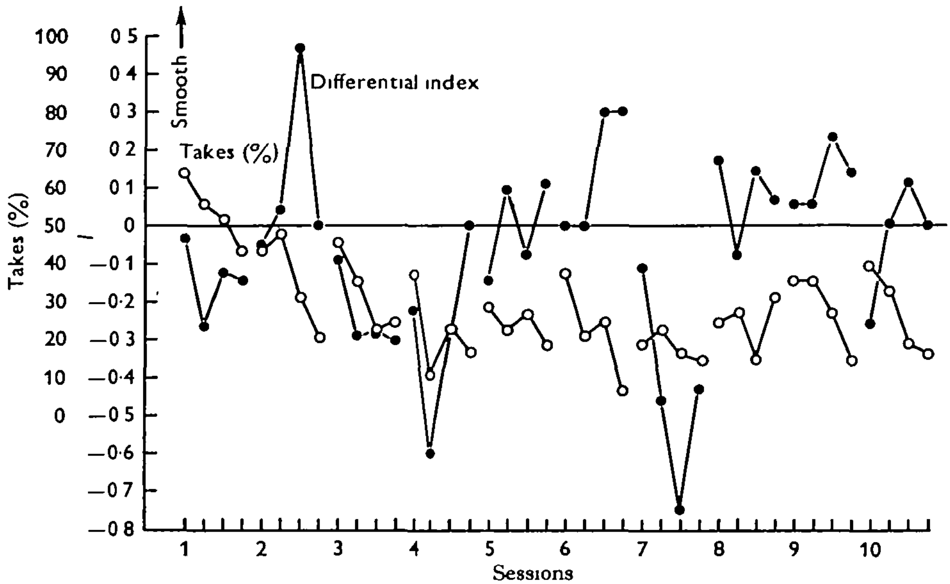

Fig. 3. An extinction experiment with twelve split-brain octopuses tested on one side, plotted as Figs. 2 and 3. These animals took fewer objects than the 'no verticals' (Fig. 2). There was no evidence of a consistent preference for rough or smooth, although in total rather more rough than smooth, objects were taken.

Table 4. *Extinction with inferior frontal system partly intact*

Animal	Takes smooth	Takes rough	% correct (smooth +)	M.I.F.	Subfr. dors.	Subfr. ventr.	Post-bucc.
OMB	4	18	41	3	3	1	0
OMD	25	33	45	0	3	1	0
OME	37	30	54	3	3	1	1
OMF	16	21	47	0	2	1	0
OMG	39	38	51	0	3	2	1
OMI	10	5	53				
$n = 6$	131	145	48·5				

% take (rough & smooth) = 28·7 %.

Octopuses with greater part of supraoesophageal lobes removed but posterior buccal and some subfrontal intact Takes of smooth and rough spheres in 80 trials with each. No rewards. The damage to median inferior frontal (m.i.f.) and to dorsal and ventral subfrontal and posterior buccal lobes on the side tested shown on same scale as Table 3. Some parts of the inferior frontal system remain.

1.4. *Extinction in octopuses with vertical lobe system and basal lobes removed*

In six animals the whole supraoesophageal system behind the posterior buccal lobes was removed. The inferior frontal system itself was also damaged. In most of them the dorsal subfrontal tissue had been removed but all retained a major part of the small cells of the ventral subfrontal. The posterior buccals were little damaged.

These animals showed a lower tendency to take than any others in the experiment (Table 4 and Fig. 4). The tendency declined sharply within each session and recovered before the next, the mean session level settling at rather less than 30 % takes after the first three or four sessions. The relative takes of the two spheres fluctuated wildly

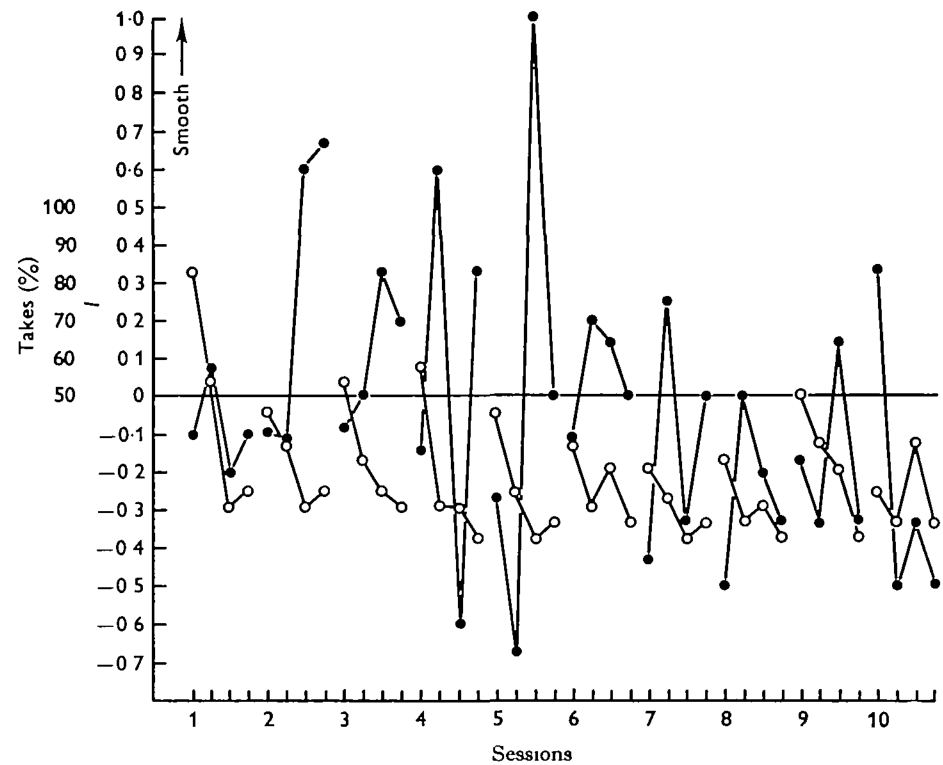

Fig. 4. An extinction experiment with six octopuses from which the basal lobes and all the overlying parts of the supraoesophageal lobe had been removed. The basal parts of the inferior frontal systems were still intact but were split (see Table 4). The animals took even less often than octopuses lacking the vertical lobes, and showed no consistent preference. ○, takes per trials (%), ●, differential index.

Table 5. *Extinction with whole inferior frontal system removed*

Animal	Takes smooth	Takes rough	% correct (smooth +)	Subfr. dors.	Subfr. ventr.	Post. bucc.
OMA	49	46	52	3	3	3
OMC	52	38	59	3	3	3
OMH	71	57	59	3	3	3
OMK	43	44	49	3	3	3
OML	57	46	57	3	3	3
$n = 5$	272	231	55·1			

% take (rough & smooth) = 62·9 %.

Octopuses with only superior buccal remaining. The whole inferior frontal system has been removed. Extinction experiment and conventions as Table 4.

within sessions but as with the split-brain octopuses, the mean showed a slight preference for rough (48·5% takes of smooth).

1.5. *Extinction with whole inferior frontal system removed*

In five animals the whole supraoesophageal brain was removed, except for the superior buccal lobe. Previous work has shown that animals with lesions of this type can still eat, but cannot be taught to discriminate in tactile experiments, where they tend to err by taking a very high proportion of all objects presented to them (Wells & Young, 1965).

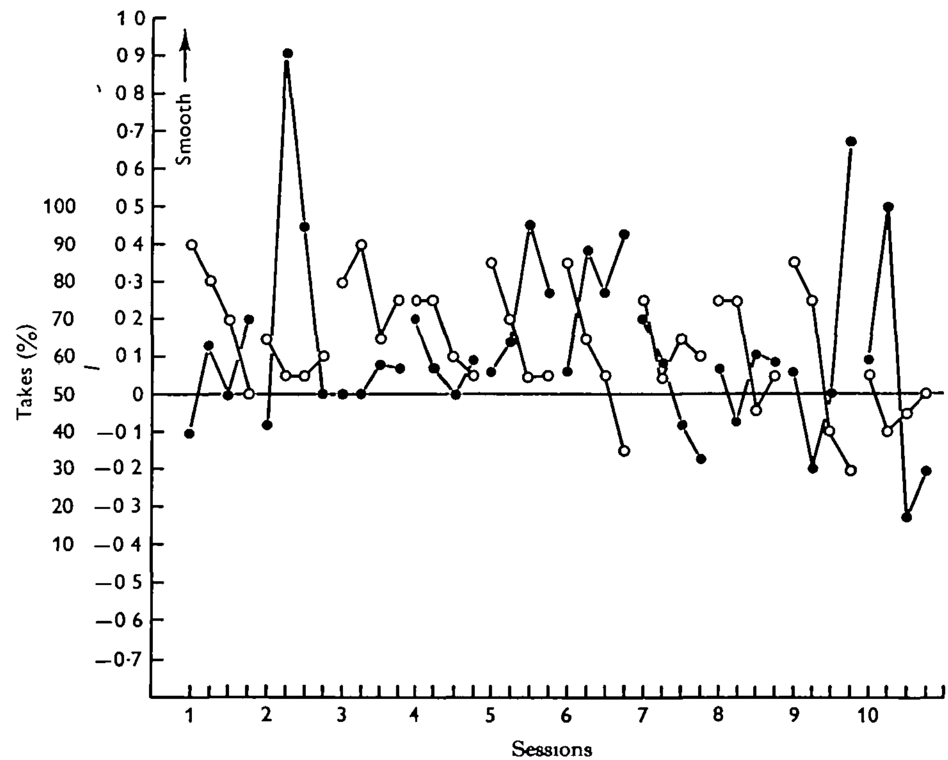

Fig. 5. Extinction experiment in five animals with the whole inferior frontal system removed as well as the basal lobes. ●, Differential index; ○, takes per trial (%).

The performance of the five animals used in the present extinction experiments was consistent in these respects. They took a very high proportion of the objects presented to them (63%) and they showed little change in behaviour as sessions continued, the overall level of take declining only slightly in the course of 160 trials (Fig. 5 and Table 5). The animals showed an overall preference for smooth (55% of all takes).

2. *Training experiments*

2.1. *Normal animals*

Since animals with the supraoesophageal lobes intact prefer the smooth object in extinction tests, one might expect training to discriminate between rough and smooth to proceed more readily where smooth was the 'positive' object. This proves to be so.

In Fig. 7*a* the performance of thirteen normal animals trained with smooth positive is compared with that of eight animals trained with rough positive. The performance of the animals is plotted in terms of per cent correct responses per sixteen takes, instead of more conventionally in terms of per cent correct per sixteen trials. The 'per take' method of plotting was adopted in order to present the data in a form directly com-

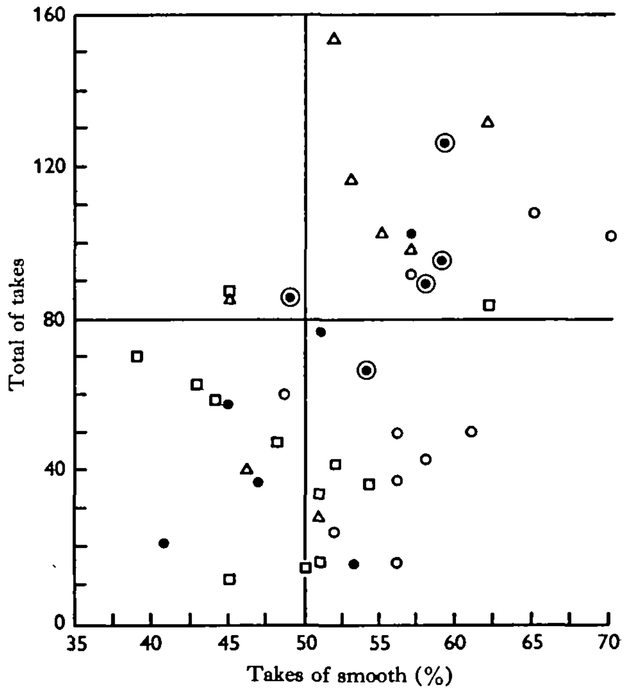

Fig. 6. Showing the performance of individual octopuses in extinction tests. Each animal had 160 trials, 80 with each test object, given at 32 trials per day in two sessions. At each session the rough and smooth test objects were presented in alternation, at intervals of 5 min. (eight tests with each). This plot summarizes the relations between lesion type, object preference and proportion of takes. ○, Normal; △, no vertical; □, split; ●, basals removed, ⊙, subfrontal removed.

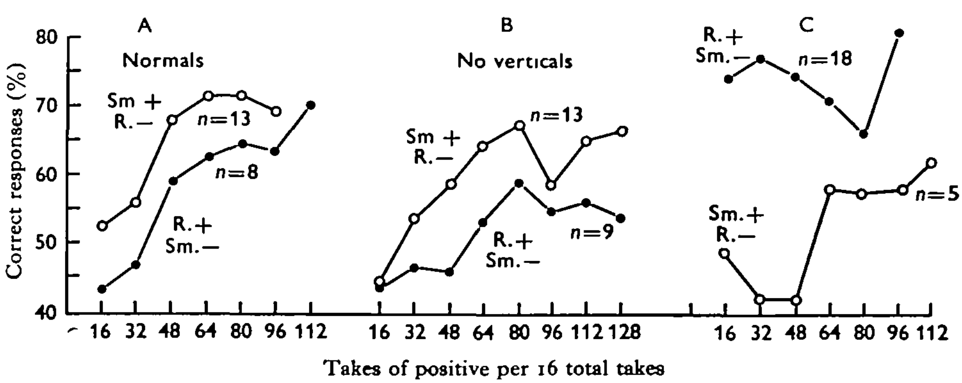

Fig. 7. The results of training experiments, comparing the performance of animals trained with smooth positive and rough positive. Note that the split-brain octopuses (C) scored better when trained to take rough and reject smooth than the reverse. The other groups of animals (A and B) scored better with smooth positive.

parable with data derived from animals with split brains or lacking their vertical lobes (Fig. 7*b* and *c*). The three categories of octopus varied greatly in the proportion of takes to trials, just as they did in the extinction experiments, with the split-brain octopuses taking least frequently. The animals are perhaps more usefully compared in terms of their change in performance per take than in the terms of change per trial.

Figure 7*a* shows that the performance of normal animals trained on smooth positive started better than that of octopuses trained on rough positive. The latter began by making less than 50 % correct responses (more smooth than rough objects taken in the first thirty-two takes). Improvement in discrimination was about equally rapid in the two series (S+ and R+) and a similar standard of discrimination was eventually reached, although the rough-positive group took longer to reach it.

2.2. *Vertical lobes removed*

Essentially the same picture emerges for octopuses deprived of their vertical lobes (Fig. 7*b*). In these the effect of the smooth preference was more marked than with normals (thirteen animals trained S+ made 72 % correct responses, nine trained R+ made 63 %), because the octopuses with no vertical lobes learn more slowly (previous references see Wells, 1965). However, there was considerable individual variation in preference and some animals showed a lesser preference for smooth than is normal. Such individual differences are characteristic of animals lacking the vertical lobes.

2.3. *Half brains*

From the extinction experiments summarized above it is clear that in split-brain octopuses there is some indication of reversal of the preference, in favour of rough. The results of training experiments using only one side confirmed that octopuses with only half the brain prefer rough. Those trained with rough as the positive sphere made mainly correct responses from the beginning of their training, so that their overall performance was as good as or better than that of normal animals trained with smooth positive (Fig. 7*c*). A similar group of split-brain octopuses, trained with the smooth sphere positive, began by making considerably less than 50 % correct responses and continued to do this throughout their first forty-eight trials (Fig. 7*c*).

The starting preference of the split-brain octopuses is more obvious than in normal animals because the animals with only half the brain learn even more slowly than animals lacking their vertical lobes. The slower an animal learns, the longer any initial bias will continue to have an obvious effect upon performance.

In the present series of experiments, no animals were trained after removal of the basal lobes. Previous experiments (Wells & Young, 1965) have indicated a preference for rough in octopuses that were split as well as having the basal lobes removed.

DISCUSSION

Figure 6 summarizes the results of the extinction experiments reported above, in terms of object preference and the proportion of objects taken. The following observations can be made.

1. Normal animals take the smooth object more readily than the rough both when unrewarded and when in training.

2. This preference is still apparent, though somewhat less marked, in animals without the vertical lobes.

3. The preference for smooth is lost in split-brain animals and in those with the basal lobes and part of the inferior frontal system removed. During training some half-brain animals showed a distinct preference for rough.

4. In normal animals and those without vertical lobes the preference for smooth was approximately proportional to the tendency to take the objects when given without reward.

A preference is either learned or innate, something that the animal has acquired by experience in the course of its own lifetime or a consequence of its inherited construction, a property due to the nature of its sense organs, manipulative effectors or to the organisation of its sensory analysing apparatus. At the present time there is no sound basis for deciding between the two types of explanation.

The sense organs concerned in rough-smooth tactile discriminations are mechanoreceptors in the rims of the suckers (Fraser Rowell, 1963). These receptors are rapidly adapting and their output feeds interneurones in the arm nerve cords, which in turn send an abstract of tactile information received to the brain. There are at least one hundred times as many receptors in the suckers as sensory nerve fibres in the arm cords where these enter the brain (Young, 1965). Recordings from the interneurones in the arm cords show that the great majority of these are 'novelty units' responding only to *changes* in the pattern of stimulation of the suckers they represent. Their response to repeated input patterns rapidly habituates. Octopuses examine objects that they grasp by touching them with the suckers, repeatedly changing their grip as they do so. A smooth spherical object will give the same pattern of stimulation wherever it is touched; a similar object roughened by grooves will not. This would lead one to expect that rough objects would the more stimulating, other things being equal. It is interesting that this is so in the animals with reduced nervous system but that normally smooth is preferred. This suggests that the normal brain may perhaps as it were compensate for the tendency to take rough, allowing for learning in either direction. The reversal of preference after lesions may be a return to the uncompensated condition.

A comparable change in preference between black and white is seen in the visual system after removal of the vertical lobes (Young, 1968). This also might be interpreted as the removal of a compensating system, although we are ignorant of the relative stimulating values of the stimuli.

SUMMARY

1. Octopuses repeatedly tested at alternate trials with rough and smooth spheres presented without reward take more of the smooth than the rough spheres. The individuals that take most often show the greatest preference.

2. The overall tendency to take decreases within each session of sixteen trials and recovers by the next session some hours later.

3. There is a slight decrease in mean takes over the first few sessions but the level then remains at about 36 % over ten sessions of sixteen trials.

4. Animals without vertical lobes tested in the same way without rewards take more often (at 60 % of all trials).

5. As with the normals there is a decline in take within each session. Extinction is therefore not exclusively the result of changes in the vertical lobe.

6. The preference for smooth is less marked in animals without the vertical lobes than in normals.

7. Animals with the supraoesophageal lobes split by a vertical cut ('half-brain animals') and animals with the supraoesophageal lobes removed except for the buccal and ventral subfrontal take fewer objects than normal octopuses.

8. The same animals show reduction or reversal of the smooth preference manifest in normal octopuses.

9. Removal of the whole of the inferior frontal system produced animals that take more often than normal, at 63 % of all trials. These octopuses showed a marked preference for smooth. The system for release of objects is defective in these animals and this may act to give the appearance of excesss of takes of smooth.

10. The fact that blind but otherwise normal octopuses prefer smooth objects was confirmed in a discrimination training experiment. Normal animals trained with a smooth sphere as positive performed better initially than those trained in the other direction, though the asymptote reached was the same for both.

11. Animals without vertical lobes showed in training about the same preference for smooth as normals but were variable. They learned more slowly than normals.

12. Half-brain animals showed a strong preference for rough in training. The animals trained with smooth positive learned very slowly and had not reached the level of those trained with rough positive after 160 trials.

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