AN ESTABLISHMENT OF ASSOCIATION IN HERMIT CRABS, EUPAGURUS LONGICARPUS.

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Introductory.

The experiments described in this paper are the result, first, of preliminary observations of a number of hermit crabs kept for some time in an aquarium at the Woods Hole Laboratory, which showed them to be quite capable of profiting by experience. In fact, the results first obtained were in general quite confirmatory of those obtained by the subsequent more systematic investigation, the method for which they indicated.

BETHE¹ and YERKES² have each made experimental studies of habit formation in the Crustacea, the former on the crab, *Carcinus moenas*, the latter on the crawfish, *Cambarus affinis*, and on the green crab, *Carcinus granulatus*. BETHE at the end of his paper relates some experiments made to determine whether or not the crab possesses psychical processes, with the result that he asserts that it does not. This conclusion is not, however, necessarily to be accepted even from BETHE's own experiments, for the reason that these at best serve to demonstrate the absence of only *one kind* of psychical phenomena, viz. those of inhibition or control; other kinds may be present. BETHE himself does not recognize that the method he employed was defective in this respect, but an account of it will, we think,

¹ BETHE, A., Das Centralnervensystem von *Carcinus moenas*. *Archiv f. mikr. Anat.*, Bd. 51, 1898.

² YERKES, ROBERT M. and HUGGINS, GURRY E. Habit Formation in the Crawfish, *Cambarus affinis*. *Harvard Psychological Studies*, Vol. I. 1903.

YERKES, ROBERT M. Habit Formation in the Green Crab, *Carcinus granulatus*. *Biolog. Bulletin*, Vol. III. 1902.

make evident the justification of our criticism. His *first* experiment was to place a crab in a basin in the darkest corner of which there was an *Eledone* (a cephalopod). The crabs, because of their instinct to hide, moved immediately into this corner and were seized by the *Eledone*. Freed from its grasp one crab returned repeatedly five times, another six, to the dark *and the enemy*, showing, as BETHE thinks, that it had not profited by experience. It is to be emphasized, however, that to have done this latter in the way BETHE thought possible, it would have been necessary that the crab *inhibit* its instinctive action. This inhibition could take place only if, first, a *representation* of the pain of the seizure by the *Eledone* were present, and second (and essentially), if the *representation* were the "*stronger*"; the other possibility, that the representation should occur and yet be overcome by the instinct, is accordingly not disproved by BETHE's experiment. The same criticism applies also to his second method that, notwithstanding maltreatment on each such occasion, the crabs repeatedly seize food when offered.

The criticism above made is quite in agreement with that principle of method for comparative psychology which is in reality very simple, but not always observed, that in any instance where the question of the presence of consciousness in any species is *admittedly* to be decided by experimentation, this question must take a *particular form*, and our efforts must be directed to the establishment of the presence or absence of some definite kind of consciousness, e. g., associative memory between constructs of two sense fields, conceptual reasoning etc.

YERKES in his experiments with the crawfish made use of the labyrinth method. The subject could escape from a box into the aquarium only by "choice of a certain passage." The "choice" consisted in or was manifested by learning (by repeated experience) to avoid the blocked passage and gain the aquarium by the most direct path. Accordingly all conflict, requiring inhibition, between the two elements or "constructs" to be associated, viz., "correct path" and "aquarium," was ab-

sent. "Correct path," as opposed to the incorrect, logically implies in these experiments "aquarium"; and its selection, as shown by the ratio of improvement from day to day may, though not necessarily, imply the representation of the construct "aquarium," but it does demand the admission that acts of recognition and discrimination, or even of what LLOYD MORGAN calls "perceptual inference" take place. These in turn presuppose necessarily, as is well known, retention and production.

Carefully excluding the possibility of the crab's merely following a path by smell, taste, or touch (although if it did *only this* one could not account for a correct after an incorrect choice had once been made) YERKES found in one case that after 40, in another that after 250, experiences no mistakes in choosing were made. In a number of cases the subject turned from, before it reached, the partition which blocked the passage, thus showing the important part played by *vision* in directing the animal in the absence of smell, taste, and touch. All of these, however, together with muscular sensations, YERKES concludes *normally* play a part in the formation of labyrinth habits. These experiments therefore seem to show that upon the basis of the "constructs" which one sense alone, viz., vision, give the crab, a consistent selection of the correct path is possible; but this is explainable it seems, even if it is considered that only a recognition of each successive part of that path and consequently a discrimination between it and the incorrect is made, and yet that no *representation* or "*reconstruction*" of "aquarium" takes place, although of course this latter interpretation is not excluded.

A method of experimentation, however, which shows that in the formation of a habit, or in the learning of a motor reaction involving two sense fields, e. g., taste and vision, it is necessary to overcome an instinct or tropism in the opposite direction, such a method, we think, would at least give more cogent grounds for accepting the presence of *representation* than one not doing this, although even here conservatism in making this claim would be the safer course.

Some Characteristics of the Hermit Crab.

The genus *Eupagurus* is easily found in the shallower waters about Woods Hole and is represented by four species, *longicarpus*, *annulipes*, *acadianus*, *pollicaris*. *E. longicarpus* was selected for the present investigation on account of its convenient size ($\frac{3}{4}$ -1 $\frac{1}{2}$ inches in length) for aquarium purposes, and because of a manifestly greater brightness. Supplementary experiments show that *E. pollicaris*, e. g., learns with greater difficulty.

Members of the entire genus inhabit, under normal conditions, the shells of gastropods, by which the abdomen is completely protected, the cephalothorax alone protruding. This peculiar mode of life is correlated with a dextral asymmetry, which extends to almost all the organs of the entire body, and which shows a very nice adaptation. This favors the view that the asymmetry is a result of life in dextrally spiral shells, exemplifying at the same time degeneration.

The establishment of the fact that these Hermits learn is not surprising in view of the complexity and fineness of their physiological sense apparatus, which is essentially the same as that of all the Crustacea, so that it is very probable that any denial of this ability to any species of the group, even upon the basis of experiment, is due to incomplete or faulty methods of investigation.

Sense Organs.

The crab has only two general kinds of sense organs, viz., eyes and sense hairs, the latter of which are, however, differentiated as to their function. These hairs, which are found in all the extremities, are epithelial in nature, and are not penetrated by a nerve, but rather this latter spreads out underneath each epithelial group and gives to each cell a fibril. These epithelial sense cells lie in a support of "Matrixzellen,"¹ and according to variations in their structure and especially position are respectively gustatory, tactile, and auditory or "equilibra-

¹ VOM RATH, OTTO. *Zoologischer Anzeiger*, No. 386, 1892.

tory." The gustatory hairs, lie as two patches of "minute curiously flat organs" on the under surface of the outer filament of the antennules, the innermost appendages, which observation shows are kept moving constantly. There are no sense organs in the mouth.¹

At the basis of each antennule is a little sac formed by an infolding of the chitinous integument, communicating freely with the water, and containing little sand grains or otoliths. Here are present a second kind of sensory hairs, connected with the central nervous system by branches of the antennular nerve, and whose function is either that of audition or of equilibrium.² The third class of hairs are tactile in function, and are especially numerous on the antennae, i. e., the second pair of appendages, although there are some on the antennules, the other appendages, and the remaining integument.

The two eyes of the crab are compound or faceted and are seated on movable pedestals. They are covered by a transparent chitinous cuticle, forming a cornea; this is divided into facets, beneath each of which there is an ommatidium with two segments (a) an outer, which is vitreous and refractive, and an inner, a short retinula, which is sensitive, thus giving a structure analogous to rods and cones. These cones are surrounded and so separated from each other by a pigment; their apex is embraced by elongated cells in the midst of which is a fibril of the optic nerve. Each facet functions as a single eye and therefore like the vertebrate eye gives no sensitive continuum but, rather, "mosaic vision," i. e., various images in juxtaposition. The eye as a whole is supposed to give a vision of distinct objects and space relations.

The brain is formed from the first three pairs of embryonic ganglia, and is therefore a "syn-cerebrum"; it supplies the eyes, the antennules and the antennae with nerves. It is connected

¹ VOM RATH, OTTO. Zur Kenntniss der Hautsinnesorgane der Crustaceen, *Zoologischer Anzeiger*, 365, 1891.

² HENSEN (Studien über das Gehörorgan, *Zeitsch. f. wiss. Zoolog.*, Bd. 13, 1863) says they are auditory, while DELAGE, *Archiv. d. Zool. Expér.*, 1887, (2), T. 5, says they are for position and equilibrium. (Cited by VOM RATH.)

by two oesophageal branches with the central nerve cord, which is represented principally by a single large thoracic ganglion or concrescence of ganglia. The thoracic portion of the nervous system is, however, symmetrical. The mandibles, or the third pair of appendages, crushing jaws, the right of which is larger, the maxillae and the maxillipeds all receive nerves. The nervous system is therefore in general so constructed that it would seem at least reasonable to expect that associations might be formed.

Experimental

The systematic experiments by which the association between the "constructs" of two sense fields, taste and vision, was established, and a "reconstruction" or reproduction subsequently shown possibly to take place, were preceded by various preparatory observations, some of which were made in the summer of 1902. For instance, it was then shown that the Hermit is remarkably *thigmotactic*, for when a shell inhabited by a crab is suspended at the distance of about twice the diameter of the shell from the floor of the aquarium, the animal is thereby made decidedly uncomfortable, protrudes nearly its entire body, feels about, and usually leaves its shell, especially if there is a vacant shell near by. Suspended at the height of from eight to ten inches the crab will remain in the shell until it dies. They are also somewhat rheotactic. New shells thrown into the aquarium are soon examined and accepted at what would sometimes seem to be a disadvantage. This constant "desire" for change, together with both a great natural rapacity and pugnacity, are indeed indications of a strenuous life even among Hermits.

Both that series of observations upon which special emphasis is placed in this paper, and that preliminary one which showed that the method adopted would probably lead to satisfactory results, were made with a very simple apparatus and in a very simple way. A number of crabs which had been kept in an ordinary laboratory glass jar aquarium about twenty inches in diameter, were made to go into a darkened portion of this that they might get their food, which consisted of a freshly

cleaned *Fundulus* held in place on a wire. The same portion of the aquarium was darkened each time just before feeding by setting down into the constantly running water a screen consisting of two thin boards fastened at right angles, leaving only an opening at each end of the vertical board wide enough for the crabs to go through one by one; around the outside of the aquarium from end to end of this portion set off by the screen was kept a piece of heavy brown paper to shut out the light coming from the other direction. The only light which could enter came therefore through the openings at each end. Sand was placed in the bottom of the aquarium, and all the conditions such as its position and that of the tap, with the exception of the putting in and taking out of the wooden screen, were kept constant during the entire series of experiments.

These were conducted in detail as follows: to establish, first, an association and, second, present an occasion for possible "reproduction" from the "after-effect" of one by the external stimulus of the other "construct."

Thirty-six crabs of the species *Eupagurus longicarpus* were placed in the aquarium on July 30th, and, first, allowed until August 6th to become accustomed to aquarium conditions; during this period they were simply fed each day with a fresh *Fundulus*, no screen being used; they seized their food most eagerly, oftentimes fighting and driving each other away from it. The death of six selected the thirty most fit individuals. The crabs were, furthermore, observed to remain in the *lightest* part of the aquarium practically all of the time, i. e., they were positively heliotropic. The positive heliotropism was confirmed by a number of control experiments with other lots and by that of Aug. 6th. The screen was inserted and all the crabs, 30 in number, placed behind it. In 10 minutes 28 had gone through the opening into the light and 27 of these were near the point of its maximum intensity.

Each day following this, the screen was inserted, a fish on a wire placed in the darkened portion, and the number of crabs going into the dark through *either one* of the entrances at the end within a given time, which was constantly shortened during

the series, counted. A crab going in and coming out again was counted as *in*, but in every case by far the greater number that had entered remained behind the screen as long as the food was there. Two stimuli to two different senses, taste and vision were thus simultaneously and contiguously presented; and if this led to an association between the two "constructs," "food" and "screen-darkness," it would necessitate the *overcoming* of the natural positive heliotropism manifested at the start, and by contrast on this background the association would stand out more prominently. After the crabs were fed each

EXPERIMENT I.

Lot 2, *Eupagurus longicarpus*.

	Total No.	No. entering.	Per cent.	Time.	Per cent. in 1'
1st day	30	3	10	15'	.66
2d day	30	14	46	20' ¹	2.3
3d day	30	15	50	75' ¹	.66
4th day	30	20	66+	15'	4.4
5th day	30	25 ²	83	5'	16.6
6th day	30	27	90	5'	18.
7th day	27 ³	26	96	3'	32.
8th day	29 ⁴	28	97	5'	19.+

¹ This long time was granted in order, if possible, that the crabs might ultimately find their way *in* as a result, perhaps, of merely wandering around in their evident endeavors to localize the source of the taste stimulus, which in every case caused considerable agitation. The *varying length of time* used throughout the series was a matter of *best adapting the means* to the end. Thus it was quite justifiable to shorten the time later to 3' if the majority of the crabs went through the openings in that time, although to do this would give manifestly more favorable results than to wait longer.

² On this 5th. as well as on each successive day up to the 9th. it was noticed that as soon as the screen was put in, and the fish was placed behind it, the crabs were much agitated and some started for the openings.

³ The three that did not go in on the previous day had been removed for the purpose of determining if possible if there was already a certain permanency of habit among the twenty-seven entering; the result was confirmatory. The three were then returned.

⁴ One had died.

day under these conditions, fish and screen were removed, and the latter was carefully washed with running sea water, as it was also each time just before using. After a few days of this treatment immediately upon the insertion of the screen the

crabs became most agitated, some hurrying and scurrying about, others making almost directly for one of the openings. A preference for the right-hand one seemed to exist and this may be connected with the right-handed asymmetry. No attempt however to investigate this matter systematically was made, and there were no 'landmarks' in the aquarium, such as stones, etc., whereby a path could be learned. The preceding tabulated results show, (1) the total number each day, (2) the number going into the dark within (3) a certain time, when fed under the condition named, (4) the per cent. entering, and (5) for comparative purposes, the per cent. entering in one minute.

EXPERIMENT II.

Lot 2.

	Total number.	Number entering.	Per cent. entering.	Time.	Per cent. in 1'
9th day	28 { death of 1 }	24	86	5' ¹	17.2
10th day	28	22	79	5' ²	17.2
11th day	28	26	93	5'	18.6
12th day	28	25	89	5' ³	17.8
13th day	27	25	93	3' ⁴	31.
14th day	27	23 { in and remained }	85	3' ⁵	28.3
15th day	27	24	89	3'	29.6
16th day	27	22	82	3'	27.3
17th day	27	22	82	3'	37.3
18th day	27	22	82	3'	27.3

¹ At the end of the 5' the fish was put behind the screen in order that the association might not be broken up by the crabs entering and finding nothing there. When this was done all but one of the eight outside, four of which had gone in and come out again, entered within 2'. This was done each successive day.

² Then fed, and in 1' all but one had entered. This shows again the constant improvement, the learning taking place in a surprisingly short period.

³ In one minute after feeding all of the seven outside had entered.

⁴ After feeding all entered in 1½'.

⁵ After feeding all but one entered in 2'.

Accordingly, after the 8th. day, evidence having been thus secured that an association between the two "constructs," food and sense-darkness, had been established, its efficiency was

further tested by simply putting in the screen with no fish behind it, and the record of the crabs entering was taken in the same way as before. The results are tabulated above.

These results, if confirmed by control experiments, must, we think, be accepted as showing conclusively that the Hermit crab of the species *longicarpus*, firstly, forms an association between two sense-constructs, which, secondly, can be interpreted as showing that the crab, subsequently, when only one stimulus is presented, *reproduces* an image of the other. The same reaction, entering the dark, which previously demanded two stimuli, is later secured with only *one* stimulus; the other therefore must either be excited or reproduced. We may say perhaps that if, when only the screen is put in as in the second series, *only visual* perception or recognition takes place, then there is no reason why the crabs should not remain where they are, in the light, which is their natural preference. The screen, which they now recognize, has however through association come to mean for them other than something to be avoided; it means "food," and this meaning is present when the food is not. The difference between YERKES' experiments and these consists, therefore, in this, that YERKES' crabs "acquired the habit" of going by a correct path from a place disliked to a place liked; the Hermits on the other hand go from a place liked to a place naturally disliked, but "artificially" liked because of food either there or—may we say—"expected" to be there. This must mean that an associative element at first external, i. e., *physical*, but now no longer *that*, is, nevertheless, now present as *internal*, and its internal presence must be due to either an excitation or a reproduction by the other stimulus. If the latter, then the Hermit may be said to remember vaguely, i. e., to *reconstruct*.

These conclusions are strengthened by the following control experiments:

EXPERIMENT III.

Lot 4. Aug. 20th. Forty crabs in a similar aquarium; the same screen was used, carefully washed each time. The previous procedure was reversed here, by placing the crabs be-

hind the inserted screen first, and feeding in the light. From the data already obtained it would be expected that in this a greater per cent. of crabs would from the start make their exit than had in the first experiment made their entrance. This proved to be the case as the following record shows :

Number of crabs.	Exit.	Per cent.	Time.	Per cent. in 1'
40	34	85.	5'	17.
40	36	90.	3'	30.
40	35	87.5	5'	17.5
40	35	85.	5'	17.
40	34	85.	5'	17.

Comparison of this with Experiment I shows that not until the 5th. day was as high a ratio approximately obtained. In both cases of course the crabs are guided by taste ; the two experiments together, therefore, serve to demonstrate the natural preference for the light, and the quicker results obtained when this works with than when against the feeding instinct.

EXPERIMENT IV.

Lot 3. This same preference was demonstrated by a second control experiment. Twenty-four crabs were placed in a large rectangular aquarium directly next to a window with a northeast exposure. Half of the aquarium was darkened by holding down with a stone a box with one end taken out. Sand was placed over the entire bottom.

Twenty observations failed to discover a single crab inside the "dark line" from edge to edge of the box. The crabs, therefore, seem to prefer the light to the darkness, at least in the aquarium.

EXPERIMENT V.

Lot 6. A third very similar control experiment was also confirmatory. Thirty crabs, the aquarium jar and screen exactly as in Experiment I were employed. The question might arise, would not the crabs possibly "learn" to go behind the screen when this was inserted even though no fish was there, the necessary feeding being done at other times. Should they do this the conclusions from Experiment I would be quite

worthless. The results were that they would not enter. Ten observations were made; in seven of these cases no crab (within 5') went further than to the edge of the entrance, which had in no experiment been counted as "in"; of the three other cases, within the period of 5 minutes, 5, 8 and 5, respectively entered, but there was no evidence of progress.

ADDITIONAL EXPERIMENTS.

Maze Experiment. Can the Hermit learn to go through a maze for its food? A simple maze was constructed of thin boards in such a way that it was necessary for the crabs, 16 being used, to enter at one end, go through to the other, enter the second passage, go back to the other end and enter the food compartment. The crabs were first given an opportunity to "become acquainted" with the maze by leaving it in the aquarium about two hours. The next day this was repeated with the result given in the first line of the table. The results are as follows:

Total No.	Successful.	Per cent "in."	Time.	Average in 1'
16	All	100	90'	.9
16	13	81	45'	1.8
16	16	81	55'	1.47
16	15	94	30'	3.13
16	8	50	30'	1.66
16	15	94	45'	2.09
16	14	88	30'	2.93
14 (2 died)	13	93	30'	3.1

This experiment was not conducted as carefully as it would be possible to make it; the crabs could not be watched all of the time, but only occasional observations and a record, as the above, at a stated time, made. The results showed, however, though perhaps not as clearly as might be desirable, that an improvement had taken place, and they have a value, as being in general confirmatory of the first experiment.

Conclusions.

The Hermit Crab, *Eupagurus longicarpus*, is capable of offsetting by experience, in a rather short time, by associating

the "constructs" of two "sense fields," vision and taste. The existence of this association is proved by its effectiveness in subsequently bringing about, with only one stimulus presented, the same reaction against a natural positive heliotropism, as previously occurred with two stimuli present. The reaction here is therefore conditioned *internally*, as well as externally. The internal condition must be identical with either the excitation of, or with that and the reproduction from the "after-effect" of the second, the "taste-stimulus;" if there is only excitation then the internal event is only physiological; if there is also reproduction then it is psychical as well as physiological.

Both interpretations agree equally well with the data obtained, for the reason that even in the second case there must be a physiological basis for the psychical events if present, and consequently, the two being quite compatible as ultimately regular and uniform series of events, there is theoretically no certain objective criterion for the presence here of consciousness.

Practically there is, however, such an objective criterion which we make use of in our intercourse with other men, and if the above data are interpreted in as strict analogy to this as possible, it seems justified to consider that the Hermit Crab "reproduces" or, if one will, remembers vaguely.

The author, as a holder of one of its "research rooms" at Woods Hole wishes to acknowledge his indebtedness to the Carnegie Institution for the opportunities thus presented for the carrying on of this and other investigations.

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