New Series, No. 184 (Vol. 46, Part 4). Price [redacted]

FEBRUARY, 1903.

THE QUARTERLY JOURNAL OF MICROSCOPICAL SCIENCE.

EDITED BY

E. RAY LANKESTER, M.A., LL.D., F.R.S.,

HONORARY FELLOW OF EXETER COLLEGE, OXFORD; CORRESPONDENT OF THE INSTITUTE OF FRANCE AND OF THE IMPERIAL ACADEMY OF SCIENCES OF ST. PETERSBURG, AND OF THE ACADEMY OF SCIENCES OF PHILADELPHIA; FOREIGN MEMBER OF THE ROYAL BOHEMIAN SOCIETY OF SCIENCES, AND OF THE ACADEMY OF THE LINCEI OF ROME, AND OF THE AMERICAN ACADEMY OF ARTS AND SCIENCES OF BOSTON; ASSOCIATE OF THE ROYAL ACADEMY OF BELGIUM; HONORARY MEMBER OF THE NEW YORK ACADEMY OF SCIENCES, AND OF THE CAMBRIDGE PHILOSOPHICAL SOCIETY, AND OF THE ROYAL PHYSICAL SOCIETY OF EDINBURGH; HONORARY MEMBER OF THE BIOLOGICAL SOCIETY OF PARIS; DIRECTOR OF THE NATURAL HISTORY DEPARTMENTS OF THE BRITISH MUSEUM; LATE FULLERIAN PROFESSOR OF PHYSIOLOGY IN THE ROYAL INSTITUTION OF GREAT BRITAIN.

WITH THE CO-OPERATION OF

ADAM SEDGWICK, M.A., F.R.S.,

FELLOW AND TUTOR OF TRINITY COLLEGE, CAMBRIDGE;

W. F. R. WELDON, M.A., F.R.S.,

LINACRE PROFESSOR OF COMPARATIVE ANATOMY AND FELLOW OF MERTON COLLEGE, OXFORD: LATE FELLOW OF ST. JOHN'S COLLEGE, CAMBRIDGE;

AND

SYDNEY J. HICKSON, M.A., F.R.S.,

BEYER PROFESSOR OF ZOOLOGY IN THE OWENS COLLEGE, MANCHESTER.

WITH LITHOGRAPHIC PLATES AND ENGRAVINGS ON WOOD.

LONDON:
J. & A. CHURCHILL, 7, GREAT MARLBOROUGH STREET.
1903.

Adlard and Son,] [London and Dorking.

CONTENTS OF No. 184.—New Series.

MEMOIRS:

QUARTERLY JOURNAL

OF

MICROSCOPICAL SCIENCE.

EDITED BY

E. RAY LANKESTER, M.A., LL.D., F.R.S.,

HONORARY FELLOW OF EXETER COLLEGE, OXFORD; CORRESPONDENT OF THE INSTITUTE OF FRANCE
AND OF THE IMPERIAL ACADEMY OF SCIENCES OF ST. PETERSBURG, AND OF THE ACADEMY
OF SCIENCES OF PHILADELPHIA; FOREIGN MEMBER OF THE ROYAL BOHEMIAN
SOCIETY OF SCIENCES, AND OF THE ACADEMY OF THE LINCEI OF ROME,
AND OF THE AMERICAN ACADEMY OF ARTS AND SCIENCES OF BOSTON;
ASSOCIATE OF THE ROYAL ACADEMY OF BELGIUM; HONORARY MEMBER
OF THE NEW YORK ACADEMY OF SCIENCES, AND OF THE
CAMBRIDGE PHILOSOPHICAL SOCIETY, AND OF THE ROYAL
PHYSICAL SOCIETY OF EDINBURGH; HONORARY
MEMBER OF THE BIOLOGICAL SOCIETY
OF PARIS;
DIRECTOR OF THE NATURAL HISTORY DEPARTMENTS OF THE BRITISH MUSEUM; LATE FULLERIAN
PROFESSOR OF PHYSIOLOGY IN THE ROYAL INSTITUTION OF GREAT BRITAIN.

WITH THE CO-OPERATION OF

ADAM SEDGWICK, M.A., F.R.S.,

FELLOW AND TUTOR OF TRINITY COLLEGE, CAMBRIDGE;

W. F. R. WELDON, M.A., F.R.S.,

LINACRE PROFESSOR OF COMPARATIVE ANATOMY AND FELLOW OF MERTON COLLEGE, OXFORD;
LATE FELLOW OF ST. JOHN'S COLLEGE, CAMBRIDGE;

AND

SYDNEY J. HICKSON, M.A., F.R.S.,

BEYER PROFESSOR OF ZOOLOGY IN THE OWENS COLLEGE, MANCHESTER.

VOLUME 46.—NEW SERIES.

With Lithographic Plates and Engravings on Wood.

LONDON:
J. & A. CHURCHILL, 7, GREAT MARLBOROUGH STREET.
1903.

CONTENTS.

CONTENTS OF No. 181, N.S., JULY, 1902.

MEMOIRS:

CONTENTS OF No. 182, N.S., SEPTEMBER, 1902.

MEMOIRS:

CONTENTS OF No. 183, N.S., DECEMBER, 1902.

MEMOIRS:

CONTENTS OF No. 184, N.S., FEBRUARY, 1903.

MEMOIRS:

The Movements and Reactions of Fresh-water Planarians: a Study in Animal Behaviour.[1]

By

Raymond Pearl, Ph.D.
(Instructor in Zoology in the University of Michigan, Ann Arbor, Michigan, U.S.A.)

CONTENTS.

---

[1] Contributions from the Zoological Laboratory, University of Michigan, Ann Arbor, Michigan, No. 58.

A. INTRODUCTION.

THE present study has for its purpose the analysis of the behaviour of the common fresh-water planarian into its component factors. It is well known that, aside from the researches of a few investigators on a small number of forms, we have little detailed knowledge of the behaviour of lower organisms. It is coming to be realised, too, that knowledge of what an animal does is just as important in the general study of life phenomena as a knowledge of how it is constructed, or how it develops. But it must be admitted that until quite recent times the study of the activities of living things was a much neglected field in biology. The publication of the 'Origin of Species' gave the biological pendulum a swing towards the study of phylogeny, from which it is only just beginning to return.

As a consequence of this concentration of interest on other subjects, we possess an accurate and full knowledge of the activities of very few lower organisms. The behaviour of the Protozoa has been quite fully described and analysed by the work of Verworn ('89) and Jennings ('97, '99, '99*a*, '99*b*, '99*c*, :00, :00*a*, :00*b*, :00*c*, :01, Jennings and Moore :02). In the earlier work of Verworn the general features of most of the reactions of the Protozoa are described, special attention being paid to the rhizopods. The reactions of the Infusoria have been very thoroughly worked out by Jennings. In the case of the Infusoria we now know exactly the mechanism of the reaction to a large number of stimuli. The reactions and general behaviour in the case of two groups of echinoderms are quite thoroughly known from the early work of Preyer ('86, '87) on the starfish and the recent brilliant work of von Uexküll ('96, '96*a*, '99, :00, :00*a*) on the sea-urchin. These few instances are the only ones in the literature where the movements and reactions of an organism, or group of organisms, have been investigated in any comprehensive "monographic" way. There is a great body of literature dealing with isolated reactions in a variety of forms, but the thorough investigation of the activities of animals in a way comparable to that in which their morphology has been investigated remains in large degree yet to be done.

It appeared highly desirable that this sort of knowledge be extended, and it was with this idea in mind that this work was undertaken. The form used, Planaria, was chosen for several reasons. In the first place, it has come to be a sort of paradigm for work on regeneration, and its biology from that standpoint is already well known. Furthermore, in some one or more of its species it is an almost universally distributed form and can always be obtained in quantities. Finally, and particularly, it is a representative of an animal type about whose activities we know only the most general facts. It is a symmetrical aquatic organism of low organisation, and its behaviour is rather complicated. The importance of possessing a detailed knowledge of the activities of a bilaterally symmetrical, free-moving, low organism will be apparent when it is considered that such an organism has never been made the subject of such a study. The behaviour of typically unsymmetrical organisms, the Infusoria, has been analysed, as has also that of some radially symmetrical animals, and in both cases there is found to be a very close interrelationship between the general form of the body and the reactions.

To investigate, then, in a comprehensive way the activities of a bilaterally symmetrical organism standing low in the animal series was the purpose of this work. The most general problem which presents itself is the establishment of the animal's position in the objective psychogenetic series. Are its activities relatively simple or are they complex? Do they fall under the same general type as those of the Infusoria or those of the higher organisms, or do they occupy an intermediate position? Another general problem of importance is whether there is any marked correlation between the behaviour and the form of the body, such as has been found to obtain in so marked a degree in the case of the Infusoria and the rotifers (vide Jennings, loc. cit.). We have in the flat-worm a symmetrical animal; are its reactions of a symmetrical type? Besides these broad fundamental problems there are, of course, a large number of subsidiary questions which readily suggest themselves in connection with a work of this sort. These need not be specifically mentioned here, but will be brought out in the course of the paper.

As to the scope of the work as actually done, the following may be said:—The general "natural history" of the animal was studied as completely as possible. All the normal movements were studied in detail. The reactions to mechanical stimuli; the food reactions and reactions to chemicals in general; electrotaxis; thigmotaxis; rheotaxis; the righting reaction; the reaction of cut and regenerating pieces; and hydrotaxis and the reactions during desiccation were investigated. No work was done on the phototaxis or thermotaxis. A study of the phototaxis was omitted for two reasons; first on account of the fact that during the progress of this investigation Parker and Burnett (: 00) reported their work on the same subject, and furthermore on account of lack of opportunity. As a result of some incidental observations made during the course of this work, it has appeared that it would be profitable to extend the work of Parker and Burnett, and this, together with a study of the thermotaxis, I hope to be able to do in the future. Another field for further work is afforded in the study of the reactions of regenerating individuals. As this subject did not fall immediately into the general plan of this work, but comparatively little attention has been given to it, yet the work done gives much promise of important results to be gained by more extended investigations.

So far as possible the details of the movements and reactions will be described fully. It is not easy to see why there is not as much need for a complete knowledge of details in physiological work as in morphological, yet in much of the recent work in comparative physiology only the most general results are reported. To gain a knowledge of the details one must do the work over again. While such more or less general papers are easy to read, and put the main results in such a form as to be easily accessible, yet it is believed by the writer that the solid foundations of comparative physiology and psychology must consist of detailed "fine" work, just as has been the case in morphology. It seems to the writer that the tendency to abandon the detailed descriptive method in favour of the extreme experimental method in biological work is unfortunate. Both ways of working are methods of getting at the truth, and, as proven by their results, both are good methods. The current notion of the sufficiency of the experimental method to the exclusion of others is not only an evident exaggeration of the facts in the case, but, in the opinion of the writer, the exclusive use of the "crucial-experiment" method in work upon the movements and reactions of organisms has in some cases hindered rather than helped us to gain a clear understanding of the phenomena. The importance of close observational work in the study of animal behaviour has been strongly emphasised recently by Whitman ('99). The aim in the present work has been to get as extensive and detailed a knowledge as possible of the behaviour of the organism by direct observation before resorting to experiments.

At this point I wish to acknowledge my indebtedness to the officials of the laboratory in which this work has been done. To Professor H. S. Jennings, under whose general oversight this investigation has been prosecuted, I wish to extend my heartfelt thanks for his uniform kindness in freely giving advice, suggestion, and kindly criticism of immeasurable value. Any adequate expression of my indebtedness to him is impossible. I further wish to express my thanks to Professor Jacob Reighard for the numerous facilities which I have enjoyed during my stay in his laboratory, and for his kindly interest, which has made work there a pleasure. Finally, I desire to acknowledge my indebtedness to Professor F. C. Newcombe, of the Botanical Department of the University of Michigan, for many valuable suggestions and advice.

B. RÉSUMÉ OF LITERATURE.

But little has been done on the physiology of the movements or on the psychology of the Turbellaria, and, as in the case of most of the literature dealing with these subjects, what has been done has been in comparatively recent years. Investigators of the old "natural-history" school which flourished before the time when Darwin's work changed the course of zoology seem not to have given much attention to planarians, while the later systematists and morphologists for the most part carefully avoided any reference to the activities of the forms which they studied.

I. Morphological and Systematic.

Among the papers devoted primarily to the systematic or morphological treatment of the group, there are occasional references to points in the behaviour of the organisms which are of importance from the present standpoint. Amon such references the following may be noted:

Moseley ('74), in a paper concerned principally with the anatomy and histology of the land planarians, devotes a section to a discussion of the habits of these forms. He comments on the "avoidance of light" (negative phototaxis) of land and aquatic planarians, and discusses the habitat and food of the animals. He reaches the conclusion that all planarians are carnivorous, but gives no account of the method of feeding. He quotes Rolleston as having found that Planaria torva and Dendrocœlum lacteum in a dish in which had been placed a freshly killed earthworm "crowded on to the worm's body and soon sucked all the hæmoglobin out of it, leaving it white and pulpy." Brief mention is made of the habit of the land planarians of secreting a mucous thread and hanging from it as a mollusc does. Finally, the method of movement of Bipalium with the head raised and waved from side to side as the animal proceeds is described. A bibliography of previous literature is given.

In another paper Moseley ('77, pp. 273, 274) gives an account of the movements and general habits of Geoplana flava, a Brazilian species. This species was found to keep in shaded and moderately lighted places. The direction of the ciliary currents was tested by placing small bits of paper on the surface of the body, and it was found that when the animal was in active movement the effective beat of the cilia on the anterior part of the dorsal surface was forward and outward, while on the posterior portion of the dorsal surface the beating was backward and outward. The currents on the ventral surface were always straight backward. The author concludes that the function of the cilia on the dorsal surface is to quickly remove foreign bodies. When the organism was at rest there was no movement of the dorsal cilia; "the animal moves to a large extent by muscular action, the body alternately contracting and expanding during motion. When moving it lifted its anterior extremity often, ... and moved it to and fro as if to fee or see its way." "When the anterior extremity of the body was cut off the remainder of the animal seemed still to move with definite purpose, avoiding obstacles and retreating from the light, while the cut end was raised and thrust in various directions as if to search for an object on which to climb."

In a brief note Zacharias ('88) mentions the occurrence of Geodesmus terrestris between the lamellæ of Agaricus deliciosus. Particular points mentioned are: the slow movement, characterised by the raised anterior end, and the hanging by a mucous thread after passing over the edge of a glass plate. Light stimulation of the anterior end with a needle induces a very strong contraction of the whole body.

Gamble ('93), in a systematic paper on marine Turbellaria, describes briefly the movements of a number of species of rhabdocœles and triclads.

Lang ('84), in his monograph on the polyclads, devotes a chapter to the habits, movements, and natural history of this group of planarians (loc. cit., pp. 631—641). While not done particularly from the physiological standpoint and not treating the subject experimentally, this work contains numerous valuable observations. Points especially treated are the habitat, colouration, food and method of feeding, defecation, movements, including swimming, copulation, respiration, regeneration, growth, and duration of life. The details in the behaviour of the polyclads recorded in this monograph will be discussed later in connection with the points on which they have direct bearing.

The most important paper dealing with the movements and general behaviour of planarians which I have been able to find in the literature is that of Lehnert ('91). This work is principally devoted to an account of the biology of three forms of land planarians, viz. Bipalium kewense, B. kewense var. viridis, and Geodesmus bilineatus. Besides the work on these land forms, Lehnert also made some comparative studies on several fresh-water dendrocœles and rhabdocœles. He gives an admirably full and detailed account of the movements of land planarians; in fact, by far the best description of these phenomena in the literature. In this account the relation of the movement to the mucous secretion from the ventral surface of the body is brought out in great detail. The principal factors in producing the movement in the case of the land planarians he gives as (*a*) ciliary movement on the ventral surface, (*b*) rhythmical contraction waves passing longitudinally over the ventral surface, (*c*) secretion of slime, and (*d*) snake-like movements of the whole body. A comparison with the movements of other planarians (fresh-water) is made. In this connection it may be mentioned that Lehnert considered rhythmical contraction waves passing along the ventral surface of the animal to be a factor in the movement of fresh-water planarians (Dendrocœlum lacteum, Planaria polychroa, and Polycelis tenuis). This I am unable to confirm from observations on the planarians which I have studied. This point will be discussed more fully later. The food and the method of taking food in case of the land planarians, Lehnert worked out very thoroughly. They were found to be carnivorous, and in the case of Bipalium the pharynx was capable of being stretched over a large piece of earthworm, so that it resembled a very thin transparent skin covering it. The relations to other phases of the environment, e.g. air, water, temperature, light, solid bodies, etc., are described very briefly.

Raspail ('93), in a brief note, mentions the feeding of a planarian.

Van Duyne ('96) mentions briefly the movements of heteromorphic forms of Planaria torva (?). He found that the parts of two-headed individuals moved independently of each other, and that each piece would move away from the other until they had completely torn apart.

Willey ('97), in a brief note, describes the structure of a remarkable asymmetrical planarian, for which he proposes the generic name Heteroplana, having the left side of the body almost completely atrophied. Regarding the locomotion of this remarkable form he says, "In Heteroplana . . . . . the locomotion is usually conducted in a somewhat one-sided fashion," and he furthermore figures the animal as constantly moving towards the left. It is to be regretted that no reference is made to how this form reacts to stimuli, as it would be of great interest to know whether the reactions are asymmetrical, and in general how they compare with the normal planarian type.

A series of papers by Morgan ('98, :00, :01) contains numerous references of importance on the movements of cut and regenerated specimens of various fresh-water planarians. He finds ('98), in confirmation of van Duyne, that in two-headed individuals each head tends to move in its own proper direction. In the case of a heteromorphic form with two heads pointed in opposite directions, this likewise held true; but one component being stronger this determined the movement of the whole. The lack of movement in certain forms of cut pieces is also noted. In his :00 paper Morgan notes the readiness with which "Planaria, sp."[1] and Planaria maculata take food, although no account is given of the method of the feeding reaction. An interesting observation, and one of considerable theoretical importance, is also reported in this paper. In an individual split longitudinally in the median line from the posterior end forward, in which the two parts were united only by a small connecting band of tissue at the anterior end, it often appeared "as though these pieces would pull apart, but as soon as the tension on the connecting band becomes too strong, the rest of the piece, by a sort of adaptive response, ceases pulling in its former direction." In the most recent paper cited (:01) Morgan corrects a statement of Bardeen[2] regarding the feeding of Planaria. It is maintained (and I may mention at this point that my own observations agree entirely with those of Morgan) that Planaria "responds freely" to food sub-

---

[1] Later identified by Woodworth as Planaria lugubris.

[2] To be reviewed later.

stances not actually in contact with it. This point will be discussed in detail later.

Lillie (: 01) brings out the fact that cut posterior parts of the body of Dendrocœlum lacteum show very little movement, and in general fail to give the typical reaction to light after removal of the brain.

Finally, there are accounts of the natural history and habits of various planarians in numerous "natural histories" and text-books. As such accounts are for the most part brief and of no great significance from our standpoint, they will not be referred to in detail.

II. Physiological.

The literature dealing with the planarians from a purely physiological standpoint is very meagre. Furthermore, for the most part it deals only with special phases of the physiology of these organisms, there being very little work attempting to bring the behaviour of planarians into relation with that of other forms.

The most important work dealing experimentally with the physiology of the movements of flatworms which I have found is that of Loeb ('94). The purpose of his work was to determine in how far the reactions of such low organisms as worms were dependent upon the brain. The planarians used were Thysanozoon brocchii, and Planaria torva. In Thysanozoon he found that if the animal were quickly cut into two pieces transversely with a sharp scalpel or scissors the anterior piece crawled on undisturbed, while the posterior piece showed no further movement. The conclusion is then drawn that "Die Spontaneität der Progressivbewegungen ist also bei Thysanozoon eine Funktion des Gehirns." This form shows no definite "geotropic" reaction, but crawls about with the axes of the body forming any angles with the direction of gravitation. The very strong "stereotropism" (thigmotaxis) of the ventral side of Thysanozoon, which always tends to keep in contact with a solid body, is noted. This reaction is found to be independent of the brain. There was found to be co-ordination between the anterior and posterior pieces of a worm in which the lateral longitudinal nerves had been cut, but in which a narrow connecting strip of tissue had been left between the pieces. In P. torva Loeb states that posterior parts of the body which have been separated by a transverse cut from all connection with the brain crawl "ebenso munter weiter, wie die orale Hälfte." The reaction of this form to changes of light intensity is discussed in considerable detail, it being shown that in strong light the organism is stimulated to active movement, while in the shade it remains quiet or moves very slowly. This was found to occur as well in decapitated as in normal worms. The "stereotropic" reaction in this form is also mentioned. In concluding, the author holds that in worms there is no "associative Gedächtniss," and hence no consciousness. These results have been recently incorporated without essential change into a larger work (Loeb : 00).

In an earlier paper Loeb ('93) first described the reactions to light of Planaria torva. These results were incorporated without essential change into the '94 paper mentioned above.

Hesse ('97), in his morphological studies on the eyes of flat-worms, devotes a section to the subject of the reactions to light of Euplanaria gonocephala and Dendrocœlum lacteum. His results are confirmatory of Loeb's, nothing of particular significance being added.

Steiner ('98) found that posterior pieces of Planaria Neapolitana (= Stylochus pilidium, Lang) separated from the brain by a transverse cut would move about freely after recovery from the operation. He believes this ability to move is conditioned by the presence of ganglion-cells in other parts of the body than the brain (along the lateral nerve-cords).

Parker and Burnett (: 00) have recently made a thorough study, using very careful experimental methods, and treating the results statistically, of the reactions of Planaria gonocephala to light. This form moves away from the source of the light. The amount of directive influence was measured. It was found that specimens without eyes, i. e. in which the anterior end had been cut off, react in much the same way to light as do normal individuals, "in that they have a tendency to turn away from the course when directed towards the source of light, and to keep in it when directed away from the source, though with less precision, and often to less extent, than planarians with eyes." Furthermore, figures are given showing that planarians from which the anterior end has been cut off move more slowly than normal animals. This is thought to be due to the absence of the eyes.

The most extensive paper dealing with the physiology of planarians is that of Bardeen (: 01). This paper is mainly devoted to a study of regeneration in Planaria maculata, but before entering upon the discussion of this subject the author devotes considerable space to an account of the anatomy and physiology of the organism. In the section devoted to physiology, the author discusses, under the caption "Environmental Activities," sensation, movement, and the central nervous system. The author makes the remarkable, and obviously incorrect, statement that the planarian is sensitive only to light and contact. A very few inconclusive experiments having reference to thigmotaxis, geotaxis (?) and hydrotaxis, are reported. The statement is made that specimens "would remain unmoved by the presence close by their side of a piece of fresh snail, a food much prized by them." Two forms of movement are described—"swimming" and crawling. The author's description of what he calls the "swimming" movement will be discussed later in this paper. Brief and very general statements regarding the reactions to mechanical stimuli are presented. Under the heading "Internal activities" are discussed deglutition, food dispersion, defecation, and respiration, in a rather loose and hypothetical way. The author makes the following contribution regarding excretion in Planaria :—

"Excretion is carried in part through the intestines by the act of defecation; in part it is doubtless carried on by an excretory system opening on the surface." A more detailed discussion of various points raised by Bardeen will be entered into in connection with the parts of this work on which they have direct bearing.

A second paper by the same author (Bardeen, :01*a*) describes briefly the normal food reactions of Planaria, and shows that a decapitated specimen will not find food material in a dish, although one such a specimen could "be made to eat if it were placed on its back on a slide in a small drop of water. Under the conditions mentioned the pharynx is usually protruded, and will engulf bits of food placed in the mouth." An experiment was performed in which the part of the head in front of the eyes was cut off. Such specimens, from which merely the tip of the head had been removed, reacted normally to food. It is also shown that specimens from which the part of the body posterior to the pharynx has been removed feed like normal worms. Regarding the method by which planarians find food in their immediate vicinity, Bardeen says (p. 176), "It is difficult to determine the source of the impulse which gives rise to this purposeful activity. It is possible that the auricular appendages here act as delicate organs capable of stimulation by slight currents in the water set up by the minute organisms that prey at once upon the flesh of the dead snail." Experiments to be reported in the course of the present paper show, I think, that the mechanical and chemical stimuli given by food are the ones which affect planarians.

c. MATERIAL.

The following species have been principally used in this study:—Planaria maculata, Leidy; Planaria gonocephala, Dugès; Planaria dorotocephala, Woodworth.[1] Of these P. dorotocephala and P. maculata have been

---

[1] Excellent figures and descriptions of these three species have been published by Woodworth, '97.

most used, both on account of their abundance and, furthermore, because P. dorotocephala is a form particularly favourable for the study of reactions. It is very active, and after being disturbed continues in movement longer than either P. maculata or P. gonocephala, as has already been noted by Woodworth (loc. cit., p. 7). I have found also that it moves faster than either of the other two species. There is a general precision and positiveness of response in its behaviour which make it especially favourable for experimental work. A large number of experiments have been made with a view to determining whether there was any difference in the reactions of these three species, but no essential difference has been found. The form of the reactions is the same in all cases. Whatever differences there are are differences of degree, such as would be conditioned by the relative sluggishness and activity.

Certain forms of reaction to mechanical stimuli, and to chemical stimuli, are rather more easily induced in P. dorotocephala than in either of the others, yet, as will be shown later, these reactions will be given, under the proper conditions, by the other species. This being the case, and since P. dorotocephala was, for reasons noted above, most used in this work, it will be employed throughout the paper as the type form, and it will be understood, when there is no statement of the species, that P. dorotocephala is the form meant.

No account of the anatomy of these forms will be given here, because it has been very fully treated in other readily accessible papers. The most important papers dealing with the morphology of the fresh-water triclads are those of Jijima ('84), Lang ('81, '81*a*), Kennel ('88), Chichkoff ('92), and Woodworth ('91 and '97).

Besides the species mentioned above, on which the most of the work was done, a number of observations and experiments have been made on several other species of triclads and rhabdocœles. The other triclad most frequently met, and whose reactions have been found to agree closely with those of the species of Planaria, is a form which agrees with the description of Dendrocœlum lacteum, except in respect to the colour. This form is usually coloured from a light grey to nearly black. The colouring is uniform. In only one specimen have I found any deviation from this typical coloration, and in that case there was a band of black pigment extending the whole length of the body along the mid-dorsal line. In width this band occupied about one third the whole width of the body. The margins were a pure white, without the faintest trace of pigmentation. This specimen was kept under observation for some time, and there was no doubt that it belonged to the same species as the grey form. The specimen struck one at once as being transitional between the ordinary white to cream-coloured Dendrocœlum lacteum, and the grey form found about Ann Arbor. Being in some doubt as to the true taxonomic position of this grey species, I shall refer to it throughout this paper as Dendrocœlum, sp.

Besides the forms mentioned, several undetermined triclads have been collected and worked with to some extent, but as no new factors presented themselves in their reactions they will not be considered in this paper.

A large rhabdocœle, which I have identified as Mesostoma personatum, O. Schm., is found rather commonly in certain localities about Ann Arbor in the spring. I have done some work on this form. Another rhabdocœle whose actions I have studied to some extent is Stenostoma leucops, O. Schm. No detailed investigation of the behaviour of the rhabdocœles was made, but as opportunity offered they were used for comparison.

The methods used in experimentation will be given under the separate headings dealing with the reactions.

D. HABITS[1] AND NATURAL HISTORY.

In the course of more than two years' study of planarians

---

[1] In this section the word "habit" will be used to signify merely those activities of the organisms which are frequently observed to occur under

numerous observations have been made on their general natural history. It is thought desirable to present a general account of this here for two reasons: first, because there is no adequate discussion of the natural history of the fresh-water triclads in the literature; and furthermore, because it will bring out prominently the phenomena for which we are seeking an explanation. In other words, it will present the problems with which this study has had to do.

I. Occurrence and Distribution.

The species of Planaria (maculata, dorotocephala, and gonocephala) used in this study have been collected mainly from the Huron River near Ann Arbor. They are found, for the most part, on the under surfaces of stones in places where the current is of moderate swiftness, and the substrate on which the stones rest is rather soft. They are also found among the fronds of such water plants as Ceratophyllum and Elodea, although less abundantly than on stones. I have obtained these species only very rarely in collections from ponds and small pools of stagnant water. They appear to be, in general, much more abundant in shallow water than in deep.

Rhabdocœles I have found in great abundance in small ponds and pools of stagnant water, and, with the exception of Stenostoma leucops, almost never in running water. Dendrocœlum, sp., is also much more abundant in stagnant water than in streams.

There is no marked seasonal distribution of the species of Planaria studied. They appear to be slightly more abundant in the fall than in the spring. I have found no evidence of any migration into deep water during the winter in the case of these forms, as has been described by Child (:01, pp. 978—981) as occurring in Stichostemma. The seasonal distribution of Dendrocœlum, sp., appears to be well marked,

natural conditions, without necessarily implying the same idea as that embraced in the term "habit" as used by the psychologists.

individuals being found in considerably greater numbers in the spring than at any other time in the year so far as my observations go. This seems to be true also of the rhabdocœles.

Relatively the most abundant species of planarians in this region are Planaria dorotocephala and maculata. The numbers of these two are about equal, with a slight advantage in favour of P. dorotocephala. Next in abundance I have found to be P. gonocephala, but this is considerably below the other two. Finally comes Dendrocœlum, sp., which I have never found in an abundance to be compared with the species of Planaria.

II. Activities.

The movements of planarians will be discussed in detail in a later section of the paper,[1] but it is desired to take up here certain general activities and relations to the environment which properly fall under the general subject of natural history.

The first of these subjects is—

a. Sensitivity.—The flat-worm is extremely sensitive to a variety of stimuli. Among the different stimuli which produce specific reactions, and to which we must therefore conclude it is sensitive, are the following:—Mechanical disturbances of the general environment (shaking, jarring, movement of water, etc.), contact (localised mechanical stimulation), chemical changes in the environment (in the widest sense, including food substances), light, the electric current, desiccation, a current of water, and heat.

Its extreme sensitivity, which makes it responsive to very slight changes in the environment, may be shown by a very

---

[1] It may be stated here, for the convenience of the reader before reaching the full discussion of the movements, that the progressive movements of triclads are of two sorts. These are (*a*) gliding movements, in which there is little or no muscular action; and (*b*) crawling movements, in which the motion is effected by muscular contractions involving the whole body. The crawling has some general resemblances to the method of progression observed in a leech of the genus Clepsine.

simple experiment. If a dish containing specimens not in any way stirred up by rough handling, but gliding along the bottom, be jarred ever so slightly, every individual will instantly stop, contract, and remain immovable. If only a single jar is given, the worms will start after only a momentary pause. A further experiment shows more strikingly the same thing. If in a dish containing water to a depth of not more than 1 to 1·5 cm. a single specimen gliding quietly is selected, and a needle is touched to the surface of the water above or to one side of it, it will be seen, if closely watched, to give the same momentary pause and partial contraction. If the needle is pushed down through the water towards the worm in any but the quietest and gentlest way the contracted state will continue. Only at the moment when quietness in the surroundings intervenes again will movement be resumed. I have frequently tried to introduce a needle close beside the animal without causing this momentary pause. With a layer of water not over a centimetre in depth covering the worm I have not been able to do this, except in rare instances. After the point is once through the surface film it may be brought nearer the worm without causing a persistence of the contraction, provided it is advanced in line with itself, i. e. not slid up laterally. In order to observe this extreme sensitiveness to disturbance of the water one must take care that the animals have not been violently disturbed just previously. Any marked disturbance or persistent, more or less violent stimulation puts the animals in a condition which may be called, for lack of a better term, "excited." Such a condition is characterised by increased rapidity of movement and increased general activity, and in this condition the animals do not give the "finer" responses,—that is, responses to weak stimuli. I shall have occasion to discuss this matter in more detail later.

This marked sensitivity and its associated behaviour are remarkably similar to what has been found by Whitman ('99) to obtain in the case of the leech Clepsine. He has further pointed out that lack of attention to this extreme sensitivity, which is apparently quite generally distributed among lower organisms, may be an important source of error in work on the behaviour.

Regarding the statement of Bardeen (: 01, p. 14) that he does not find that Planaria "is sensitive to anything but light and contact," nothing need be said here. The detailed accounts of the reactions of the organism to a variety of stimuli which follow in this paper are in themselves a sufficient criticism.

b. Secretion of Mucus.—There is secreted at all times over the surface of planarians a sticky slime, apparently of the nature of mucus. This secretion is increased when the animal is irritated, and is under normal conditions more abundant on the ventral than on the dorsal side. If a needle or fine glass rod is touched several times on the surface of the body its end becomes covered with this secretion. For this reason it is necessary in applying localised mechanical stimuli to wipe the mucus off the end of the needle frequently, in order to obtain good results. Similarly, if one is using a sharp scalpel to cut the animals, if the edge is left in contact with the surface of the body any length of time before the decisive cut is made, the edge will become so coated with mucus that a clean cut is impossible; instead, the animal will slip from under the knife.

When the animal moves about it leaves behind a more or less heavy string of this mucus, so that if several specimens are placed in a clean glass dish the bottom will, in a short time, become covered with a network of interlacing mucus threads. The same phenomenon occurs in other Turbellaria and among the Nemerteans (cf. Child, : 01, and Wilson, : 00). The threads when first secreted are so transparent as to be invisible, but in larger quantities they appear opalescent, and may be picked out of the dish with forceps.

The function of this secretion in locomotion is evidently to attach the body to the substrate. Secretions for such a purpose occur widely among aquatic organisms.

The mucus also undoubtedly plays an important part in the attachment of the animal to the under side of the surface film. When the worm leaves the surface film in open water, i. e. when it cannot reach any solid body, it hangs by the mucus thread in much the same way that a terrestrial mollusc, like the common slug, does when it passes through the air from a higher to a lower point. This observation I have made many times, though generally in an indirect way. As has been said before, the mucus thread is invisible when first secreted, so that when a worm leaves the surface film it seems to glide freely through the water. If, however, one passes a needle horizontally through the water immediately above the posterior end of a worm which has just left the surface film, it will be seen that at a certain point (where the needle strikes the thread) the end of the worm will be jerked to one side. Furthermore, one may with care pick up the invisible mucus thread with forceps and raise the whole worm, provided the attempt is made before the anterior end reaches the bottom. I have seen specimens of P. maculata crawl back upon the thread after going a part of the way down to the bottom, and again regain a position on the surface film. The same thing is frequently done by slugs. When the animal has fully reached the bottom, connection with the thread which has served to suspend it in the water is usually broken by several sharp jerks of the posterior end of the body from side to side.

The relation of the organism to this slimy secretion is much the same in the land planarians, according to the observations of Lehnert ('91). He distinguishes in case of these forms "Kriechfaden," "Brückenfaden," and "Gleitenfaden" formed from the slime, the distinction being based on the relation of the thread to the surroundings. The "Kriechfaden" are the threads left behind as the organism moves over a continuous solid body, and the "Gleitenfaden" are the threads on which the animal hangs in passing through the air from a higher to a lower level. Both these forms of threads I have found in case of the fresh-water planarians. The "Brückenfaden," which are formed by the land planarians when they pass from one solid body to another at about the same level, I have never observed in case of fresh-water planarians, though I see no reason why under proper conditions they would not be formed. Lehnert (loc. cit., p. 17) says, "Die Wasserplanarien bilden wie die Landformen ihren Kriech-, Brücken-, und Gleitfaden." He also noted that Polycelis tenuis was able to crawl back upon a mucus thread after passing for some distance down over it.

Nothing like the formation of "cysts" from this mucus, such as Child (:01, pp. 989 to 993), found in the case of Stichostemma, has been observed in the case of planarians. Its only biological significance in these forms is in relation to movement, as pointed out above.

In connection with the subject of mucus secretion it may be well to point out the tenacity of the attachment of the flat-worm to the bottom. It will be found in attempting to dislodge the animal that the extreme anterior end and the extreme posterior end stick very firmly to the substrate. Whether this holding is the result of a sucker-like action of the ends of the body, or is due merely to the stickiness of the mucus, I have been unable to decide. It is easily possible that the muscles could be so contracted as to form out of either end of the body a practical sucker, but whether this is done or not it is impossible to say. Woodworth ('97) has described a permanent anterior adhesive disc in Dendrocœlum lacteum, but considers that this "is not a true sucker, nor does the animal employ its anterior end for the purpose of attachment to any greater degree than the posterior or lateral margins of its body, along the ventral surface of which numerous mucus glands have their openings. In truth, it is the margins and posterior end that adhere more firmly to a support; often when the animal is forcibly removed from the sides of the aquarium the parts of the margin or the posterior end will adhere so firmly to the glass that the points of attachment are drawn out into digitate processes." I incline to the view that in Planaria it is the mucus which attaches the organism to the support, although it must be said that the appearance is at times strikingly as if the anterior and posterior ends acted as suckers.

c. Periods of Activity and Rest.—There is in the case of freshly collected planarians a certain periodicity in the activities. First, there is the rather marked difference in the amount of activity in the night and day. It has been stated by a number of investigators that planarians were probably nocturnal in their habits, i. e. more active at night than during the day. This can easily be seen to be the case in the following way:—In a dish containing a large number of planarians, together with some plant material like Ceratophyllum, usually comparatively few specimens will be seen during the day. Nearly all will be in among the fronds of the plant material in a quiet condition. If, however, one comes into the laboratory at 8 p.m. or later at night, so that (in case of winter days) there has been two and a half or more hours of darkness, a large number of the specimens will be found on the sides and bottom of the dish in active movement. Again, one will frequently find in the morning that the specimens are scattered about all over the sides and bottom of the aquarium dish at rest. By noon many of these will have disappeared, or, in other words, gone in among the plants, where they are protected from the light.

Besides this day and night periodicity there is another fact that may be mentioned; this is that during the day, at any rate, they seem to be incapable of continuing movement more than a certain, not very great, length of time. Then a period of rest must intervene. Thus one may see a specimen which has been moving about come to rest, and after a length of time, varying from a comparatively few minutes to several hours, it will start into spontaneous movement again, and repeat the whole cycle over and over. It seems that the periods of quiet are really for the purpose of resting, i. e. the animal seems to be quickly fatigued by its own movements. This is indicated by the fact that if one stirs up a specimen, and sets it into activity again just as soon as it comes to rest, the periods of spontaneous activity will become progressively shorter, until finally the worm will only move a very short distance before coming to rest again. The periods of activity are longer and more frequent in P. dorotocephala than in any of the other species I have studied.

d. Formation of Collections.—There is a well-marked tendency for specimens of planarians to form well-defined groups or collections when they come to rest on an open surface like the bottom or sides of a glass dish, or on the under side of rocks, under natural conditions. Of course, this is in part a result of their reaction to light, as has been noted by Loeb ('94). Besides this there seems to be some other factor at work, for in the same dish one frequently finds several localised collections from one to two inches in diameter in different parts of the dish. In these collections the specimens may be closely packed together, and with some specimens overlapping and lying partly over others, yet in the species I have studied a looser arrangement of the character shown in fig. 1 is the more usual one. On the under surface of stones such groups are frequently seen; two or three may be found on the same medium-sized stone. In this case light as a factor cannot be present, since the conditions of all with reference to this stimulus are equal.

FIG. 1.—Diagram showing the appearance of a collection of resting planarians.

We have, then, here a case of what appears superficially to be "social instinct."

e. Movement on Surface Film.—As is well known, flat-worms and a number of other animals frequently move about on the under side of the surface film at the top of the water. On account of the flexibility of the support, motion under these conditions is very slow, and usually, after having been on the surface film for a short time, the worm will loosen its hold and pass down to the bottom in the way which has been described above. The worms do not remain customarily in the angles formed by the surface film with the side of the dish, as does Stichostemma (Child, :01), but instead pass out at once on to the free surface. Further, the flat-worms never push through the film at the side of the dish and pass up out of the water as the nemertean does. The occurrence of planarians on the surface film is not the result of any thigmotactic reaction (using thigmotactic in the sense ordinarily understood), but is brought about by a simple reflex act, and is the result of the configuration of the surface of the water and the side of the dish. This will be brought out in more detail later. It is probable that fresh-water planarians, in their normal habitat, very rarely take up a position on the surface film. Among other organisms (Entomostraca, Hydra, etc.) this habit probably has a much greater biological significance than in planarians (cf. Scourfield, '94, :00, :01). When on the surface film the worm behaves in nearly every respect as it does when on the bottom. The head is frequently raised (with reference to the worm) and waved about in the water just as occurs in the normal movement. That the situation is a more or less abnormal one, however, is shown by the fact that, so far as I have observed, the worm never comes to rest on the surface film, but instead, always keeps in active movement till it leaves it.

The means by which the animals maintain their position on the under side of the film is undoubtedly the mucous secretion from the ventral surface. This is very sticky, and holds the animal to the film, the surface tension being sufficiently great to support a considerably greater weight than that of a flat-worm.

It is interesting to note in this connection that the land planarians are able to move about on the top of the surface film of water to a limited extent (cf. Lehnert, loc. cit., p. 16). The immediate means of support here, as in the case of the fresh-water planarians, is the mucous secretion.

The leaving of the surface film by means of the mucus thread described above apparently does not take place if it is possible for the same result to be accomplished in any other way. Before it occurs the worm usually stretches the anterior end down into the water, and turns it in all directions. If it comes in contact with something solid the anterior end becomes attached to this, and pulls the posterior end of the body away from the film. If nothing solid is within reach the worm will usually, after a time, drop down on a mucus thread as described.

III. Food.

Planarians will take almost any sort of animal food very readily. I have used mainly, in the feeding experiments, crushed pieces of fresh-water molluscs, such as Physa, Planorbis, etc. One of these molluscs, removed from the shell and placed in a dish containing a large number of planarians, will, in a short time, be literally covered with the worms feeding. If a worm is gently lifted off the pile the greatly stretched pharynx will be brought into view. The worms will eat any other kind of animal tissue (fresh meat, parts of insects, pieces of fresh-water worms, etc.), so far as I have observed, the only condition being that the meat must be fresh. As will be shown later, the juices from the food act as chemical stimuli, so that it is necessary that the tissue be crushed or bruised so that its juices can escape into the water. A partially crushed specimen of Planaria, even though still able to move about, will be seized upon and eaten as quickly as any other food. I have several times seen specimens thus eaten. It is, in fact, possible, with a little patience, to make a specimen eat a small piece cut off the posterior end of its own body! This eating of each other does not occur, so far as I have observed, unless an individual is bruised so that some of the tissue underlying the epidermis is exposed. Under these conditions juices escape from the body and act as stimuli on the other worms. Under normal conditions contact of one individual with another does not start the feeding reaction, which is a purely reflex phenomenon, capable of being started only by a certain set of stimuli. Promiscuous cannibalism, such as Child (:01) suspects to occur among individuals of Stichostemma, I have seen no evidence for among the Turbellaria.[1]

In the feeding the worm lies fully distended, with the posterior two thirds of the body on the meat, or whatever else is being used for food; the pharynx is extruded, frequently to nearly half the length of the body, and its end is attached to the meat. During the feeding the very anterior end of the worm is attached to the bottom of the dish, provided the piece of food is not so large as to make this impossible.

Besides the animal food which the worms will take so readily, they also normally, probably to some extent, feed on vegetable matter, although I have not been able to induce the typical food reactions (to be discussed later) with vegetable material. The evidence for the statement that vegetable food is used by planarians is of two sorts: (*a*) specimens are frequently found extended on the stalks of water plants, with the pharynx extruded and attached to the stalks; and (*b*) the fæces which have been observed immediately after defecation have been found to consist largely of finely divided plant tissue. It would appear, however, that

---

[1] Bardeen (:01, A, p. 176) says, "Strong planarians often prey upon weak ones. In such instances the strong individual attaches its pharynx somewhere upon the body of the weak one, usually near the head." I have never seen even the largest specimens eat smaller ones unless these latter were bruised in some way.

vegetable food is not alone sufficient to keep the animals in good condition, for specimens kept in an aquarium dish with plenty of living plant material, on which they stay the greater part of the time during the day, will steadily grow smaller unless animal food is given them.

The food is in part digested, or at any rate softened, and physically changed outside the body. A piece of mollusc, on which a number of worms have been feeding for some time, has a white, fluffy appearance, similar to that of meat after partial gastric digestion. This is apparently brought about by a secretion poured out of the end of the pharynx. The necessity for some such action is apparent, because the flat-worm has no teeth or other means of separating a portion of ordinary tough fibrous tissue off from a mass so that it can be swallowed. This can be done, however, if the mass is first softened and partially dissolved. There are certain other evidences that a secretion is poured out from the pharynx during the feeding process. These will be taken up in another connection.

After the worms have fed undisturbed for a certain length of time they will leave the meat, and, after a short period of activity, come to rest.

The worms are able to live for a considerable length of time (at least two months) without food, although they continually grow smaller during this time. This marked decrease in size while starving has been noted by several observers, and especially studied by Lillie (:00). This author finds that the decrease in size is accompanied by a simplification of structure—a sort of "development backward," such as has been described by Patten ('96) for abnormal embryos of Limulus.

IV. Defecation.

The process of defecation has been observed by Bardeen (:01). The process consists of three or four general contractions involving the whole body, during which the contents of the intestine can be seen to be in rapid motion. Soon after the beginning of the contractions, which are in character different from any other of the movements of the body which I have observed, and which cannot be adequately described, the intestinal débris is shot out of the pharynx. The force of the expulsion is so great that the fæces spread out in the water some considerable distance from the opening of the pharynx. I have observed the process only a few times; apparently it occurs only at infrequent intervals.

V. Summary of Factors in Behaviour.

From the above sketch the behaviour of the flat-worm can be seen to be of considerable complexity. The movements show many variations in character, rate, and direction. The animal shows apparent preferences for certain situations while avoiding others. It reacts to a variety of stimuli in ways which, on the whole, further its preservation and well-being perhaps as well as if guided by careful thought. It chooses its food, taking certain things and passing by others. It forms gatherings of a sort which apparently indicate that the flat-worm prefers to be in the company of his fellows; in other words, it seems to have something of "social instinct." On the whole, as the further analysis will show, it fits itself to its environment by its activities in a way which would not be discreditable to a being possessed of considerable powers of reasoning.

Our problem now is to analyse, as far as possible, this complex behaviour into its component factors. Each activity will be taken up in detail and subjected to thorough scrutiny, to determine its essential nature, and whether it may not be resolved into simple components. With this analysis completed, it will be possible to assign the organism a definite position in the objective psychological scale. With the internal psychological factors—those of which there is no objective criterion—we shall not attempt to deal. The purpose of the paper is to furnish the data which may be obtained by an objective study of the phenomena: precisely what these imply as to internal factors would doubtless be a subject of dispute among psychologists of different schools.

E. Normal Motor Activities.

Under this heading will be included all the purely motor phenomena of the organism. This will include the movements (without reference to special reaction to stimuli), the coming to rest, and the general resting condition of the organism.

The movements naturally fall into two categories; (*a*) locomotor movements, and (*b*) non-locomotor, including such movements as contractions and expansions and the like.

I. Locomotor Movements.

As has been mentioned above (p. 19), there are two sorts of locomotor movements, the gliding and the crawling. The gliding is the smooth, even motion by which the flat-worm slips about over surfaces without showing a perceptible ripple of muscular movement. This is the characteristic movement when the organism is not particularly stirred up. The crawling is the characteristic movement when the animal is, or has been recently, strongly stimulated. It is a purely muscular movement.

a. Gliding.—The movement which I have called gliding is apparently the same as that which has been called "swimming" by Bardeen (loc. cit., p. 15), yet it must be stated that in all of my observations on a very large number of planarians I have never seen anything corresponding to some of the details which this author mentions in this movement. In the first place, he speaks of the worms moving progressively when not in contact with a solid body, i.e. of a movement freely through the water. This I am unable to understand, as I have never seen the slightest indication of the organism moving freely in the water without contact with a solid body or something which served the purpose of a solid (viz. the surface film). The only possible exception to this is the passage of the animals from the surface film to the bottom on a string of mucus, as described above. Furthermore, so far as I can find in the literature, no one else has ever seen a fresh-water triclad swim freely through the water.

The movement takes place with the body in contact with a surface either of a solid or of the surface film. There is, of course, between the ventral surface of the body and the surface on which it is moving, the thin layer of mucus which is constantly being secreted. It is in this mucus layer rather than the free water that the cilia beat.

This gliding movement is, so far as I have been able to ascertain, brought about by the action of the cilia on the ventral surface. There may also be some very slight muscular movement of the ventral body-wall comparable to that in the foot of a mollusc like Physa, which assists in the locomotion; but in the case of the flat-worm this factor, if it exists at all, is very insignificant. Only in a few instances have I been able to satisfy myself that any such movement was taking place, and then it did not have the characteristic rhythm seen in a mollusc. If this factor has any effect at all on the gliding movement it must be an extremely slight one.

The cilia beat strongly backward, i. e. towards the posterior end of the body. I have not been able to induce any reversal of the ciliary beats in these ventral cilia. Bardeen (loc. cit., p. 15) states that when the head is suddenly drawn back from some object the movement of the cilia on the antero-lateral margin of the head is reversed, and further suggests that "this reversed action may possibly be set up by the mechanical friction of the water." It would appear that the suggestion is the correct explanation, and that this is not a true reversal of effective beat.

The cilia which are mainly effective in producing the gliding movement are distributed on the ventral surface of the body, as shown in Fig. 2. There is a band down the centre of the body, which widens out at the anterior end so as to cover nearly the whole of the ventral surface of the head. The beat is the strongest down the median line of this band, and diminishes in intensity towards either edge until at the margins there is no ciliary movement at all. At the anterior end the cilia near the side of the head beat backwards and at the same time inward towards the median line, so that the currents take the course indicated by the arrows in that region in Fig. 2. The distribution and action of these cilia were made out by stirring finely powdered indigo in the water, and then either directly observing the ciliary action on these suspended particles as the animal glided on the surface film, or by indirectly observing it in a mirror placed below the bottom of the glass dish in which the worms were. Both of these methods gave the same results, and showed very clearly the distribution of the effective cilia.

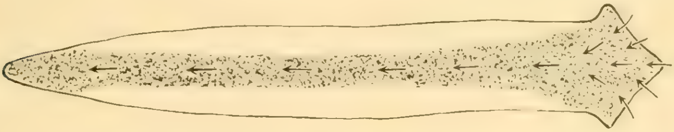

Fig. 2.—Diagram of the ventral surface of Planaria, to show the distribution of cilia. The stippled area is that which bears cilia. The arrows indicate the direction of the ciliary currents. (The pharynx is omitted for the sake of clearness.)

I have found no evidence of ciliary action on the dorsal surface of the body. Around the margins of the head there are cilia, but in other parts of the body, either on the dorsal surface or the edges, I have found no evidence of their presence. Particles of indigo dropped on the dorsal surface of a worm will remain in the same place for hours at a time. This is in striking contrast to the conditions in the land planarians as described by Moseley ('77), where the dorsal surface is thickly covered with cilia, which serve the purpose of keeping the body freed of foreign matter.

In the gliding movement the head is raised slightly from the bottom so as to form an angle with the rest of the body.

This position is shown in Fig. 3. As will be brought out later, the head is a particularly sensitive portion of the body, and apparently its elevation is related to its sensory function, in that it practically brings the head into close relation with a large environmental field. The head is not held in a fixed raised position, but is in constant though slight movement whenever the animal as a whole is moving. These "feeling" movements ("tastende Bewegungen") of the head are very characteristic. The head as a whole is raised and lowered, and turned from side to side, while at the same time the antero-lateral margins are moved up and down and extended and retracted. These "feeling" movements of the head region are usually very slight, and escape notice except under close observation. When the organism is much stirred up, however, they may become quite apparent. Their purpose is evidently to increase the chances of receiving stimuli, so that any stimulus in the neighbourhood may be quickly received. Constantly different sensory surfaces are presented to the environment. The head region acts in movement as a single great tentacle-like organ which is constantly testing the environment as the animal proceeds. At the same time the auricles are fully extended and raised. I do not think that this marked sensory activity functions so much for the protection of the organism against harmful environmental influences as it does to give prompt notice of useful stimuli,—for example, stimuli due to the presence of food material. In general it would not appear that such an organism as the flat-worm runs as great risk of elimination from enemies as it does from not finding food material for its own support. In the ctenophore Mnemiopsis Leidyi, whose reactions I have studied, no trace was observed of a reaction adapted to the purpose of getting the organism out of dangerous surroundings, but its only specific

FIG. 3.—Diagrammatic side view of a gliding planarian.

reaction is one which would bring it towards any food material which might be encountered.[1] While, as will be shown later, there is in the case of Planaria a reaction which is adapted to getting the organism out of danger, yet it is not called forth by so weak a stimulus as is the food reaction, and it is evidently for the purpose of receiving stimuli of the lowest intensity that the "feeling" movements are adapted.

In addition to the slight "feeling movements" of the head, described in the preceding paragraph, the organism frequently in the course of its gliding raises the whole anterior part of the body off the bottom and waves it about in the water. The portion of the body so raised may include the whole anterior half. The gliding is usually entirely stopped or very much decreased in rate while these waving movements are taking place. The head is swept from one side to the other and raised high in the water, covering a considerable area. This movement is also undoubtedly for sensory purposes.

In the gliding movement the body back of the head is kept in an approximately straight line; that is, there is no sinuous bending of the body such as is observed, for example, in Stichostemma (Child, loc. cit., p. 981), or at times in the movement of the earthworm. Furthermore, I have never observed any regular undulation of the margins of the body during movements such as take place in case of many polyclads, e. g., Leptoplana tremellaris (cf. Lang, '84). Bardeen (loc. cit., p. 15) seems to imply that such motions occur, and are an aid in the locomotion, but I am unable to confirm this statement. There are, of course, slight movements and changes of contour of the margins of the body, but they are not of a prominence or character to warrant thinking that they in any way contribute to the propulsion of the animal. In fact, it seems more probable that they are in part passive results of the motion of the whole body, and

---

[1] A brief preliminary account of the reactions of Mnemiopsis has been published in 'Science,' N. S., vol. xii, No. 311, pp. 927, 928, : 00.

in part the expression of local changes in the tonic contraction of the muscles.

In the gliding movement the body is in close contact with the surface along which the animal is moving. When an animal passes from the resting condition into movement one can see the body lengthen and flatten so as to hug the surface. By observing with a compound microscope an animal gliding along the vertical side of a dish so that the edge is brought sharply into view, the closeness of the contact of the margin of the body with the surface can be well seen. Furthermore, in specimens in which the posterior part of the body has been split longitudinally in the middle line to a point just behind the head, it is found that the half of the body which is determining the direction of the movement is always in close contact with the surface, while the other half only lightly touches it.

It would appear from all the observations which have been given that the gliding movement is brought about in the following way :—The ventral surface of the body constantly secretes mucus in greater or less quantity. This mucus can be shown experimentally to be very sticky immediately after it is secreted into the water. As it is secreted under normal conditions it immediately sticks to the surface on which the animal is reposing. Thus there will be constantly between the animal and the surface on which it is moving a layer of mucus which is adherent to the substrate. We can think of the lowest part of this mucus layer where it is stuck to the surface as of denser consistency than its upper layers which are in contact with the animal. In this upper layer of the mucus the cilia are beating and constantly pushing the animal forward. Of course, what really takes place is that the cilia are pushing the secreted mucus backward, but as this layer of mucus becomes fixed to the substrate as soon as it is secreted, the practical result is that the animal is pushed ahead. This relation is shown in Fig. 4. A represents a side view of a gliding worm ; D is the substrate ; C the cilia on the ventral side of the organism ; and B the mucus secretion, represented disproportionately exaggerated in thickness. This sticks to the surface of the substrate, and the backward beating of the cilia drives the worm ahead.

1. Rate of Gliding Movement.—There is no very marked difference in the rate of the gliding movement in case of the species of Planaria studied. On the whole, specimens of P. dorotocephala move more rapidly than do those of the other two species, but there are large individual differences in this matter. Active specimens of Dendrocœlum, sp., move much faster than any other planarians I have observed. Large specimens of this form will sometimes glide along with simply amazing rapidity, not showing the slightest tremor of the surface of the body.

As to the absolute rate of the crawling, some statistics

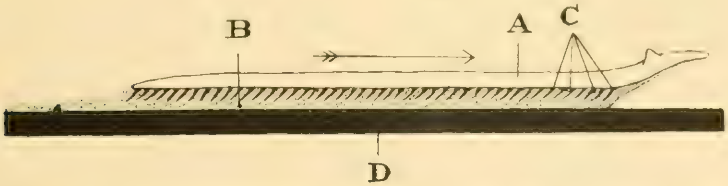

FIG. 4.—Diagram to show the mechanism of the gliding movement. A represents a specimen of Planaria seen from the side; B, the layer of mucus secreted by the animal. (This layer is represented as greatly exaggerated in thickness in proportion to the animal.) C, cilia. D, the substrate. The arrow indicates the direction in which the organism is moving. For further explanation see text.

have been collected and will be presented. The statistics were obtained in the following way:—A paper was ruled into centimetre squares; over this was placed a flat Petri dish containing the worm to be tested. Normal active specimens of P. maculata were used, and nothing was put into the dish but fresh clean water. The experiments were performed at night, and the source of illumination was a 16-candle power electric light enclosed within a ground glass globe. This lamp was 35 cm. above and 35 cm. distant in a horizontal direction from the centre of the dish, so that the light struck the animal at an angle of approximately 45° on its dorsal surface. The worm was allowed to get into an even, normal glide, and then to come around, as it usually would in a short time, so that it was headed in the direction of the light. Then the time which it took the worm to glide three centimetres was taken by means of a stop-watch. If the animal started crawling, or abruptly changed its direction, the trial was ruled out. The average rate in millimetres per second determined in this way from twenty trials on two individuals is 1·34. This rate is considerably higher than those obtained by Parker and Burnett (:00) for P. gonocephala. In that form they found a rate of 1·04 mm. per second in the case of individuals moving toward a horizontal light; 1·12 mm. per second when movement was away from a horizontal light, and 1·08 mm. per second when the animals were moving under a vertical light. There seems to be a well-marked correlation between the size of individual and the rate of gliding, as would be expected on general grounds, and is apparent from merely qualitative observations on the movement. One of the specimens from which observations were taken was 11 mm. long when extended, and its rate of gliding was 1·48 mm. per second; while the other specimen, which was only 6 mm. long when extended, showed a correspondingly slower rate of 1·23 mm. per second. The statistics are, of course, very meagre, and are not offered for any other purpose than to give a concrete idea of the approximate rate of the gliding movement. A thorough quantitative study of this matter of the rate of movement in planarians and other related organisms, and of the effect of different agents on the rate, would, I believe, be very interesting, and might lead to valuable results. I hope to be able to make such a study at some future time.

Lehnert (loc. cit., p. 17) gives a table of the rate of movement (presumably in the case of the fresh-water forms the rate of the gliding movement) of several species of flat-worms. He gives no account of how the data were collected, but his values may be inserted here for the sake of comparison. His rates for Bipalium kewense and B. kewense viridis are—Usual rate, 1 to 1·33 mm. per second; occasional rate, 1·83 mm. per second. This agrees very closely with the rate for P. maculata given above (1·34). His rates for Geodesmus bilineatus and Dendrocœlum lacteum are considerably slower (0·5—0·66 mm. per second and 0·75—1·33 mm. per second respectively). Polycelis tenuis (1·66—1·83 mm. per second), Planaria polychroa (2·16—2·5 mm. per second, exceptionally 3·33 mm. per second), and Mesostomum tetragonum (2·66 mm. per second) show a markedly faster rate than the forms I have studied.

Regarding the effect of different agencies on the rate of the gliding movement no special study has been made, and I can only report a few incidental observations. Such a study should be made by exact quantitative methods, and this I have not had the opportunity to do. What the effect of light on the rate is, it seems to me, impossible to say with entire certainty. Cole and myself[1] have found that light of great intensity (that obtained from a projection lantern with an electric arc as its source of illumination) causes a definite increase in the rate of gliding, but this increase has not been measured. The results of Parker and Burnett do not help us to answer this question of the effect of the intensity of light on gliding, as they are concerned only with the direction of its rays. The well-known phenomenon of "Unterschiedsempfindlichkeit" for light which Planaria shows (Loeb, '93, et al.) would indicate that increased light causes increased rapidity of movement. The electric current causes a very marked diminution in the rate of gliding in the weakest intensities which affect the organism at all. The effects of chemicals on the rate of gliding are not altogether uniform. Solutions of all chemicals tried with this point in view, when above a certain strength, caused a marked diminution in the rate of the gliding, or else an entire inhibition of it, and the substitution of some other form of movement. The action of weak solutions varied with the different substances. Very weak acids slightly increased the rate. Weak sugar solutions had no observable effect so far as rate of movement was con-

---

[1] Unpublished observations.

cerned. Copper sulphate causes an entire inhibition of the gliding movement in moderately weak solutions, even when these are not immediately fatal. Weak mechanical stimuli applied at the posterior end of the body cause a slight increase in the rate of gliding, but this is not marked, as any decided stimulus in this region of the body causes the crawling motion to supervene.

It is probable that the various agents affect the rate merely by causing changes in the general tonus of the animal. There is much evidence to support the view that the rate of gliding of an individual is a direct function of its tonic condition. Thus in the resting condition, which is characterised by a general lowering of the tonus, as will be brought out later, there is little, if any, ciliary movement. Again, after operations which result in lowering the tonus, the gliding is very slow or entirely absent.

2. Direction.—The direction of the gliding is, so far as my observations go, always forward. I have never been able to make the animal glide backward. This is in agreement with the finding of Child (: 01) in the case of Stichostemma. It, of course, indicates that the effective beat of the cilia cannot be reversed. In the case of the planarians on which this work was principally done, a lateral change of direction of movement is not brought about by the stronger beating of the cilia on one side. In other words, when the animal turns to one side it does so by a muscular bending of the body in that direction, and not by ciliary action. In an undetermined species of triclad, however, I found that the most usual method of turning towards one side was by the stronger beating of the cilia on the opposite side of the body. As an individual was gliding along the bottom of the aquarium dish it would swerve off at an angle to its former course without bending its body in the slightest observable degree.

b. Crawling Movement.—The second form of locomotor activity, the crawling movement, is distinctly a muscular movement. It takes place only when the animal has been stimulated in certain ways, and is of much less frequent occurrence than the gliding.

The crawling is always induced when the posterior end of the body is strongly stimulated. The characteristics of the movement are as follows :—If the posterior end of a worm which is gliding smoothly along is touched with a needle the posterior half of the body immediately contracts longitudinally ; an instant later the anterior end stretches out far in front and fastens to the substrate. Then there is a longitudinal contraction which begins just back of the head and runs posteriorly. This, of course, at once draws forward the posterior part of the body, and as this comes forward and gets a hold on the surface on which the animal is crawling, the anterior end is again extended far in front and attached to the substrate. This process is repeated until the animal settles down into the regular glide again. It consists essentially in a stretching out of the head followed by a pulling of the body forward by an active muscular contraction. When the animal is very strongly stimulated the portion of the body posterior to the pharynx usually takes no part in the crawling after the first general contraction. In fact, the posterior half of the body may even be held slightly raised off the bottom, while the region between the head and the origin of the pharynx is actively expanding and contracting and sending the body ahead. These strong expansions and contractions of the anterior end which make up the crawling movement may follow each other in rapid succession as described above, or there may be a considerable interval between one contraction and the next. In this interval the body as a whole keeps moving ahead as a result of the ciliary action ; that is, the gliding movement continues during the crawling, so that the latter may be regarded as an additional movement for the purpose of advancing the animal faster than the gliding alone can do it. The crawling may take place, however, with the ciliary beat entirely stopped.

The duration of the crawling movement after it is induced is usually rather short. A single strong stimulus at the posterior end of the body—such, for example, as is given by running a needle through the body—will not usually cause more than three of the strong contractions of the crawling movement, and then the animal will relapse into the usual glide. The limits in this matter I found to be from a single contraction and expansion as a minimum up to six or seven as a maximum. This is, of course, in response to a single stimulus only. By repeating the stimuli the animal may be made to continue the crawling indefinitely.

The effective rate of this form of progression is faster than that of the gliding movement. The crawling rate of one of the worms used for the measurement of the rate of gliding (the specimen 11 mm. long) was measured in the same way as was the gliding rate. The worm was stimulated with a needle at its posterior end just enough to keep it crawling, i. e. prevent it from settling into the regular glide. The average rate of the crawling was found to be 1·66 mm. per second. Merely qualitative observation shows that the worm gets along somewhat faster in the crawling than in the gliding.

1. Direction.—The crawling may take place so as to carry the animal either forward or backward. The backward crawling is induced by very strong stimulation of the anterior region of the body. It does not always occur even after such stimulation, there being apparently some individual differences among the specimens in this respect. One factor which will call forth persistent backward crawling is partial desiccation. If the dorsal surface of the organism is allowed to dry, it will attempt to crawl backward violently. The mechanism of the backward crawling is just the reverse of that which obtains when the animal moves forward. The posterior end is extended and fastened to the bottom; then a wave of contraction, starting in this case from the posterior end, draws the remainder of the animal backwards, and then the posterior end is again extended. The backward crawling is usually induced when the worm is excessively stimu-

lated or injured at the anterior end. This movement almost always occurs when the head is cut off, and may usually be induced in such decapitated specimens for a considerable period after the operation by stimulating the anterior end. The backward crawling is not so rapid as the same movement forward. The reason for this appears to be that the posterior end is unable to take so firm a hold upon the bottom as does the anterior end. The backward crawling is usually not very long continued, the animal soon coming to rest. The inability of the animal to glide in a backward direction should, of course, be noted in this connection. Strong chemical stimulation of the anterior end will cause the backward movement to appear in some cases. Light, so far as I have observed, will not, nor will the electric current. There is considerable variation as to the appearance of this backward crawling. Some individuals cannot be induced to do it at all, or only in a very slight degree, while others will crawl backward for considerable distances after injury to the anterior end. It appears to be a complex of reflexes which under normal circumstances is inhibited, and only appears in any pronounced way under comparatively rare conditions. It is not, as might be expected, a method ordinarily used by the organism to get out of danger. This is one of the cases quite frequently met where an organism has among its available assets, so to speak, a reaction which is well adapted to a certain end, but of which use is not made at all, or but very little.

2. Stimuli which induce Crawling.—It may be said in general that almost any strong stimulus applied to the posterior portion of the organism causes the forward crawling movement to appear. Mechanical and strong chemical stimuli applied in this region will do this. Light, either of ordinary intensity, or of such high intensity as that from an arc light, so far as I have observed, will not cause the crawling movement. The electric current does cause it, but greatly diminishes the rate. Any operative treatment—as, for example, cutting the body in two in the middle—almost in-

variably causes the portion in front of the cut to advance by the crawling movement, and, as has been mentioned in the preceding section, at the same time frequently causes the posterior piece to crawl backward. There is no reason to suppose that the operative procedure acts in this respect in any other way than merely as a strong mechanical stimulus applied at the point of the cut. Other stimuli which induce the backward crawling have been taken up in the preceding section.

c. Movement on the Surface Film.—Motion on the surface film is practically confined to the gliding movement. This gliding is slower in rate than that on the bottom, largely on account of the greater flexibility of the surface on which the animal is moving. While the mechanism of the movement is the same in the two cases, the surface film is elastic, and does not give so firm a basis as does a solid body. The effect of this elasticity of the film is very well seen when the animal attempts to change its course and turn to one side. The film offers little resistance to the posterior end, so that this cannot easily serve as a fixed point for the anterior part to turn about. Furthermore, in case the anterior end is left in contact with the film when the turn is attempted, as is usually the case, there is almost as much resistance against this turning of the anterior part as there is resistance to hold the posterior end fixed as a pivot support. The consequence is that the worm is unable to change its direction of movement quickly when on the film, and it has to go through a succession of muscular twists and jerks towards one side before the result is attained. I have not been able to induce well co-ordinated crawling movements in a worm while on the surface film. The preliminary contraction of the posterior part of the body occurs when that region is stimulated, but the subsequent stretching out of the head and drawing up of the body does not usually follow. I have tried stimulating both the exposed ventral surface of the animal and the dorsal surface from below, but neither method is effective. The reason for this is probably to be found again in the elasticity of the film. The anterior end is unable to get any firm attachment so that the rest of the body may be drawn forward. Furthermore, similar resistance is offered to the stretching of the head forward as to the turning of it towards one side.

When the animal is gliding on the surface film the same raising of the head (with reference to the worm, of course: in this case, a lowering with reference to the centre of the earth) and waving it about in the water occurs as under normal circumstances. In some cases two thirds or three fourths of the whole body will be thus raised and waved about, extending itself to its utmost capacity, and apparently seeking some solid body on which to attach itself. In these cases only a small portion of the very posterior end of the body will be left in contact with the film to support the whole.

On coming to the side of the dish when gliding on the surface film, the worm almost invariably leaves the film and turns down the side of the dish. The reaction which is the cause of this and of the organisms passing from the side of the dish on to the film will be brought out later.

d. Relation of Movements of Triclads to those of other Forms.—In respect to their movements, the triclads studied occupy a somewhat intermediate position between certain other groups. The rhabdocœles are in general characterised by free movements in the water, brought about by cilia covering the whole body. Their movement in general features resembles that of the holotrichous Infusoria. A type showing well this class of movement among the Turbellaria is Stenostoma leucops. The movement is not at all or very little dependent upon muscular activity. On the other hand, the movement of many of the polyclads is characteristically muscular. An example of this is found in the case of Leptoplana tremellaris, where the movement is largely effected by the rhythmical beating of the margins (cf. Lang, '84). In fact, this form of movement has become so well developed in these animals that we may think of the margins of the body as special locomotor organs. Ciliary action plays little if any part in the movement of such a form. It is to be noted, however, that both the rhabdocœles and the polyclads are capable of performing true swimming movements, i. e. movements free in the water without contact with any solid body. In the fresh-water triclads, especially of the genera Planaria and Dendrocœlum, the cilia have become much diminished in comparison with the rhabdocœles, and are restricted to a portion of the ventral surface only. Consequently they are not numerous and strong enough to support and move the disproportionately heavier body freely through the water. The movement of the cilia merely serves in these forms to propel the body while insufficient to support its weight. Consequently we find the principal form of movement to be a gliding over the surfaces of solid bodies.[1] On the other hand, the fresh-water triclads have not attained the high development of muscular locomotion which the polyclads have. There is a purely muscular movement in their case, but it is not by far the most important form of locomotion, and is not so highly developed as is that of the polyclads. Evidently, then, the fresh-water triclads seem to form a transitional stage in respect to locomotor phenomena between the rhabdocœles on the one hand, where purely ciliary locomotion obtains, and the polyclads on the other hand, where we find the locomotion largely if not entirely muscular. Whether this has any phylogenetic significance is not certain.

The land planarians occupy a position very similar to that of the fresh-water forms so far as their movements are

---

[1] I do not wish to imply, in this discussion of the different forms of movement as related to the number and distribution of the cilia, any belief that structure gave rise to function or function to structure. I wish merely to point out the evident correlation which exists in the matter. It seems to me most probable that structure and function changed together; but in this, as in many other similar cases, positive evidence is lacking, and consequently attempts to settle the phylogenetic development of the phenomena would appear to be fruitless.

concerned. There is, however, a noteworthy difference between the two groups. In the movements of the land planarians the muscular factors (rhythmical wave motion of the ventral surface, and snake-like movements of the whole body) are more important relatively to the ciliary component than in the fresh-water forms. In these land planarians there is evidently the beginning of the characteristic rhythmical wave motion of the part of the body in contact with the substrate, which reaches its highest development in the case of the Mollusca.

II. Non-Locomotor Movements.[1]

Under non-locomotor movements will be included the phenomena of contraction, expansion, "feeling movements," movements of the pharynx, etc. The purpose of discussing these phenomena, which are not immediately included in the general standpoint, is to give an account of their mechanism which may be referred to in succeeding portions of the paper. These movements are the physiological foundations on which the locomotor movements and the reactions are based, and it is necessary to determine their mechanism in order to bring the analysis of the behaviour to completion.

a. Contraction of the Body.—By the term "contraction of the body," when applied to forms like the flat-worm, is usually meant the shortening of the body lengthwise. In the flat-worm this movement is brought about by the contraction of the longitudinal muscle-fibres. It may involve the whole body or only a portion of it. Most frequently only a part of the body contracts longitudinally after stimulation; thus, if the anterior end is rather strongly stimulated in the middle line, the resulting contraction will usually involve only the anterior third of the body. In this longitudinal contrac-

---

[1] In discussing the musculature I have used throughout the nomenclature of Jijima (loc. cit.), in whose paper a very full description of this system will be found. I have identified in sections of P. maculata the following groups of muscle-fibres:—(*a*) outer longitudinal, (*b*) circular, (*c*) oblique (?), (*d*) inner longitudinal, (*e*) dorso-ventral, (*f*) transverse.

tion all the sets of muscle-fibres other than the longitudinal must be relaxed completely, because as the animal shortens it grows broader and thicker, which would be impossible if the ring, or transverse or dorso-ventral musculature, also contracted. The longitudinal musculature is apparently better developed and more effective on the ventral side of the body than on the dorsal, because after very strong stimulation of the anterior end there is a well-marked tendency for the middle portion of the body to be raised and the head somewhat curled in under it. This relation is shown diagrammatically in Fig. 5. This curling under of the head does not appear to be a specific reaction, but, on the contrary, merely an expression of the fact that the ventral musculature is capable of shortening its side of the body more in maximal contraction than the dorsal side. Jijima (loc. cit., p. 378) finds, from a histological study of the musculature, that the bundles of fibres in the main longitudinal muscle layer are thicker on the ventral than on the dorsal side.

FIG. 5.—Diagram showing the appearance in side view of a maximally contracted planarian.

b. Extension of the Body.—The mechanisms by which extension of a soft-bodied animal is brought about are probably very different in different groups. In the case of the flat-worm extension is produced by the contraction of the circular muscular layers surrounding the body, and of the transverse and dorso-ventral systems of musculature. Probably also the oblique musculature, when present, assists, by its contraction, in the extension of the body. The mechanical necessity for extension of the body, after contraction of these muscles, is readily apparent. If the body, for simplicity's sake, be considered a cylinder, contraction of circular muscles must cause it to lengthen, while with the form of body which really exists in the flat-worm, the contraction of the well-developed dorso-ventral fibres must bring about the flattening seen in the fully extended gliding animal.

Probably by far the most important sets of muscle-fibres for producing the general extension are the dorso-ventral and circular. It is to be noted that contractions of any of the sets of fibres may take place in localised regions, producing extensions or contractions of that region, according to the set affected. The sensory, or "feeling" movements of the head are brought about in this way.

The extension, and probably also in large part the extrusion of the pharynx is brought about by contraction of its well-developed circular musculature.

In the case of the marine mollusc, Aplysia limacina, Jordan (: 01, pp. 11—15) has recently shown that extension is brought about in an entirely different manner. It results from passage of fluid from vesicles in the skin into the spaces in the body parenchyma when the body muscles are relaxed. When the animal contracts this fluid (blood) is pressed out into the vesicles, which become very much extended and swollen; then, when the muscles are relaxed, the elasticity of the walls of the vesicles forces the fluid back into the body, and thus causes its extension. As a result of this method of expansion it is possible to kill the animal fully extended by the use of such poisons as cocaine.

It is not unusual to consider the fully extended condition of such an organism as a flat-worm as one of approximate relaxation. Instead of this, it is, in fact, a condition in which a certain part of the musculature is in a state of well-marked tonic contraction. This furnishes a reason for the fact that it is impossible to kill these animals in a completely extended condition by the use of poisons which tend to produce a relaxation of the muscles. Under these circumstances the animals take on the typical relaxed form, which is quite different from that of extension.

c. Rest.—Inasmuch as a very large, if not the larger portion of the life of a planarian is spent in a condition of rest, it will be well to discuss this matter; and it may, perhaps, best be taken up under the general heading of "activities," although really the opposite of activity.

The appearance of the worm when resting is, as has already been mentioned, quite different from its appearance in the active condition. The body is shorter, wider, and thicker. The ordinary contour of the head is almost entirely lost, and in place of the sharply pointed anterior end of a form like P. dorotocephala, the end is evenly rounded. The auricles disappear almost entirely, and their position is indicated only by the difference in the pigmentation at that part of the dorsal surface. The lateral edges of the body frequently have a wavy line instead of the straight one of the active condition. The anterior end of the body is in contact with the bottom, and not raised as in movement. The general appearance of a resting planarian is shown in Fig. 6.

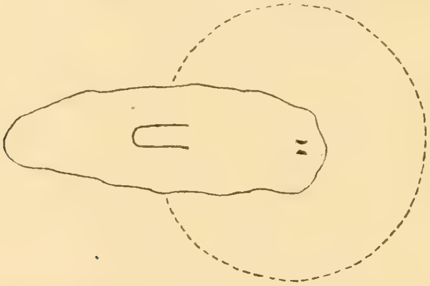

FIG. 6.—Diagram showing the typical appearance of a resting planarian. The dotted line bounds approximately the area covered in the "testing movements" which precede the coming to rest (cf. text).

The coming to rest of a gliding animal is usually done in a very characteristic way. First, the animal glides more and more slowly for some distance before reaching the point at which it will finally stop. The distance before reaching the stopping place in which the worm glides appreciably slower is not, however, in most cases very considerable—usually not more than two or three times its own length. It is to be noted that this slower gliding which precedes the coming to rest is not in form or rate distinguishable from the other slow gliding motion of the worm which is not followed by rest. In other words, a specimen may glide slowly for a long time without stopping, so that one cannot prophesy with certainty from the rate of movement whether the specimen is soon coming to rest or not. The coming to rest is practically always preceded by a period of slower gliding, but all slow gliding is not immediately followed by rest. After a brief period of this slower gliding the worm suddenly stops, and the posterior half of the body remains fixed in precisely the same position. The anterior half of the body is slowly moved about over the bottom from side to side, the head being touched frequently to the bottom or any other solid object in the neighbourhood. The anterior part in this "feeling" movement moves about the posterior part as a fixed point, the latter very rarely changing its position after it has once stopped. The thoroughness of this "testing" of the surroundings by the sensory anterior end varies much in different cases, but in practically all cases one can see some indication of it. I have in some instances seen it done very thoroughly, so that the whole surroundings within a radius of 3 mm. were gone over. Finally, when this is done the animal comes to complete rest, and assumes the typical relaxed condition shown in Fig. 6. The apparent significance of the "testing" movements at the time of stopping is that it is a piece of protective behaviour. The worm examines the surroundings before coming to rest, to see if there is anything dangerous (either of a solid nature or a harmful chemical) in the immediate neighbourhood. Whether or not this explanation is the true one, and further, whether natural selection developed this reaction for protective purposes, seems to me to be very doubtful, for reasons brought out in another place (cf. pp. 542 and 543). In some cases I have seen the worms come to rest by simply stopping without any appreciable trace of the "feeling" movements, but this is not the usual procedure. In coming to rest in one of the collections already mentioned, the "feeling" movements are usually very well marked.

There is a well-marked tendency for the planarians studied to come to rest in such a way that the long axis of the body forms a right angle, or nearly a right angle, with the lines of the force of gravitation. The cases in which the organisms come to rest with the long axis forming an angle of less than thirty degrees with the line of gravitation are rather few. Of course, when they come to rest on the bottom, the angle formed is approximately ninety degrees. A large number of observations on individuals which came to rest on the sides of dishes of various shapes have given the general result stated above. There are, of course, exceptions, but there is, after making due allowance for these, a tendency to a horizontal position as the position of rest. This is the only behaviour of the organism which bears any resemblance to a geotactic reaction. Another tendency, less marked than the former, is for the animals to come to rest in the angle formed by the sides and bottom of the dish. Not only do specimens come to rest lying directly in the angle, as shown at A in fig. 7, but also, and more frequently, they lie in such a position that a part of the body is on the side of the dish and a part on the bottom, as shown at B, fig. 7. In this position the animal usually lies obliquely rather than at right

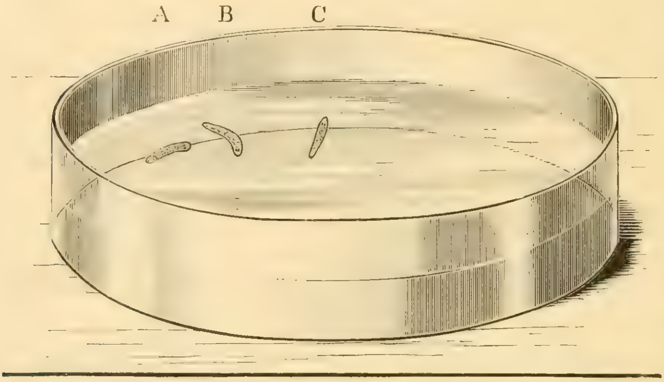

Fig. 7.—Diagram showing the positions taken by planarians coming to rest in a dish (see text).

angles to the line of the junction of the side and bottom of the dish. The animals usually come to rest in this position after they have been gliding on the side of the dish. When they come to rest from movement on the bottom of the dish, a position frequently taken is that shown in C, fig. 7, where only the very anterior end is in contact with the side. This coming to rest in the angle of a dish is apparently a reaction which agrees with those usually called thigmotactic reactions. But it is not, as has been stated by several writers, due to a tendency to get more of the body in contact with something solid, than is in such contact under usual conditions; for in the case of an organism like a flatworm, it is impossible for any more of the surface of the body to be in contact with a solid when it is bent, as shown in Fig. 8, A, than when it is flat, as in B. There is the same amount of surface in contact in either case. The ventral surface of the flat-worm is strongly positively thigmotactic under all circumstances, and the dorsal surface negatively thigmotactic, but this does not help us understand why the animal comes to rest frequently in angles. This behaviour of the flat-worm in dishes is due to the same sort of reaction as that which causes them to come to rest on unevennesses on rocks, and also causes the same phenomenon in a more marked degree in the case of *Littorina*, as recently described by Mitsukuri (:01). The common factor in the reaction in all cases is that different parts of the body are brought into such positions that they form unusual angles with each other. Since this phenomenon is distinctly different from any embraced by the term thigmotaxis as used in its true sense, it seems desirable that it be

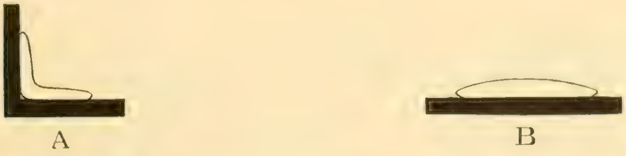

FIG. 8.—Diagrammatic cross-section of a planarian at rest—A, in an angle; and B, on a plane surface.

given a specific name. I would propose for this reaction the term goniotaxis.[1]

When a flat-worm starts from a resting condition the nature of the movement, i. e. whether gliding or crawling, depends in large measure on the intensity of the stimulus which starts it. If the resting animal is rather strongly stimulated it will start at once into a crawling movement, which changes to gliding after three or four, or fewer, contractions, provided the stimulus is not again renewed. It is possible by the use of a very weak stimulus to start the resting animal off at once into the gliding movement, or with only the faintest indication of a single crawling contraction. When the animal starts spontaneously into movement it usually begins at once with the glide. When starting spontaneously the glide is usually preceded by some of the "feeling" movements of the head end, such as precede the coming to rest. The purpose of these is evidently the same as in the former case. Any sort of strong stimulus will start the resting animal into movement.

The physiological condition of the resting animal is, as has already been mentioned, one of relaxation. All of the muscular systems of the body are in an apparently completely relaxed condition. This is evidenced by the form of the resting animal, which differs from that of one in movement, in being shorter, wider, and thicker, and in not showing such features as the auricles, or the pointed tip of the head. This relaxed condition is evidently one of lowered tonus, as may be determined by simple observation. Stimuli of an intensity which would cause a marked reaction in an individual in an active condition, will produce no effect on a resting animal. This point has been tested with a variety of stimuli, including mechanical, chemical, food, etc., and the markedly lower tonus of the resting animal is very evident. The reactions which are produced, provided the stimulus is made strong enough to be just effective, are weak. Of course, if the stimulus is above a certain strength, or is con-

---

[1] From γωνία = angle.

tinued for some time, the animal will become generally stirred up and glide or crawl away. This condition of lowered tonus in the resting animal reminds one of the conditions found in sleep in the higher animals. There, as in this case, the general sensory and muscular tonus is greatly reduced, and there seems to be no good reason why the resting condition of these lower organisms may not be considered and called "sleep." The two things appear to be fundamentally the same physiologically, and would appear to serve the same purpose. Furthermore, there is no apparent reason why the lower organisms should not have as great a need as the higher for periods of rest or sleep, during which the anabolic processes are in considerable excess over the katabolic. The fact that some lower organisms are so balanced physiologically that they apparently do not require such periods of rest is not conclusive evidence that other low organisms must be similarly balanced. So far as is known to the writer, there has been comparatively little attention paid to the physiological condition of lower organisms during different phases of their activities. An animal which is not moving is loosely said to be in a "resting condition," when in many instances, as in Clepsine, the quiet animal is in a condition of heightened rather than lowered tonus (cf. Whitman, loc. cit.).

As was noted in the section on "Natural History," the periods of activity of Planaria are separated by periods of rest of greater or less length. The time spent in the resting condition, at least during the daytime, is considerably greater, on the average, than that spent in movement. Probably, however, this is reversed during the night, when the activity is greater than during the day. This periodicity in the activity is just what would be expected if there is a necessity for rest at intervals as in the higher animals.

The causes which immediately induce the coming to rest may now be considered. The principal cause, as has been indicated above, is that the animal becomes fatigued by movement, and its general tonus becomes lower and lower. As a result of this it must remain relaxed for a certain time in order that recovery may take place. When in the course of the activity of the animal its general tonus gets below a certain point it stops, the actual process of coming to rest being a more or less gradual one. A strong piece of evidence in favour of this view is the fact already given in the section on "Natural History," namely, that if the animal is stirred up and made to start moving again immediately after coming to rest each time, it will be found that the periods of activity become progressively shorter. Furthermore, when the general physiological condition of the organisms is weakened by keeping them for a time in the laboratory, it is found that the periods of rest become progressively longer in proportion to the periods of activity. The general "predisposing condition" to the coming to rest is then probably a lower tonus due to fatigue. The immediate causes determining the exact place chosen are of three sorts. First, and probably most important of these, is the intensity of the light. It is well known that planarians tend to come to rest in regions of comparatively low light intensity, the reaction having been first noted by Loeb ('93), and called by him "Unterschiedsempfindlichkeit." This factor seems to be the most important of any in determining the region in which the animals come to rest, both under experimental conditions and in the natural habitat. In aquarium dishes placed close to a window, and containing considerable plant material, the worms will be found resting practically always in the half of the dish away from the window. The largest number of individuals will be entangled in the plant material, and usually for the most part invisible; while of those specimens resting on the sides and bottom of the dish the greatest number will be found in such places that there are heavy masses of plant material between them and the window. A few will come to rest far around on the sides of the dish where the glass itself cuts off some of the light. This last position has been mentioned by

Loeb as the one most frequently taken by planarians in a dish containing only water. This behaviour towards light is not, however, an absolutely precise reaction. Many times during experiments I have seen specimens come to rest in the very lightest parts of the dish and remain there; but in general this reaction will cause most of the animals to gather in shaded areas. It is probably the principal factor in causing the animals to take positions beneath stones in their natural habitat.

The second immediate cause in determining where the animals shall come to rest is the goniotaxis mentioned above. If an animal in the proper physiological condition of reduced tonus comes to an unevenness in the surface on which it is moving, it will in most cases come to rest there. This, again, is not a very precise reaction; not sufficiently so as to make it possible to predict beforehand where any given individual will stop. In this case, just as in the case of light, much depends on the animal's physiological condition, and when in the proper condition they may come to rest on a perfectly smooth surface. Thus in a dish individuals will always be found at rest on the smooth sides and bottom, yet there is a distinctly marked tendency, when the animals are put under experimental conditions and closely observed, for them to come to rest in the angle of the dish. This reaction probably also plays a considerable part in the habit of coming to rest among the branches and leaves of the plant material. In the natural habitat it is undoubtedly the factor which causes them to take positions on the uneven parts of stones. It may be that the immediate cause of the stopping in this case is the increased resistance to movement afforded by the unevenness of the surface. This, acting on an animal in a fatigued condition, might give the necessary stimulus for the stopping.

The third factor in determining where the animals shall come to rest is one about which I am doubtful. There seems to be some evidence, from the behaviour of the animals themselves, that in the formation of the groups or collections previously mentioned (pp. 533, 534) there is a sort of chemokinesis. That is to say, the presence of some chemical substance in the water causes the animals to stop. The evidence for this factor will be taken up with the discussion of the formation of collections. It probably does not play any part in determining where a single individual shall come to rest outside of a collection.

It must be emphasised that all of these three factors are secondary in importance as compared with the physiological condition of the animal, which may be said to prepare it for the resting state. An active animal, in which the tonus is at or near the maximum, will pass through regions of low illumination, uneven surface, or collections of other individuals without stopping. Only when the animal is in the right general condition do these factors come in to determine the precise point where the stop shall be made.

1. Formation of Collections.—Since the formation of collections is dependent on the animals coming to rest in a certain area, it may properly be taken up in this section. The collections are fairly well-defined groups of from six or eight up to twenty or more individuals. The general appearance of such a group is shown in Fig. 1. The individuals composing it have no definite orientation, but are scattered about with the anterior ends directed in whatever way they happened to be pointed when the individuals stopped. The distance separating the individuals varies much in different cases. In some cases it may be as much as a half-centimetre, or again may be the width of an individual worm or less. This formation of collections of this sort might be considered the result of a "social instinct" by animal psychologists of the Binet school. Actually, it appears to be due to two simple reactions taken in conjunction with the general physiological condition of the individuals composing it. The first of these reactions is that to light. That is to say, when individuals come to a comparatively restricted area of a certain degree of illumination, if they are in a certain condition of reduced tonus, they stop. Those which are

very active pass on through the region, but necessarily in course of some time several individuals will have stopped, and a group will have been begun. When once started another reaction apparently enters to assist in enlarging it. This reaction appears to be due to some chemical substance, and belongs to the class of reactions which Engelmann has suggested should be called "kinetic," in this case chemokinesis. It would appear that planarians excrete or secrete some chemical substance towards which they are themselves positively chemotactic, and which also causes them to come to rest. When several individuals remain quiet in a small area this substance, of course, accumulates and affects other individuals passing. That some such a substance is separated from the bodies of the animals is evidenced by two phenomena. First, in the case of the food reaction, which will be taken up in detail later, it is found that after one or two individuals have attached themselves to a piece of food material and begun feeding the mass of food and planarians is a much more effective stimulus to positive chemotaxis than is the same food substance alone, even though it may have remained in the water a greater length of time. The "zone of influence" (vide infra, p. 626) of the food and feeding individuals together is much wider than that of the food alone. Specimens are affected at a greater distance from the food and react more sharply. As a result of this, dense aggregations of planarians will be formed in a comparatively short time after the first two or three individuals have found a bit of food. As there is no reason to suppose that the action of the food itself is different in the two cases, we must conclude that the greater effectiveness of the food and feeding individuals is due to some chemical substance coming from the organisms themselves.

The second line of evidence for the existence of a reaction to a chemical in the formation of collections is found in the behaviour of specimens coming near a group of individuals resting on the bottom of a dish. When some distance away from the outer boundary of such a group a gliding animal will frequently be seen to give a well-defined positive reaction, and turn towards the group. The reaction is of precisely the same character as that given by the organism to weak chemicals (to be described later), and the behaviour convinces one observing it that the specimen is stimulated by some chemical diffusing out from the group. After turning towards the group the specimen will glide into it and usually come to rest, in the manner which has been described above.

What the nature of the chemical substance present in the region about the groups is, I have not been able to discover. Neither rosolic acid nor methyl orange is discoloured by it. Whatever its nature, it must be in an extremely diluted state. This seems evident for two reasons: first, because it does not affect delicate indicators; and second, because it does not have any effect on active specimens of Planaria. A large number of experiments have been performed to test this latter point, but always with the same result. Unless the individuals were in the proper predisposing condition of lowered tonus, they would pass by or through groups of other individuals without giving any reaction.

Attempts to produce, artificially, collections of planarians in chemicals have been unsuccessful. I have tried various solutions (such as sugar, weak alkalies, etc.) to which the organisms showed a well marked positive chemotaxis when tested by other methods, but have not been able to get any formation of collections in them. The animals would give the positive reaction on coming to the edge of the diffusing chemical and pass into it, but would not come to rest. This failure to produce collections artificially is not surprising when one considers the number of conditions necessary for the production of the desired result. The organism must be in just the right physiological condition, the chemical must be of a certain concentration, and finally, it must be located in an area of a certain light intensity. It is practically almost or quite impossible to fulfil all these conditions at the same time in an experiment.

The coming to rest in the collection seems to be due simply to the direct effect of the chemical on the organism. There is no evidence that the animals are held in the group as a result of a negative reaction to the surrounding water, as is the case in the collections formed by the infusoria (cf. Jennings, '99, *b*). The method of formation of collections in chemicals in the case of the infusoria is as follows:— Specimens swimming about at random come to the edges of drops of chemicals purely by chance. If, for example, the chemical happens to be a weak acid, the specimens will pass into the drop without giving any reaction. When, however, they reach the opposite edge of the drop and attempt to pass from the chemical back into the water they are stimulated, and give their usual motor reaction. This turns them back into the drop, in which they are, as it were, "caught in a trap." As a consequence of this method of reaction a very dense collection will be formed in a short time. With the flat-worm the case is very different in that an active individual frequently passes into and out of one of these collections without showing the faintest trace of a reaction on either side. The only way in which any stopping in the region is brought about by a chemical is by a chemokinetic reaction. The fundamental difference in the reactions of the two groups of organisms on which this difference in the matter of forming collections is based will be brought out in the section on the reactions to chemicals.

To sum up, the formation of collections of individuals seems to be due, in the first instance, to the tendency of the organisms to come to rest in areas of a certain degree of intensity of light, and in a lesser degree to a tendency to turn towards and come to rest in areas containing some substance secreted or excreted by the worms themselves. A prerequisite in the formation of collection, as in the coming to rest under any circumstances, is a proper physiological condition of reduced tonus.

There does not appear to be any special biological significance to this tendency of the animals to collect in groups.

The behaviour is not of any evident benefit to the organisms, as it is in the case of infusoria, where it is apparently closely connected with the obtaining of food. On the contrary, it seems to be, at least potentially, a harmful thing, because any accident or enemy would affect a number of individuals rather than a single one when they were so collected.

d. The Effect of Operations on Movement. — It may be well to put together in one place the results which were obtained with reference to the movements from animals which had been cut in various ways. From these we can form some idea of the relation of the nervous system of the planarian to its movements.[1]

The immediate effect of any operation is that of a very strong mechanical stimulus applied to the same part of the body, and the sort of movement resulting in each piece depends on the position of the cut. The details of this immediate effect will be described in connection with other mechanical stimuli. What concerns us here is the permanent after-effect of operations on the movements. We can best get at this matter by taking up some specific cases.

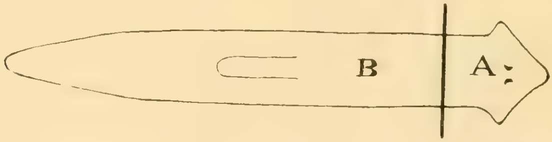

FIG. 9.—Operation diagram. The heavy straight line indicates the cut made. For results see text.

---

[1] All the operations were performed with a sharp scalpel, in most cases with the specimen in a dish of water. In some cases the worm was transferred to a drop of water on a soft board for the cutting, but in all cases where immediate observations were wanted, the operations were performed in the dishes used for the experiments. The only difficulty in performing operations on planarians arises from the fact that if the edge of the knife is allowed to rest on the surface of the body for even a very short time before the cut is made, it will become covered with the sticky slime from the animal, and then any clean cut is impossible. The edge will slip off the back of the worm without penetrating.

If a planarian is cut squarely across the body in the region a short distance behind the head, as indicated in Fig. 9, the anterior piece will continue to move after the operation at approximately the same rate as the whole animal did before. After the immediate effect of the operation is past the glide is its ordinary movement, and it will go about the dish and behave in general like a whole individual. At the outstart its periods of activity and rest are distributed about as in a normal individual, or, in other words, its power of spontaneous movement is not impaired, at least for a time. On the other hand, the posterior piece comparatively soon comes to rest after the operation. Its gliding movement is slower, and the periods of rest become longer and longer in comparison with the periods of activity. Its power of spontaneous movement becomes very greatly diminished within a comparatively short time after the operation, and it remains in the relaxed resting condition during the greater part of the time spent in the process of regeneration. When this posterior piece does glide about soon after the operation its anterior end is usually raised off the bottom considerably higher than is the head of a normal flat-worm under similar circumstances. This is shown in Fig. 10. There are no "feeling" movements of the anterior end of such a piece, but instead this end is held very stiffly in the raised position.

FIG. 10.—Diagrammatic side view of a decapitated specimen performing the gliding movement.

If, instead of making the cut so close behind the head, it is made back in the middle region of the body, the anterior piece behaves as before, i. e. like the normal animal. The posterior piece, however, moves slower than did the corresponding piece in the previous experiment, and it comes to rest sooner after the operation, and remains quiet longer.

In the same way cuts may be made nearer and nearer the posterior end; the posterior piece will move more and more slowly, and come to rest sooner. At the same time the anterior pieces will appear more and more like the normal. In both sets of pieces the crawling movement may be induced by proper stimulation of the posterior ends.

Oblique transverse cuts produce the same results as do direct ones. The same laws hold as to the movements of the pieces. In case a strip is cut from the side of the body, as shown in Fig. 11, the smaller piece A curls up, and does not make any further progressive movements, although it remains alive, and will eventually regenerate in most cases. The main part B contracts on the cut side, and hence becomes curved in that direction after the operation. It is able to move about, but at a somewhat slower gliding rate than normal, and in a path curved towards the cut side. In case a worm is slit down the middle line at the anterior end, as in Fig. 12, it is able to glide, but at a slower rate than normal. It performs the crawling movement in response to stimulation at the posterior end, and each half of the head performs feeling movements independently of the other half.

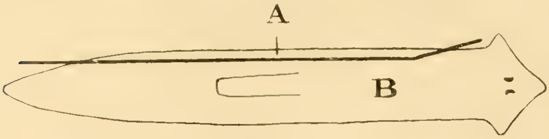

Fig. 11.—Operation diagram. Heavy lines indicate the cuts made. For results see text.

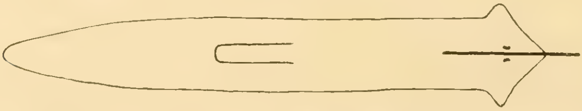

Fig. 12.—Operation diagram. The heavy line indicates the cut made. For results see text.

An individual slit up in the middle line from the posterior end, as in Fig. 13, glides at approximately the normal rate, provided the cut is not carried too far forward. If the cut extends into the head region the gliding becomes immediately slower. Such a specimen performs the crawling movement upon stimulation of the posterior end of either piece, but in a peculiar way, which will be described later.

Putting all these results together, we see that there is a general tendency for animals on which operations have been performed to glide at a slower rate than normal. In some of the pieces this tendency is very slight, and frequently hardly noticeable. In others the movement is very much slower than normal. In all cases the periods of rest are longer during the time of regeneration than normally. This tendency for the animals to remain quiet during regeneration increases up to a certain point as regeneration proceeds. A piece of a planarian may be quite active for three or four hours after the operation, while during the following three or four days it will scarcely move at all. After the regeneration is practically complete the worm will begin to move about again approximately as it normally does. During the regenerating process the anterior pieces, bearing an uninjured head, are much more inclined to move about than are the posterior parts. These latter usually remain entirely quiet during regeneration.

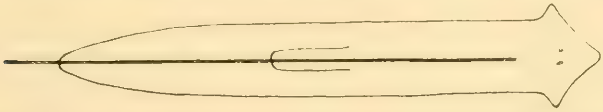

FIG. 13.—Operation diagram. The heavy line indicates the cut made. For results see text.

This behaviour of the posterior parts during regeneration appears to be distinctly purposive, and to belong to the class of phenomena called regulatory. The general tonus of these pieces is immediately lowered by the operation, and consequently they keep quiet. Yet at the same time the processes of morphallaxis and, in many cases, growth begin at once, and proceed very vigorously till the missing parts are restored. If we consider that the worm or part of a worm has at the beginning a certain sum-total of energy available for all activities, including movement, growth, morphallaxis, and all its other vital processes, then it would appear that the performance of any single set of activities in excess must cause a corresponding diminution in other activities. This is exactly what we find to be the case with the regenerating planarian. While the processes concerned in regeneration are at their maximum activity, we get a decided reduction in the amount of movement. It would seem, then, that a large part of the energy which is ordinarily expended in movement is used after operation or injury in the processes of regeneration. As the regeneration nears completion more and more energy is available for, and used in movement. This would seem to be a sort of "energy regulation." The behaviour is evidently further beneficial in the case of the posterior pieces, because their anterior ends are very insensitive as compared with the head of the normal animal, and if they moved about they would certainly be more apt in the long run to get into difficulties than if they remained quiet.

It may be well in closing the section to point out the relation of the nervous system to the movements. Loeb (:00) has maintained that "if we divide a fresh-water planarian, for instance Planaria torva, transversely, the posterior half, that has no brain, crawls just as well as the oral half. Spontaneity in Planaria torva is, therefore, by no means a function of the brain." If by "crawl" in the first sentence we understand "glide" to be meant, the statement is not strictly accurate. The posterior pieces do not "move just as well as the oral" (anterior), but, as has already been brought out, more slowly. For a very short time after the operation the statement would in some cases be correct, but it certainly would not be twenty-four hours later, according to all the observations I have been able to make on the subject. As for the spontaneity of the movement, that also becomes very much lowered with the loss of the brain, as I have attempted to show above. The very much lessened activity of posterior pieces of planarians has been mentioned by Lillie (:01, pp. 132, 133).

From my own observations it seems clear that the principal function of the brain of Planaria with reference to movements is to maintain the tonus of the ciliary system. That neither the crawling nor the gliding movements are specific functions of the central nervous system is evident, because both sorts of movement may take place after its removal. Yet all my observations tend to show that after injury to or loss of the brain the gliding movement becomes, almost immediately, markedly slower. This relation is especially well indicated by the experiments noted above on splitting the animal longitudinally from the anterior and the posterior ends. In the one case the gliding movement becomes at once distinctly slower, while in the other case there is only a slight difference in the rate, evidently conditioned by the fact that only comparatively few of the cilia can get a hold, so to speak, so that they can function. The force of the argument will be impressed if one glances at the relative size of the cuts in Figs. 12 and 13, and then remembers that the rate of gliding of the specimen figured in Fig. 13 is faster than that of the one in Fig. 12. With the co-ordination of movements, including the crawling, the central nervous system has very little to do in the case of Planaria. With regard to the spontaneity of movement it is difficult to decide in how far the brain functions. It is certain that regenerating anterior pieces show more spontaneous movement than do posterior pieces, yet the anterior pieces are behind the normal worm in this respect. The brain probably plays some part in the performance of normal spontaneous movements, but, as has been pointed out, in these operation experiments the whole matter is very definitely related to the regenerative process, and loss of substance plays nearly, if not quite as great a part as loss of nervous system.

Summarising, we may say that—1. For the performance of the crawling or gliding movements the brain is not specifically necessary. These movements are normally co-ordinated in the absence of the brain.

2. The maintenance of the tonus of the ciliary system (which produces the gliding movement) is a specific function

of the brain, and is, further, its most important function so far as movement is concerned.

3. The brain plays a certain part in the production of spontaneous movements.

F. Reactions to Stimuli.

I. Reactions to Mechanical Stimuli.

Since the reactions which are given by Planaria to mechanical stimuli are in a sense the foundation on which the reactions to other stimuli are based, it may be well to consider them first. After thoroughly working out the reactions to mechanical stimuli we have a very definite clue to practically all the animal's behaviour.

a. Methods.—For rough, general work with mechanical stimuli a needle or a sharp-pointed scalpel may be used as the stimulating agent. For the finer work in sharply localising the stimulus, I at first made use of pieces of glass tubing drawn out to capillary fineness. This method was not, however, satisfactory, as the glass was too stiff to admit of reaching all points of the body under some circumstances. Furthermore, this stiffness, together with the sharpness of the end, made it almost impossible to give the animal a moderately strong stimulus without wounding it. A far better plan was found to be to fasten with sealing-wax a moderately stiff piece of human hair to a piece of glass tubing, the latter to serve as a handle. With such an arrangement the stiffness of the stimulating point can be varied by varying the length of the hair. Danger of wounding the animal is avoided, yet repeated strong stimuli may be given, while, further, the flexibility of the hair makes it possible to stimulate the animal at any point and from any desired direction.

An annoying difficulty in connection with this work was the clinging of the slimy secretion of the body to the point used for stimulating. Once coated with this slime the sharpest point will slide off the body without giving any effective stimulation.

b. Description of Reactions.—The reactions can best be described by taking up in order the typical results following stimulation of the different parts of the body.

1. Stimulation of Head Region.—If a planarian gliding along on the bottom of a dish be touched with a needle on one side of the head, it will, under normal circumstances, in the majority of cases, turn the head and anterior one fourth of the body away from the side stimulated, and continue gliding along in the new path determined by the turning of the anterior end. This "turning away" reaction, or, as we may call it for economy of words, negative reaction, will always be given if the stimulus is made sufficiently strong. There is a certain intensity of stimulation below which the negative reaction may or may not be produced, depending on the physiological condition of the individual, but above which it always occurs. If, again, a normally gliding planarian be selected for stimulation, and this time the stimulating point (preferably something finer and more flexible than a needle) be touched very lightly to the edges of the sides of the head or the auricles, we get, provided the specimen is in the proper physiological condition, a very graceful and striking reaction, quite different from that obtained in the former case. This time the flatworm will stop for the briefest instant, turn the head and a little of the anterior end of the body towards the side stimulated, and at the same time raise the head from the bottom, until finally the tip of the head points exactly towards the point from which the stimulus came, and then glide forward in that direction. This "turning towards" or positive reaction is given only in response to very weak mechanical stimuli, and then only when other conditions are favourable. It is a very precise and characteristic reaction when it does appear.

Having outlined the two main reactions following mechanical stimulation in the head region, we may proceed to consider each of them in more detail.

a. Reactions to Strong Stimuli.—The negative reaction is the characteristic reaction given to all strong stimuli, whether mechanical or of some other sort. It is, further, the same type of reaction which most organisms with fairly well-differentiated reactions give in response to strong stimulation. It takes the animal away from what might be a dangerous object.

In Planaria the portion of the body which takes part in the turning away varies with the strength of the stimulus to a certain degree. Stimuli just strong enough to call forth the negative reaction will cause only the head to be turned away. The first turn away of the definite reaction never includes any of the body back of the pharynx, so far as I have observed, except in the case of very strong and repeated stimuli. In the typical and most often observed form of the negative reaction the portion of the body which turns away is that anterior to a point about halfway between the level of the eyes and the point of origin of the pharynx. This is shown in Fig. 14. With stronger stimuli the point of turning is farther back on the body.

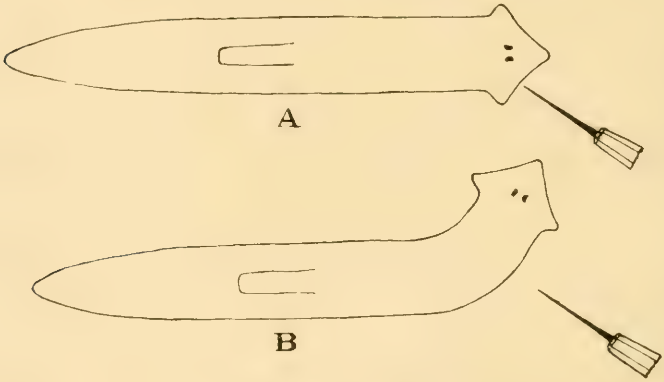

Fig. 14.—Diagram showing the form of the negative reaction to mechanical stimuli. A shows the position just before the stimulus is applied, and B the position after the reaction.

The number of degrees through which the head is turned in the negative reaction depends on the intensity of the stimulus. With stimuli just effective in calling forth the reaction the turn is only slight, and since it affects only the head end the direction of movement of the whole animal may be scarcely changed at all. The amount of turning of the anterior end is typically from 30° to 40°.

There is in the negative reaction a pause at the instant of stimulation, preceding the turning away. The first effect of the stimulus is to cause the animal to stop its relatively rapid movement. This pause may be so slight as to be almost imperceptible in the case of comparatively weak stimuli, or, on the other hand, may lengthen to a quite noticeable interval when the stimulus is very strong. It is a characteristic feature of both the positive and negative reactions of planarians, and is evidently due merely to the fact that before a reaction (i. e. something involving a change of motion) the former movement must stop.

The effect of localisation of mechanical stimuli in the head region may next be considered. As has already been mentioned, stimulation of the sides of the head produces the positive or negative reaction according to the intensity of the stimulus. There are no special regions of specific sense-organs connected with either of these reactions. The negative response is given after strong stimulation of any part of one side or the other of the head and, so far as it is possible to observe, just as decidedly after stimulation of one part as of another. It is of interest to know what happens after stimulation of the head in the median line. It is very difficult to get a stimulus exactly in the median line, but one may come very near it by stimulating the dorsal surface of the head in the region between the eyes. The reaction produced is a longitudinal contraction of the anterior part of the body, drawing the head back away from the stimulus. The head is then turned to one side or the other as in the usual negative reaction, and the animal starts ahead again in the new direction. The side towards which the turn is made after median stimulation is indeterminate—that is, there is no tendency to turn in more cases towards one side than towards the other, as has been found by Frandsen (:01) to be the case with Limax. This is what would be expected in the case of the flat-worm, because it is a perfectly bilaterally symmetrical organism. Probably what actually determines which way the organism shall turn after attempted median stimulation is the fact that the stimulus really acts a little to one side or the other, and the turning is really the negative reaction.

By repeatedly stimulating the anterior end of a worm with moderately strong mechanical stimuli its reactions may be modified. In the beginning of such a series of stimulation the worm turns away farther and farther from each succeeding stimulus, at the same time remaining at the same place in the dish, i. e. not making any progressive movements. This process tends to make the animal describe a circle away from the stimulus, about its posterior end as a fixed point. It never completely describes a circle, however, but after several stimuli have been given, to which it has responded progressively more vigorously, it finally jerks back with a strong longitudinal contraction, and turns the anterior end through a considerable arc, so that it points in an entirely different direction. This final strong reaction in the majority of cases turns the anterior end towards the side from which the stimulation is coming, or, in other words, in an exactly opposite direction to that of the previous reactions. This reaction appears as if, after the animal has tried in vain to get away from an uncomfortable stimulus by its ordinary reaction, it finally tries a wild jump in the opposite direction. This curious change in the reactions induced by a repetition of strong stimuli I have observed many times. It indicates the effect of the organism as a whole on its reflexes. As von Uexküll (:00, p. 73) has well brought out, we must consider that in the case of a higher organism, like a dog, the animal moves its legs, while with a lower organism whose activities are reflex—for example, the sea-urchin—it is really the "legs" (i. e. locomotor organs) which move the animal. In the flat-worm the movements of the whole organism are determined by definite stereotyped reflexes, yet in such exceptional cases as the one just described the organism as a whole takes control, and does something quite different from what the normal reflex fitted to the case would accomplish.

Very strong mechanical stimulation of the anterior end, such as to wound the animal, causes a very much more vigorous reaction than the ordinary negative one, and of a slightly different form. The animal contracts strongly longitudinally, and, as a result of the heavier musculature on the ventral surface, curls the head in under the body. Then the anterior end is turned to one side through a larger angle than is usually the case, and the worm straightens out in this new direction. The point of importance to be noted in this reaction to maximal stimuli is the curling under of the head. The turn away from the side stimulated frequently is so great as to turn the animal squarely about, so that it heads in the direction opposite to that before stimulation. Besides this effect of maximal stimuli just described, they may also produce a change in the movement from gliding to crawling. The crawling does not usually follow stimulation of the head end of the body, but it is possible in some cases to produce it by very strong stimulation here. I have also been able in a normal animal to induce crawling backward by very strong and continued stimulation of the anterior end of the body. This backward crawling, when it occurs, is of the same character as the same movement in a forward direction, except that all the factors are reversed. It has been described above (cf. p. 551). It is much more easily produced after certain operative procedures, and in connection with them further details regarding it will be brought out.

The negative reaction, i. e. that to strong stimuli, is given more frequently than any other in the course of the activity of the individual, and apparently does not depend on the presence of any special physiological condition. It is given in response to stimuli covering a wide range of intensity. The lower liminal value of the stimulus producing it (there is apparently no upper limit) varies to some extent with the physiological condition of the individual. Thus in some specimens at certain times stimuli which would ordinarily produce a rather strong negative reaction will call forth nothing but the positive reaction. This condition is only a transitory one, and the reason for it seems to be a heightened tonic condition of the animal. Specimens exhibiting this relation to rather strong stimuli are always very active, and move about with great rapidity, frequently raising the anterior end of the body and waving it about through the water as they glide along. Persistent strong stimulation of the organism rapidly changes the general physiological condition. This is not more true of stimulation applied to the head region than of strong mechanical stimulation of any part of the body. The animal becomes "stirred up" generally, moves about with increased rapidity, its sensitiveness to stimuli becomes diminished, and it will give only the negative response to stimulation of the anterior end. This change in the physiological condition of the animal as a result of continued stimulation of any sort, as in a series of experiments, is a matter of great practical importance in connection with reaction work. One may get totally different appearances from an individual which has been "stirred up" from what are seen in the case of one which is in the normal condition. This is only one of a number of factors which must be taken into account in work on the reactions and behaviour of an organism if one is to obtain trustworthy results. It is almost an absolute necessity that one should become familiar, or perhaps better intimate, with an organism, so that he knows it in something the same way that he knows a person, before he can hope to get at even an approximation of the truth regarding its behaviour.

β. Reactions to Weak Stimuli.—The positive reaction is the characteristic reaction given to all weak stimuli. It is an orienting reaction in the sense that it brings the anterior end of the animal in a position such that it points approximately towards the source of the stimulus. On account of its fineness of adjustment with reference to the strength of the stimulus and the general physiological condition of the animal, it is a response which might be very easily overlooked in a superficial examination of the behaviour. As the worm gives this positive reaction in response to a gentle stimulus, turning the head towards the source of stimulation, and at the same time raising it, it gives one the impression that it is seeking something, and such the behaviour would doubtless be called by some animal psychologists. This impression is enhanced by the fact that if the head does not come in contact with the stimulating object at the first reaction, the animal advances in the direction from which the stimulus came, with the anterior part of the body raised and waving from side to side in the water.

As has been mentioned, the reaction is very delicately adjusted physiologically. In the majority of cases the animal must be in a comparatively quiet condition,—that is, not "stirred up" or excited, and gliding smoothly at the ordinary rate, in order that the reaction may appear at all. The stimulus must ordinarily be very weak, and given so as not to disturb the animal by abruptly changing the surrounding conditions. It is possible to produce the reaction by the use of a needle or scalpel point if sufficient care is taken, but better results are obtained by the use of a hair as the stimulating point. The point should be lightly touched to the edge or dorsal surface of the head, and then quickly drawn a short distance away. Even when all these precautions are taken one may fail to produce the characteristic response. I have frequently found that the same specimen which at one time would give the positive reaction in a very definite and characteristic way to every light touch on the head could not be made to show it a few hours later. This shows how closely it depends on general physiological conditions. On the other hand, specimens will frequently be found that for short periods of time (two or three hours) can hardly be induced to give any other response to mechanical stimulation of the head. Stimuli strong enough to be far above the usual upper liminal value for this reaction will call it forth. Such specimens show the reaction in a much more pronounced type than is usually the case. After a stimulus has been given they will turn towards it, and if the source is not touched immediately they will remain in the same spot waving the head about the region from which the stimulus came, at the same time stretching the anterior end of the body far out in all directions, precisely as if in search of the stimulating body. Usually this hypersensitive condition passes off in a short time, and the animals behave again in a more normal fashion. It was thought that possibly this condition was due to hunger, but experiments[1] devised to test this question indicated that this was not the case. We can only say that it is due to some intimate physiological condition, the exact nature of which we do not know. Another fact which may be mentioned in this connection is that sometimes a specimen in normal condition will give the positive reaction in response to a certain strength of stimulus only a part of the time. Other trials result in entire indifference on the part of the organism. Of course, it is not possible to give mechanical stimuli always of the same strength, yet with the closest possible approximation to this by an experienced operator, some of the trials will not affect the animal in any way except to cause a slight local contraction at the point on the head stimulated. The worm glides along without any change in rate or direction. Altogether we must conclude that the reaction is one which is very closely dependent on the existence of certain definite internal conditions as well as the external ones.

The typical course of the reaction is, as has been described, first a momentary pause, followed by a turning of the head towards the stimulus, accompanied by a raising of the anterior part of the body. From this typical form of the reaction there are many variations. The raising of the anterior end from the bottom just before and during the time it is being

---

[1] See section on "Reactions to Food and Chemicals."

turned towards the source of the stimulus may be entirely omitted. In this case the head is swept around towards the stimulus without being any further raised from the bottom than in the ordinary glide. The duration of the pause immediately following stimulation is likewise subject to great variation. It may be so diminished as to be imperceptible, the worm sweeping the anterior end around through the water without any change in the rate of the glide. The amount of the turn varies with the point of application of the stimulus, the head being turned just far enough to point in the direction from which the stimulus comes. This orientation, if we may so call it, is generally quite exact. If the stimulus is near the middle line on the edge of the head the turn will be only through a few degrees, while if the auricles are touched it will amount to nearly 90°. This fact indicates the remarkably well-developed co-ordination of the reaction. There is a great deal of variation with regard to what takes place after the turn has been made, and the anterior end is directed towards the stimulus. If the stimulating point is removed immediately after stimulation, so that the animal does not touch it by means of the first reaction, a normal specimen will usually lower the head and continue gliding in the new direction. As has been mentioned, however, in some cases a specimen will continue "feeling" about in the locality for some time. If the stimulating point is held in about its original position after the stimulus has been given, the first reaction will in most cases bring the head into contact with it. In this event the animal usually moves the tip of the head about over the hair (or other point) for a short time, and then drops back to the bottom and continues gliding. In other cases it will clasp the anterior end about the hair (as in the feeding reaction to be described later), and then in a moment start gliding up over it. When this happens the hair or needle may be moved about in the water or even lifted out of it, and the animal will not let go its hold and drop off. If the needle is held quiet, however, the animal will in a short time glide down off it and proceed on its way along the bottom. This behaviour when the animal is able to reach the stimulating object is evidently the action which most frequently occurs in natural environmental conditions.

With regard to the localisation of the stimulus producing this reaction, I may say that I have been able to produce it by proper stimulation of any part of the edge or dorsal surface of the head region under favourable circumstances. It seems to be more certainly produced—that is, in a larger number of cases—by stimulation of the auricles than of any other part of the head, and it may be that in this is to be found an indication of the chief function of these sense-organ bearing structures. At any rate, this is the only indication of a special function for them which I have been able to discover. The positive reaction given in response to light stimulation of the dorsal surface of the head is necessarily somewhat different from the typical reaction which has been described. In this case there can be no turning towards one side, because if this were done the head would not be directed towards the source of the stimulus. Instead, what takes place is this: the head is sharply raised and twisted, so as to form a part of a spiral in the region posterior to the head. This brings the anterior end into a position pointing towards the source of the stimulus, and at the same time the ventral surface is brought around so as to be, in most instances, the first portion of the body to touch the stimulating point. This reaction, following stimulation of the dorsal surface of the head, is not an easy one to obtain. I have succeeded best in producing it in the case of individuals in the hypersensitive condition mentioned above.

With regard to the strength of the stimulus necessary to call forth the positive reaction, only very relative statements may be made. Unfortunately we have no method of measuring the intensity of such weak mechanical stimuli as are used in work on lower organisms. Our only idea of the strength of the stimulus must come from the reaction of the organism itself. It must suffice to say, regarding the reaction under discussion, that in an animal in a condition of hypersensitivity I have been able to produce the reaction by the weakest stimuli which I was practically able to give. Under normal conditions of sensitivenes it takes a slightly stronger stimulus. No absolute value can be given for the upper limen of the reaction, beyond which it does not appear, but gives place to the negative reaction. This value varies greatly with different individuals. The general statement may be made that the positive reaction is the characteristic response to stimuli of very low intensity, and its production is very closely dependent on the proper gradation in the intensity. This dependence is so close that it is possible to obtain a part of both the negative and positive responses combined in the same reaction by the use of a stimulus of the proper intensity. I have been able in a few very favourable cases to produce by a single stimulus a pronounced raising of the head, such as is characteristic of the positive reaction, followed by a turning away from the source of the stimulus. Now the raising of the head is no part of the typical negative reaction, and, furthermore, was done in the very characteristic way in which it occurs in the positive reaction. The stimulus which produced it was evidently about intermediate in intensity between what, in the case of the particular animal used, would have called forth either the positive or negative reaction, as the case might be. This experiment shows in a very striking and conclusive way that in both the positive and negative reactions we are dealing with a complex of reflexes, since here a part of one of the reactions is associated with a part of the other. This point will be alluded to again in another connection, and its significance more fully pointed out.

The evident purposeful character of the positive reaction is plainly apparent. It is a reaction admirably suited, on the whole, to bring the organism into contact with beneficial things, such as food, etc. It seems to me that it must be by far the most important reaction of the animal in the struggle for existence. In the conditions under which planarians live a reaction which gets it food, or helps to, is of far greater importance for the survival of the individual than a reaction which takes it out of danger; for, so far as observation can show, the dangers it encounters are relatively few. It does not move over large areas of territory, and, so far as is known, it does not furnish a considerable part of the food supply of any other organism. Altogether its chief struggle for existence would seem to consist in obtaining subsistence for itself, and for this the positive reaction to mechanical stimuli would appear to be an important aid. As will be shown later, the food reaction proper consists largely of this same response.

We may now pass to a consideration of the—

2. Reactions to Stimuli applied to the Middle Region of the Body.—I use the term "middle region of the body" to distinguish that portion extending from the posterior border of the head to about the middle of the pharynx. The separation of the body behind the head into a "middle" and a "posterior" region is based entirely on physiological considerations, and is not defined morphologically.

a. Reactions to Strong Stimuli.—Strong mechanical stimulation of the middle region of the body along the lateral edges causes, in the first instance, a local contraction of the body in the immediate region of the stimulus. This local contraction is well marked; much more distinct than that in the head region. If the stimulus is sufficiently strong, and especially if the stimulating point is applied to the edge from above rather than from the side, the previous gliding movement will be changed to crawling. This will continue for a brief interval, usually from two to four crawling contractions being given; then the animal will relapse again into the glide, provided the stimulus is not repeated. In the case of a strong stimulus applied to the side of the middle region of the body, especially if the stimulus is several times repeated, we get the negative reaction—a turning away from the side stimulated—just as in the similar case in the head region. The nearer to the anterior end of the middle region the stimulus is applied, the more easily will the negative reaction be produced, while back in the pharyngeal region it follows even strong stimulation in fewer cases. In all cases where this reaction is not produced the direction of movement is either unchanged by mechanical stimulation, or the anterior end may be brought around very slightly towards the side stimulated as a mechanical result of the local contraction on that side. By repeating the strong stimuli on one side of the middle region, summation effects similar to those described above as taking place when the head is similarly treated are not produced. The animal crawls faster and faster away from the stimulus. Its direction of movement is changed, but usually not more than thirty to forty degrees. We see here evidence of precise response to localisation of stimulus. Stimulation of the head causes the animal to turn to one side, and, in case the stimulus is very strong, to contract longitudinally strongly before doing so. As we go back from the head in the middle region of the body, the tendency to crawl rapidly ahead away from the stimulus increases. At the same time the turning away from the stimulus becomes less and less marked the farther back it is applied. In no case do we get any strong retraction of the anterior end, which, in case of stimulation of the middle region of the body, would tend to bring the animal, or at any rate a part of it, into further contact with the stimulus.

Strong stimulation applied to the dorsal surface of the middle region of the body causes the animal to change from the glide to the crawl. This change of the form of motion may be regarded as a specific reaction in response to strong stimulation of the middle or posterior regions of the body. Stimulation of the dorsal surface of the middle region does not change the direction of the movement unless the stimulus is applied near the lateral margin, in which case it may cause the negative reaction, as mentioned above.

β. Reactions to Weak Stimuli.—Weak mechanical stimulation of the sides of the middle region of the body causes, in the first instance, a small local contraction at the place stimulated, without any effect on the general direction of movement of the whole organism. Under favourable circumstances, however, it is frequently possible to get a quite different result by the use of a weak stimulus on the lateral margins of this region. Specimens of Planaria may be induced to give the characteristic positive reaction described above by stimulation of a point as far back as the middle of the pharyngeal region. The stimulus inducing it is of the same intensity and character as that which will produce the same result in the head region.

Some experiments bearing on this point will be reported in full, on account of their important bearing on theoretical questions to be taken up later. These experiments were to

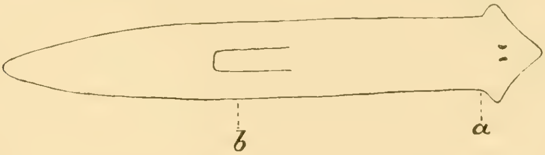

FIG. 15.—Diagram to show the portion of the side of the body (*a b*) within which weak stimulation produces the positive reaction.

test the effects of weak stimuli on the sides of the middle region of the body, especially with reference to the relation of the physiological condition of the individual to its reactions. The experiments were performed on large specimens of P. maculata, and the region of the body stimulated was that from *a* to *b* in Fig. 15. Most of the stimuli were applied in the region between the auricles and the origin of the pharynx. The stimuli were given by moving the point of a fine scalpel along the bottom of the dish till it came into contact with the margin of the body. In this way no general disturbance was produced. The attempt was made to make the stimuli of as nearly as possible the same intensity each time. The results were classed as positive, negative, or indifferent, according as the specimens gave the usual positive or negative reaction, or kept their course without change, showing only the local contraction. The first series which I will report was on an individual which was in a condition of great excitation, moving about with more than normal rapidity, and generally "stirred up." The results of twenty-three stimulations on this specimen were—

Expt. I.	Positive responses	1	Specimen in state of excitation.
	Negative responses	0	
	Indifferent responses	22	

A similar experiment with another individual in an entirely normal unexcited state, gliding at a moderate rate, gave the following results :

Expt. II.	Positive responses	20	Specimen in normal condition.
	Negative responses	2	
	Indifferent responses	13	

The striking preponderance of the positive reaction in the case of the unexcited individual is notable. The same individual used in Experiment II was now "stirred up" by poking it violently about the dish with a needle for about five minutes. It was then allowed to settle into a glide which was at a more rapid rate than normal, and another series of stimulations was made, with the following results :

Expt. III.	Positive responses	1	Specimen in condition of excitation.
	Negative responses	3	
	Indifferent responses	8	

Here, again, the indifferent responses are in excess, and there are practically no positive reactions. The specimen was again "stirred up" in the same way as before, and another series taken.

Expt. IV.	Indifferent responses (trials 1 to 11 inclusive)	Specimen in state of excitation.
	Positive responses (trials 12 and 13)	
	Negative responses (0)	

The specimen was again stirred up in the same way and another series taken, with the following results:

Expt. V.	Indifferent responses (trials 1 to 9 inclusive)	Specimen in state of excitation.
	Positive responses (trials 10 and 11)	
	Negative responses (0) .	

The positive responses in all these experiments were very definite and characteristic. I have obtained the same results in many other series of experiments, which need not be recorded in detail. The experiments show very clearly that in order for the animal to give positive responses to weak stimuli it is necessary that it be in an unexcited condition. These results have also an important bearing on the question of the mechanism of the positive response, in that they show conclusively that the reaction does not depend on the stimulation of special sense organs located in the head regions alone.

Weak mechanical stimulation of the dorsal surface in the middle region of the body is usually without any effect other than the causing of a slight local contraction at the point stimulated. If any specific effect on the whole animal is produced, it is merely a change from the gliding to the crawling movement, such as results from strong stimulation in the same region.

3. Reactions to Stimuli applied to the Posterior Region of the Body.—By "posterior region of the body" I mean that part of the body from the pharyngeal region to the posterior end. This region is not sharply marked off physiologically from the middle region, and it is impossible to say in any given individual at just what level the demarcation will be found. The physiological distinction between the two regions is founded on the fact that it is possible by unilateral stimulation of the middle region of the body to produce a change in the direction of the movement of the animal as a whole, while in case of the posterior region,

as will be shown, this cannot be done. On this account it will not be necessary in the description of the reactions to sharply distinguish between the effects of stimulation of the margins and of the dorsal surface, as has been done in the previous cases.

Strong mechanical stimulation of the posterior region of the flat-worm produces as a specific reaction an immediate change from the gliding to the crawling movement. The direction of the crawling is the same as that of the gliding; that is to say, the worm keeps on in a straight line, taking itself directly and in the quickest possible way away from the stimulus. The duration of the crawling movement following stimulation of the posterior region varies with the relative intensity of the stimulus and the physiological condition of the specimen. The most usual number of the strong, crawling contraction waves following strong stimulation is three or four. We may get a smaller number than this, and very frequently do, but in the species studied I have very rarely seen more than four of the general contractions following a single stimulus. This is evidently all that would be necessary under normal circumstances, since four of these strong contractions will carry the animal a considerable distance ahead, and probably out of reach of the stimulating agent. The weaker the stimulus is, the fewer are the contractions and the shorter the distance crawled. In some individuals it is at times almost impossible to induce the crawling movement except by repeated stimulation. Such specimens will merely draw up the posterior end in a single crawling contraction after stimulation, and then immediately relapse into the glide. If a strong stimulus is repeatedly given at the posterior end the crawling is continued, becoming more and more rapid. This is the only effect of continued stimulation in this region, there being no summation effect corresponding to that produced by stimulating the anterior end. No different effect is produced by stimulating the margins of the posterior region of the body from what takes place when the point stimulated lies near the middle line. There is no turning towards or away of any part of the body. The lack of any special effect of unilateral stimulation is not surprising, for the reason that rapid movement in a forward direction will get the animal away from harmful stimuli affecting this region, in the long run, more quickly than any other. Further, there would be no advantage in the production of a positive reaction by stimuli at the posterior end. If we think of these reactions as having been developed by natural selection there would be no possibility of such a reaction having arisen, for the reason that practically any favourable stimulus would be encountered by the anterior end before it possibly could be by the posterior. Very weak mechanical stimulation of the posterior end of the body causes only a local contraction at the point stimulated.

4. Reactions to Stimulation of the Ventral Surface.—In the descriptions of the reactions to mechanical stimuli up to this point we have been considering stimuli applied to the dorsal surface and to the margins of the body. It may be well to describe briefly what the reactions in response to localised stimulation of the ventral surface are. This matter can best be tested when the animal is moving on the under side of the surface film, with its ventral side uppermost. It might be supposed before the trial was made that this habit of the animal would afford ideal conditions for testing its reactions to ventral stimulation, but, as a matter of fact, the conditions are anything but ideal. The flexibility and elasticity of the surface film makes it almost impossible to touch it with a stimulating point anywhere within a radius of a centimetre about a planarian without causing the animal to be jerked bodily to one side or the other, quite sharply and for some little distance. This is, of course, a mere mechanical effect, which takes place with lifeless bodies also. Furthermore, as has been mentioned in an earlier section, it appears to be very difficult for planarians to quickly change the direction of their movement when on the surface film (as is necessary in reacting to stimuli). On account of these

conditions it is very difficult to get any certain and trustworthy results from the stimulation of the ventral surface. My results have been as follows:—strong stimulation of the anterior end on one side of the middle line causes the negative reaction just as when the stimulus is applied at a corresponding point on the dorsal surface. For mechanical reasons the response is not as extensive as when the animal is on a solid, but there seems no doubt of its character. The positive reaction to weak stimuli I have not been able to produce in any certainly recognisable form in response to stimulation of the ventral surface, but I think this negative result is due probably to the external conditions, and not to a real failure of the organism to react. Strong stimulation of the posterior end of the body causes the gliding to change to the crawling just as under other conditions. Very strong mechanical stimulation of the ventral surface of the body causes the animal to let go its hold and pass down to the bottom.

5. Reactions of Resting Specimens to Mechanical Stimuli.—A resting specimen gives no response whatever to weak stimuli which are still strong enough to produce a definite reaction when the worm is in the active condition. The stimulus is simply below the threshold of the resting animal's sensitiveness. To stronger stimuli the reactions correspond in form with those given by the active animal, but are less pronounced. For example, rather strong stimulation at the anterior end induces a weak negative reaction; similar stimulation of the posterior end sets the animal off into the crawling motion. Strong stimulation of any part of the body besides producing the characteristic reaction for that region (that is the negative reaction) will also in most cases start the animal into movement. This will always be the case if the stimulus is of sufficient strength, or is several times repeated. As would be expected from the low sensitiveness of the resting flat-worm, it is impossible to call forth from it any positive reaction.

6. Reactions to Stimuli given by Operative Pro-

cedure.—Evidently when a planarian is cut the cutting induces a strong stimulation, which is of the same kind as that induced by ordinary mechanical stimuli, only much more intense. The immediate effects of operations may then be taken up in this section.

If we take first the typical case given by cutting the animal transversely in two in the region between the posterior border of the head and the origin of the pharynx, and make the cut by a single stroke of a sharp scalpel, we find that the effect on the anterior piece is precisely the same as that of an ordinary strong mechanical stimulation of the same place. That is, this piece merely changes from the gliding to the crawling movement, and after giving three or four crawling contractions settles down again into the glide. This is the same result essentially as that obtained by Norman (: 00) and earlier by Loeb ('94 and : 00). In the behaviour of the posterior piece in this experiment under discussion there is a great deal of variation. In about 70 per cent. of all cases in which I have observed the results of such an operation, the posterior piece crawled backwards as a result of the cut. In the remainder of the cases the piece either stayed in the same place and contracted violently, or else glided ahead. The amount of the backward crawling when this occurs varies greatly, from a short distance involving only one longitudinal crawling contraction to several times the length of the worm, the movement lasting in this latter case for over a minute. In order that this backward crawling may appear in a well-marked and distinct form it is necessary that the posterior piece be above a certain size. Very small posterior pieces after operation usually remain quiet.

A cut so made as to split the anterior end of the body in the middle line in most cases causes the worm to crawl backwards just as does a transverse cut. In some cases this, as well as other operations, merely causes the animal to contract violently and squirm about at the same place. Splitting the posterior end of the body in the middle line causes the parts on either side of the cut to give violent longitudinal contractions, while the worm as a whole starts crawling ahead; that is, it changes from the gliding to the crawling movement.

Oblique cuts produce essentially the same effects as would transverse cuts in the same part of the body, i. e. forward crawling of the anterior piece, and usually backward crawling of the posterior piece. This is true unless the cuts are very oblique, so as to form very acute angles with the sagittal plane of the body. In such cases the effects produced more nearly resemble those obtained in complete longitudinal splitting of the body. If the body is split completely into two parts longitudinally, there is usually very little progressive movement of either piece afterwards. The pieces contract strongly on the cut sides very soon after the operation is performed, so that they take on the form of a bow, which in many instances becomes a nearly complete circle. This being the case, any progressive movement, either by gliding or crawling, is nearly or quite impossible. Cuts involving only a small portion of one side of the body produce, if in the anterior region, the characteristic negative reaction given to other strong mechanical stimuli, while if in the posterior region they cause the crawling ahead.

Cuts made on the resting animal produce essentially the same effects as on the gliding specimen. Unilateral cuts have the same effect in producing the negative reaction.

7. The Effect of Mechanical Hindrance to Movement.—A series of experiments was performed on Dendrocœlum, sp., with reference to the behaviour of the animal when progressive movement was made impossible, and yet the animal was stimulated strongly at the same time. These conditions can be realised by thrusting a needle through the centre of the body from above, and then holding it fixed in position. The results of this procedure varied somewhat, according to the portion of the body through which the needle was thrust. In case the hindrance is in the posterior region of the body, e. g. at a point just behind the posterior

end of the pharynx, the effect immediately following the thrusting in of the needle is a strong longitudinal contraction of the whole body. After this first strong contraction the animal remains perfectly quiet in the contracted form for a varying length of time (in some cases as long as five minutes, but usually less). After this period of quiet a series of rhythmical waves of contraction pass longitudinally over the still contracted body. The purpose of these waves is evidently to loosen the restraining object by making the hole in the body through which it passes larger. This is the same behaviour that I have observed in the deposition of the large egg. This process of rhythmical longitudinal contraction is continued for a time; then the animal stretches to its extreme length, attaches the anterior end to the substrate, and attempts to crawl away. The movement of the anterior end is precisely the same as in crawling. The animal turns and twists and struggles violently in this attempt to crawl away, and the cilia beat strongly. If the needle occupies a position near the edge of the body this first struggle will usually be sufficient to tear the body loose from the needle, so that the animal may then move ahead freely. Such specimens will, of course, have a large jagged wound in one side of the body, which, however, closes in and heals in a short time. In case the first struggle of the extended animal to crawl ahead is not effective, that is if the needle is too far in towards the centre of the body to make the tearing out possible, the animal, after continuing the struggle for a time, contracts strongly longitudinally and goes through the whole series of stages of quiet, rhythmical, longitudinal contraction and attempted crawling again. The only difference between the first and succeeding series of trials is that the stages in which the animal is strongly contracted longitudinally tend to become shorter with each repetition.

In case the needle is thrust through the body in front of the pharynx, the strong longitudinal contraction appears as before, and is followed after some time by an extension of the part in front of the needle, while the rest of the body remains quiet and contracted. This short anterior region, including hardly more than the head, goes through the crawling movements, but on account of its small size is very ineffective so far as pulling the body away from the needle is concerned. In my experiments I have never seen any worm succeed in getting free from a needle put through the body in this position.

This general behaviour of the animal in response to restraint of movement is very interesting, especially in the cases where the restraint is at the posterior end, as showing the relation between the behaviour and the capability of regenerating. The organism tears itself loose from a restraining body with entire nonchalance, as it were, and its confidence is well founded because no permanent harm comes from the action. The lost and wounded parts are regenerated and healed in a short time. The behaviour takes advantage of the ability to regenerate. Whether the form of behaviour (pulling away from restraining objects) or the power of regeneration and reparation appear in the organism first we cannot say, for either might very well follow, in a more or less remote causal connection, the other. What we do know is that at present there is a very nice condition of mutual adaptation between the two things.

The effect of the hindrance of a rather light weight at the posterior end of a worm is to induce the crawling movement. This can be seen in case the animal is feeding on a small piece of food material, and, as frequently happens, starts into movement before the pharynx is withdrawn. The piece of food attached to the end of the pharynx is dragged along behind, and the movement is the crawling. Frequently, also, in feeding experiments pieces of food will get stuck to the posterior end of the worm by means of the mucous secretion of the body, and these have the same effect in inducing the crawling movement.

Having now obtained a descriptive basis we may pass to a discussion of some general features of these reactions. We may first take up—

c. The General Features of the Reactions to Mechanical Stimuli.—From the above description it appears that the nature of the reactions to mechanical stimuli depends upon several factors. These are—

1. The intensity of the stimulus.
2. The localisation of the stimulus.
3. The physiological condition of the organism.

The reactions given may be of several different kinds, depending on the factors mentioned above. These are chiefly as follows:

1. The resting individual may begin locomotion.
2. The gliding movement may be changed to the crawling movement.
3. The forward movement may be transformed to movement backward.
4. The animal may turn away from the source of the stimulus (the "negative" reaction).
5. The animal may turn towards the source of the stimulus (the "positive" reaction).

It is evident that the reactions last named—the negative and positive reactions—are the most important and most interesting from the theoretical standpoint. It is of the greatest interest to note that these two qualitatively opposite reactions are induced merely by differing intensities of stimuli, the stimuli being otherwise identical throughout.

It is to be noted further that the positive and negative reactions have the characteristics of purely reflex acts. Each reaction has a perfectly definite and characteristic form. While, in some cases, which of the two reactions will be given in response to a particular stimulus depends on the physiological condition of the organism, yet it is practically always either one or the other of the typical reactions. Only very rarely do we get any deviation from the type forms, and in such cases the reaction is evidently a combination of easily recognisable components of the two typical complexes of reflexes.

These two reactions are evidently not single simple reflexes, but are complexes of several simple reflex acts. It may be well to present in tabular form the different components in each of these reactions, indicating by the position in the table the relations of the parts.

Component Phases of the Reactions to Mechanical Stimuli, with special reference to the Head Region.

Positive.	Negative.
A. Momentary stopping of previous movement. Referred to as "pause" or "hesitation" in description.	A. Same as in positive.
B. Longitudinal extension of the anterior end to greater or less extent. Amount depends on previous extension. Usually distinctly noticeable.	B. Longitudinal contraction of anterior end of greater or less intensity. Tends to make A appear more pronounced and longer in duration.
C. Turning towards one side, viz. that stimulated. This side is defined by the position of the source of the stimulus, not structurally. Sharp "orientation."	C. Turning towards one side, viz. that not stimulated. Defined as in positive. No sharp "orientation."
C′. Raising of anterior end. This takes place at the same time as C.	
D. Movement towards stimulus. Direction determined by position taken by anterior end at termination of C.	D. Movement away from stimulus. Direction determined as in positive.

Time relations are indicated by vertical position in the table. Components occurring at the same time are included in braces.

Each of the components before D may be considered as a single reflex, and thus there are in one case four and in the other case three simple reflexes which go to make up the whole reaction. That these reactions are composites of the distinct parts is evidenced, first, by direct observation of the reactions themselves; and second, by the fact that it is possible by varying the strength of the stimulus to produce only certain parts of the whole reaction without the remainder, and, furthermore, that a part of one reaction may in rare instance be combined with a part of the other (v. sup., p. 587).

d. Mechanism of the Reactions.—A question which is of the greatest importance in all work on the reactions of organisms is, what is the mechanism of the reaction? In the case of the flat-worm this becomes, what is the neuromuscular mechanism of the reactions? Very little direct evidence bearing on this question can be obtained from the reactions themselves. Taking the positive and negative reactions as they occur, there are several different sets of muscles and of nerve connections by means of which they might conceivably be brought about. The best evidence on the question is the indirect evidence from operation experiments, in which parts of the mechanism are injured or removed.

1. Relation of the Brain to the Reactions.—The first specific problem which may be taken up may be stated thus: is the brain necessary for the performance of the normal reactions to mechanical stimuli? Or, in other words, will a planarian from which the brain has been removed react normally to stimuli? This question can be answered from the study of specimens which have been cut in two transversely, and consequently we may proceed at once to a description of the reactions of the pieces resulting from such an operation. A typical specimen is cut in two transversely at the level of a point about halfway between the head and the origin of the pharynx, as shown in Fig. 16. As has been mentioned above, the cut itself acts as a strong mechanical stimulus, and the immediate effect of the operation is to set both pieces crawling, the anterior one ahead and the posterior one usually backward.

If now the pieces are allowed some hours to recover from the immediate effect of the operation, and then stimulation is tried, the following results are obtained:—With the anterior piece A, containing the brain, the results are entirely similar to those obtained in case of the normal animal. Strong unilateral stimulation of the head causes the negative reaction, weak stimulation of the same sort the positive reaction. Stimulation at the posterior end causes the crawling movement to appear, and altogether the appearances are essentially the same as in the normal complete specimen.

The posterior piece B (lacking the brain) behaves in a somewhat different manner. If the anterior end of this piece is given a stimulus of moderate intensity anywhere on the cut surface the piece will usually start crawling straight backwards. This is almost always true for a short time after the operation, and is especially well shown in such specimens as started crawling backwards as a result of the cut. When from twenty-four to forty-eight hours have elapsed after the operation this tendency of posterior pieces to crawl backward on stimulation of the anterior end begins to grow less marked, and, as regeneration proceeds, finally disappears. In many such posterior pieces I have been able to produce this backward crawling in a very pronounced form, and of comparatively long duration (three or four minutes at a time). The character of the movement has been described above. If the stimulus is applied to one side or the other of the anterior end of such a posterior piece, instead of squarely against the cut surface, a well-marked negative reaction is produced; that is, the anterior end turns away from the stimulus just as a whole animal would. The reaction is very definite, and of precisely the same character as the normal negative reaction. The only difference to be observed is that in proportion to the strength of the stimulus the reaction is not so pronounced as in the

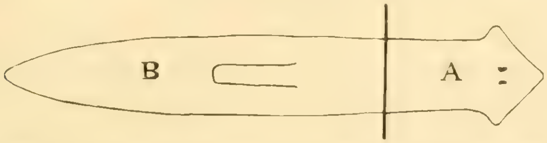

FIG. 16.—Operation diagram. Heavy line indicates cut.

normal animal, this being due to the generally lowered tonus in such a piece. I have not been able to obtain any positive reaction (i. e. turning towards the stimulus) in such a posterior piece after operation. Stimuli which are at all effective produce the negative response. This experiment has been tried many times, but always with the same result; the positive reaction never appears. If the posterior end of such a posterior cut piece is stimulated the crawling movement is produced just as in case of the normal complete animal. As has been noted in connection with the movement, there is a general reduction of tonus in the posterior pieces resulting from transverse cuts. This low tonus involves not only the motor functions, resulting in slower movement, but also to a less extent the sensory functions. Such a piece is somewhat less sensitive to mechanical stimuli than normally. The cut surface is more sensitive to mechanical stimuli than any other part.

Now it will be seen from the above description of the reactions of a piece from which the brain has been removed, that the most striking difference in the behaviour of such a piece from that of a normal animal is to be found in the absence of the positive reaction.

There are three conceivable possibilities as to the cause of the absence of the positive reaction in pieces from which the head has been removed. First, the positive reaction might be due to the stimulation of certain sense organs which are removed by the operation. But this is decisively negatived by the fact that in an entire worm stimulation of points posterior to the level of the cut removing the anterior end will cause the positive reaction.

Second, it might be conceived that the reaction is brought about by a special localised muscular mechanism, which is removed or destroyed by the cut. But there is no evidence of the existence of such a mechanism; and further, it will be shown later that the ordinary musculature of the body, which is of course uninjured in the posterior part, is sufficient to bring about the reaction.

Finally, the positive reaction might in some way be a specific function of the brain, which is removed by the operation. As the evidence seems to be decisive against the first two possibilities this seems probably true. Is this because the brain contains a special "centre" whose function it is to produce the reaction?

There is no reason to think of the reaction as a function of the brain in the sense that that organ forms a centre which originates the impulses which cause the reaction. On the contrary, it seems much more probable that the loss of the brain causes the loss of reaction for the following reason. It has been shown that removal of the brain causes a general lowering of the tonus of the organism, and further that the appearance of the reaction in a normal animal is closely dependent on the tonic condition of the organism. Probably, then, the chief reason for the non-appearance of the positive reaction in posterior pieces is that in these the conditions of general tonus are so changed by the loss of the brain that the reaction is no longer possible. Expressing it in another way, the animal is too sluggish to give the positive response. This being the case, it would be expected that it might be possible to induce the positive reaction in a decapitated specimen provided the tonus were raised in some way. As a matter of fact, as will be shown later, positive reactions to certain chemical stimuli have been observed in a few cases (cf. p. 649). In its form and mechanism the positive reaction is not directly dependent upon the brain.

Summing up the evidence on the relation of the brain to the reactions of the flat-worm, it may be said that all the reactions to mechanical stimuli shown by the normal animal, with the single exception of the positive reaction, are given by specimens from which the brain has been removed. The relation of the brain to the positive reaction is, in large part, so far as evidence can be obtained, an indirect one, viz. it is necessary for the maintenance of the proper tonic conditions of the organism. Thus far there is no evidence of any special "centre" functions of the brain, similar to those supposed to exist in the cortical centres, for example, of a mammal.

2. The Neuro-muscular Mechanism.—In the negative reaction to mechanical stimuli the anterior end of the body is turned sharply away from the source of the stimulation, while in the positive reaction it is equally sharply turned towards the source. These relations immediately suggest the following questions :—Is the negative reaction the result of a crossed impulse, which, originating at the point stimulated, crosses over to the other side of the body and causes the contraction of the longitudinal muscles on that side, thus producing the turning away from the stimulus? What is the course of the nerve impulse which produces the positive reaction? What sets of muscles are concerned in the production of each reaction?

The discussion of the negative reaction may be taken up first. If the nervous impulse producing this reaction crosses the body to produce a contraction on the side opposite from the stimulus, the experiment cited in the section above shows that this crossing cannot occur entirely in the brain, but must also occur in some part of the body posterior to the brain; or at any rate, be capable of so doing in a quite normal fashion immediately after removal of the brain. In this experiment where the body has been cut in two behind the brain, the posterior piece performs the negative reaction in a quite normal way immediately after the operation. This experiment may be carried farther, and the animal cut in two transversely in places nearer and nearer to the posterior end of the body. In all of these cases, until the piece becomes too small to show definite movements of any sort, the negative reaction may be obtained by strong unilateral stimulation. This shows conclusively, then, that if the negative reaction is to be considered a crossed reflex, there must be all along the body a series of cross-commissures which are at all times ready to bring about in co-ordinated perfection a result with which they have never previously had anything to do. This conclusion seems inevitable because, as has been shown above, unilateral stimulation of the posterior region of the body in a normal individual does not cause the negative reaction, but instead merely causes the animal to move ahead faster by crawling. If these paths for the crossing of impulses which are so immediately effective after the operation are present in the uninjured specimen, one would expect the reaction to be of quite a different character from what actually occurs. A stimulus applied near the posterior end would naturally cross over at once and produce a bending on the opposite side at the same level. Or the stimulus might diffuse, so that the entire opposite side would be affected and the worm would become uniformly curved on that side. But as a matter of fact we find that the turning affects only the anterior portion of the body. If it is urged that after operation the crossing of impulses takes place through the general protoplasm the difficulties encountered are no less, for it must be shown how passage of an impulse through the protoplasm to cause a perfectly well co-ordinated reaction can appear so quickly and produce such perfect results at once. If tested immediately after the operation, before the general lowering of tonus is felt, the reaction time for the negative response of a posterior piece of the body will not differ appreciably from that of a normal worm. Now, according to the views of the advocates of the theory that after operations involving loss of nervous tissue, impulses may be conducted through the general protoplasm, it is held that such conduction is always at first appreciably slower than in nervous tissue. It would also seem on purely a priori grounds that this must be true.

Thus it is seen that there are serious objections to the view that the negative reaction is the result of a contraction on the side of the body opposite to that stimulated—that is, that it is a crossed reflex. The question now arises, if the reaction is not produced in this way, in what other way can it be produced? Evidently it is quite possible that the anterior part of the body can be turned away from the stimulus by a lengthening of the side stimulated, quite as well as by a shortening or contraction of the opposite side. We may now consider the evidence as to whether or not the turning away is actually due to a lengthening of the side stimulated.

Very little evidence can be obtained regarding this from observation of the normal moving animal, because the general appearance in the turning would be the same whether it were due to a shortening of one side or a lengthening of the other. The results from certain sorts of operation, however, give definite evidence on the question.

A specimen split longitudinally in the posterior end, as shown in Fig. 17, *a,* and the cut was extended forward to the posterior border of the head region. Several days were allowed for recovery from the shock of the operation, care being taken to prevent the two parts from growing together again. By this time the cut edges had healed well, and the specimen was in good condition for experimentation. The results of mechanical stimulation were as follows: strong stimulation of the head or anterior part of the body on either side caused the negative reaction; the anterior end turned away from the stimulus. But it was possible to tell in this case which of the two pieces or halves of the body were effective in producing the turning. It could be seen clearly that the half stimulated, immediately on stimulation, flattened

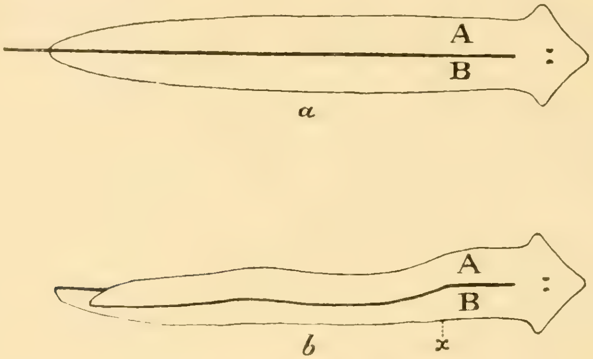

Fig. 17.—*a.* Operation diagram. *b.* Showing side A supported on B. For further explanation see text. (The pharynx is omitted for the sake of clearness.)

out slightly ventrally, thus bringing the ventral cilia in close contact with the bottom, as is necessary for their effective working. At the same time it lengthened along its outer side, thus forcing the anterior end around towards the side opposite from the stimulus. That the "side opposite" had nothing to do with the turning could be observed in many cases directly, for this side (B) would remain in an almost entirely relaxed condition after the stimulus was given, and not get any effective hold on the bottom so that it could affect the movement. It was further possible by a little manipulation to get the piece B laid over on A so as to be practically entirely supported by it, as shown in Fig. 17, *b*. If with such conditions the worm was stimulated rather strongly on the A side of the head, it gave a strong negative reaction, the point about which the turn was made being as far back as *x*. Evidently with part B up on the dorsal surface of A, and consequently having no hold on the bottom, it could have no effect in the reaction. The reaction must have been due to the side A alone. The same thing could be shown by very gently lifting on a needle the side B so that it was not in contact with the bottom, and then stimulating A, when again the negative reaction occurred. This experiment I have repeated with variations many times, but always with the same result, showing that the side stimulated is the effective one in producing the turning.

It may be mentioned here that the effect of strongly stimulating the posterior end of either of the two pieces of a specimen slit in this way was to cause a local contraction of the piece stimulated, and a crawling movement of the short portion of the body in front of the slit. This crawling was not very effective, since so small a portion took part in it, but it is of interest to note that what crawling appeared involved only the uncut part of the body.

It being established that the side stimulated produces the turning, the question may be raised, how, supposing in these longitudinally split individuals that this side does produce the reaction, is it known that it does this by lengthening along its outer margin rather than by actively contracting on its inner cut margin? This question may be answered by operative experiments of a different character. If the side stimulated, acting independently, produces the reaction by lengthening on its own outer side, then an isolated longitudinal half of the body ought to be able to give only one reaction wherever stimulated, or, in other words, it ought always to turn towards the same side. Furthermore, such a piece ought always to turn towards the cut edge, since only on the side opposite to this has it a margin possessing the necessary circular muscles for extension (vide sup., pp. 556, 557). On the other hand, if the contrary view is correct, that the turning away is due to contraction of the longitudinal muscles on the side opposite that stimulated, then such an isolated longitudinal half of the body ought to be able to turn either way, according to the localisation of the stimulus, since there are longitudinal muscle-fibres along the cut edge as well as along the other. We may determine from experiments which of these two views is correct.

Fig. 18.—Showing the appearance of a longitudinal half of a planarian when at rest.

Unfortunately, it is impossible to get any clear evidence on this point from entirely separated longitudinal halves of the worm. When a planarian is split in two lengthwise each of the pieces immediately becomes strongly contracted longitudinally on the cut side, the apparent purpose of this reaction being to reduce the exposed surface at once to a minimum. After this strong contraction has taken place, giving the piece the form shown in Fig. 18, no further progressive movement can take place, and the general tonus becomes immediately very much lowered. In view of these facts it is impossible to get any very trustworthy results from the stimulation of such a piece.

There is another operation, however, which, while it does not isolate completely two longitudinal halves of the body, yet does separate into longitudinal halves the essential reacting parts, namely, the head regions. This is the splitting of the worm in the middle line for a short distance back from the anterior end, as shown in Fig. 12. After this operation the two anterior pieces move about violently and independently for a time, taking all the various positions shown in Fig. 19. The animal soon recovers from the immediate effects of the operation, glides about in a normal way, only at a rather slow rate, and responds well to stimuli. The anterior piece keeps comparatively straight, there being much less tendency to contraction on the cut side than when the split extends the whole length of the body. The reactions of such a specimen to mechanical stimuli are as follows. To stimuli applied at the posterior end along the sides of the body the reactions are precisely the same as those already described for the normal individual. Stimulation in the regions *a a* (Fig. 20) of moderate or strong intensity produces the negative reaction. The organism turns away from the

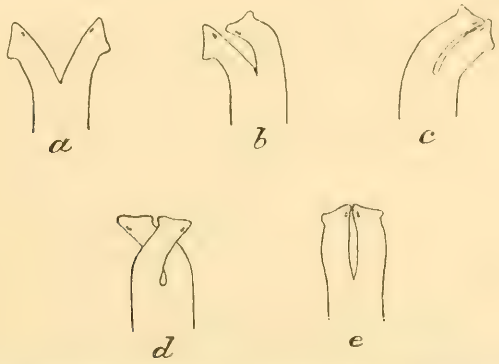

FIG. 19.—Diagram showing the different positions taken by the two components resulting from longitudinal splitting of the head.

side stimulated quite as promptly and in the same way as does a normal specimen. If now the cut edges A and B (Fig. 21[1]) are stimulated in the same way (a needle may best be used for this) the specimen will always turn towards the stimulus. This can best be brought out by describing a typical case in which a series of fifty stimulations in the regions A and B were made on a favourable individual cut in this way. In thirty-nine of the reactions the animal turned towards the stimulated side. That is, if the stimulus was applied at A the animal turned in the direction of the arrow *a*; while if B was the stimulated edge the reaction was in the direction of the arrow *b*. In eight of the remaining eleven trials the reaction was indifferent. The animal stopped at stimulation and then started moving straight ahead again, the stimulus evidently having been ineffective so far as special reaction is concerned. In only three cases out of fifty did the specimen turn away from the stimulus. Since it required the greatest care in manipulation to give the stimulus to one cut edge without touching the other side, especially in view of the fact that the animal was moving all the time, it seems very probable that in these three cases a stimulus was accidentally given to the side which it was not intended to stimulate. The same general result of turning

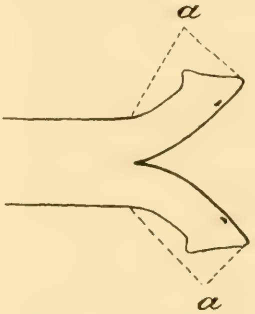

FIG. 20.—Operation diagram. See text.

---

[1] After this operation the two parts of the head usually take the position shown in this figure after the first spasmodic movements following the operation have ceased.

towards the stimulus when applied to the cut edge was obtained in several other series with this same specimen, and many times with other specimens similarly mutilated. It will be seen that this is the result which would be expected if the turning away is due to lengthening of the side stimulated. Stimulation of either side of the cut portions, inner or outer, causes turning in the same direction, and that direction is the one in which turning would be caused provided each piece did actively lengthen on its outer side. There seems to be no reason whatever, if the turning away were due to contraction of the side opposite that stimulated, why the specimen should not turn away from stimuli applied to the cut inner edges. This it does not do. There seems to be no escape, then, from the conclusion that the turning

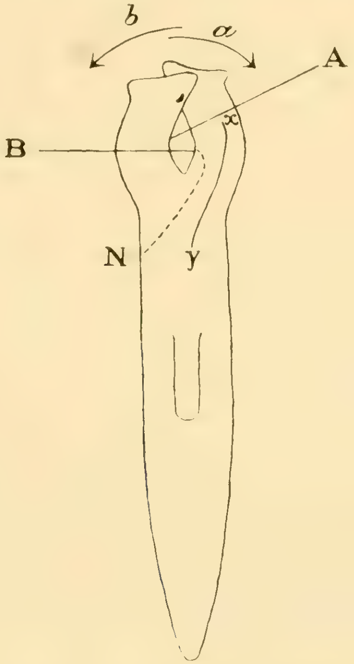

Fig. 21.—Diagram to show the reactions to mechanical stimuli and their mechanisms in the case of a specimen in which the head has been split longitudinally. For further explanation see text.

away from the stimulus (negative reaction) is due to a lengthening of the side stimulated.

It may possibly be objected to the last experiment that the impulse from a stimulation at, for example, B (Fig. 21) took the path indicated by the dotted line in that figure, and caused a contraction on the left side of the body, so that really the observed turning was the result of a contraction on the side opposite that stimulated. To this objection it may be answered that by stimulating different points along the edge B it is possible to cause the point about which the turn occurs as a pivot to be located anywhere along the line $x\,y$. It is very evident that contraction of muscles in the region N can have nothing whatever to do with turning of the right piece about the point x. So this objection is without force.

As the process of regeneration of a cut longitudinal half of the body goes on, the piece will straighten out from the curved form it takes after the cut is made, and it is consequently possible to obtain specimens in which the regeneration of the missing half of the body has produced only a very small amount of new tissue, and which are at the same time nearly straight in outline and able to make progressive movements. The reactions of such partially regenerated specimens are of importance as throwing light on the normal mechanism of the reactions. The reactions of a typical specimen of this sort may be described in detail. On October 10th, 1901, a small piece of the anterior end of a specimen of P. maculata was isolated. The piece was cut as nearly as possible in the form shown in Fig. 22, *a*. On October 16th the piece had the form shown in Fig. 22, *b*. A narrow strip of new tissue had formed down the right side, and the formation of the outline of the head and of the right eye was just beginning. At this time the reactions of the specimen were as follows. Stimuli applied at y caused the head to turn sharply away from the stimulus (typical negative reaction). This reaction was quite like that given by a normal individual stimulated in the same way. Stimulation at x, however, produced no trace whatever of a negative reaction. On stimulation at this point the specimen contracted longitudinally, and then started moving ahead again in exactly the same direction in which it was going before stimulation. It was impossible to induce any turning away following stimulation of the side *x*, although this was tried many times.

Now it is evident that this specimen comes very near to being an isolated longitudinal half-planarian. All the structures of the original one half are present, and there is only a very little of the other side of the body produced in the line of new tissue, down the originally cut edge. In this new tissue there is probably very little differentiation, and the muscle layers are not well formed. It was brought out above (p. 610) that an isolated half of the body ought to be able to give only one reaction, or, in other words, ought to be able to turn the body in only one direction in response to stimulation, provided this turning is due to an extension of the stimulated side. We find precisely this result in the regenerating specimen just discussed. It turns away from stimuli applied at *y* because on that side are present all the muscles necessary for extension just as in a normal animal. It does not turn away from stimulation of the side *x* because it has not the necessary muscles for extension on that side. On the view that the turning away is due to contraction on the side opposite that stimulated, there is no reason why stimulation at *x* should not cause the animal to turn away from the stimulus, because the opposite side (*y*) has all its muscular mechanisms intact.

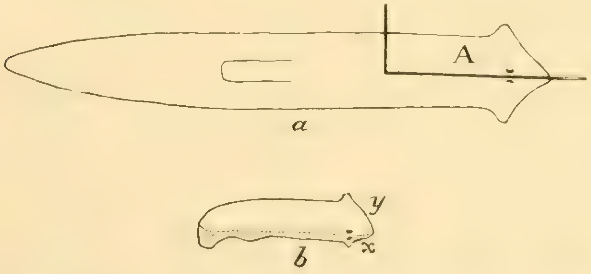

FIG. 22.—*a*. Operation diagram. *b*. Piece which regenerated from A in Diagram *a*. The new tissue is indicated by stippling.

The reason why the specimen in this last experiment does not turn towards the stimulus when stimulated on the side x, is apparently because the regeneration has proceeded only far enough to produce just enough new tissue to form the beginning of a new side to the body. This new side receives the stimulus and is sufficiently potent to determine the reaction of the whole (the straight longitudinal contraction), but is lacking in the mechanism necessary to produce its own proper reaction, the negative reaction. On the other hand, in the case of the individual with the split anterior end, each piece turns towards the stimulus after stimulation of the cut edge because here only one half the organism is present either to be stimulated or to react; there is not even the beginning of the formation of a new side along the cut edge.

Putting all the evidence together, I think it must be regarded as demonstrated that the turning away from the stimulus in the negative reaction to mechanical stimuli is due to an extension of the side of the body stimulated. This extension is brought about by the contraction of the circular and dorso-ventral muscle-fibres—probably also assisted by the transverse and oblique systems of fibres—in the region stimulated. This reaction is a simple reflex act involving only the side stimulated. The normal organism, so far as this response is concerned, is to be considered as composed of two identical, but in a certain sense independent longitudinal halves. Thus, representing these halves diagrammatically, as in Fig. 23, *a*, the evidence presented indicates that stimulation of one side of the worm, as A, causes a reaction in that side, and, so far as essential features of the directive reactions go, only in that side. The movements of half A after its stimulation determine and, in fact, cause the reaction of the whole animal. Furthermore, these longitudinal halves retain their individuality as halves if they are isolated from each other. A separated half-worm (longitudinal) reacts as a half-worm, just as it did when in connection with the other half in the body, and not, as might perhaps be expected on a priori grounds, as a whole worm. It reacts as a whole worm only after a new half has been regenerated along its cut edge. The various stages in the change from the reactions as a half-worm to those as a whole worm can be followed step by step as regeneration proceeds. The new tissue formed along the cut edge very quickly takes on some of the functions of a side. When only a narrow strip has been formed it serves for the reception of the stimulus, and hence stops the reaction of the opposite side, as in the experiment last discussed. To make the meaning more clear, reference may be made to diagrams *b* and *c* of Fig. 23. In *b* is represented, in a straightened position, the half B of a normal worm immediately after being separated from the other half, while *c* represents the same half after regeneration has begun and a strip of new tissue has been formed down the cut edge. Now stimulation of the cut edge of *b* causes the anterior end of the piece to turn towards the stimulus, i. e. to give its own proper negative reaction (cf. experiment given above on slitting anterior end). This is because in this case it is side B that is stimulated, although along its inner edge. Stimulation along the right-hand edge of *c* does not cause the turning towards the stimulus, because in order that this

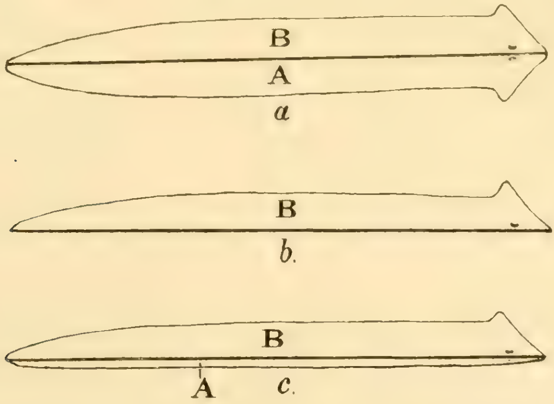

FIG. 23.—Diagrams to show the relations of the halves of the body of Planaria to the reception of stimuli, and the reactions thereto. See account in text. (The pharynx is omitted for the sake of clearness.)

may take place it would be necessary for the side B to give its proper negative reaction. It cannot do this because it is not directly stimulated, but the new very small side A is stimulated. This side may not have the necessary muscles to give a negative reaction itself—as in the experiment described above,—yet may receive the stimulus and so indirectly prevent B from reacting. Another way of expressing this same fact is by saying that in regenerating longitudinal halves of planarians the physiological middle line remains at the line of the former cut edge for some time after regeneration has begun.[1] In connection with this discussion of the reactions of half-animals it is greatly to be regretted that Willey ('97) did not get any data on the reactions of the remarkable form Heteroplana. In this form we have a natural "half-planarian," or very nearly that. One side is so greatly atrophied as to be practically absent. It seems to me very probable that this organism would react to stimuli in much the same way that a longitudinally split specimen of Planaria, which had begun to regenerate, does.

I do not wish it to be understood from the analysis of the negative reaction which has been given that I intend to maintain that in this reaction the side opposite that stimulated never contracts longitudinally. It probably often does this, especially in cases of very strong stimulation which cause a general excitation and reaction of the whole body. I have merely wished to show that the fundamental basis of the negative reaction is the extension of the side stimulated. It seems to me quite possible that it may be shown by close analysis in other cases that supposedly crossed reflexes are not fundamentally such at all.

We may now pass to a brief consideration of the mechanism of the positive reaction of the planarian to mechanical

---

[1] I have records in my notes of experiments which show that in the case of oblique cuts the physiological middle line remains at the cut edge until after the new head is well formed in the new tissue on the oblique edge. Lack of space forbids detailed description of these experiments here.

stimuli. As has been shown above, removal of the anterior end of the body containing the brain causes the disappearance of this positive reaction, and this result is probably due rather to the lowering of tonus than to the removal of any special centre having the causation of this reaction as its function. Additional evidence on this view that lowering of the tonus is the chief cause of the disappearance of the reaction is found in the fact that other injuries to the head, such as longitudinal splitting, which produce a lowering of the general tonus, also cause the disappearance of the positive reaction.

This very close dependence of the reaction on the general tonic conditions of the organism makes its analysis difficult, but it seems most probable that its mechanism is as follows:—a light stimulus, when the organism is in a certain definite tonic condition, sets off a reaction involving (1) an equal bilateral contraction of the circular musculature, producing the extension of the body; (2) a contraction of the longitudinal musculature of the side stimulated, producing the turning towards the stimulus (this the definitive part of the reaction); and (3) contraction of the dorsal longitudinal musculature, producing the raising of the anterior end. In this reaction the sides do not act independently, but there is a delicately balanced and finely co-ordinated reaction of the organism as a whole, depending for its existence on an entirely normal physiological condition. It is to be noted, however, that the definitive part of the reaction, namely, the turning, is a response of the side of the body stimulated. This point is one of fundamental importance for the general theory of the reactions.

The mechanism of the other reactions to mechanical stimuli are evidently very simple. The crawling movement, which must be considered as the specific reaction to mechanical stimulation of the posterior region of the body, is due to rhythmical contraction of the longitudinal musculature. The only other reactions to mechanical stimulation are local contractions, whose mechanism is evident.

e. Features in the General Behaviour of the

Organism which the Reactions to Mechanical Stimuli explain.—That much of the behaviour of planarians in their natural surroundings is the result of the reactions above described is very evident to any one watching them. Among specific features of this sort in which these reactions play a part may be mentioned the escape from enemies or harmful surroundings, the getting of food (to be discussed in detail later), the localities chosen for coming to rest, the behaviour on meeting solid obstacles in the path of movement, the passing on to the surface film, etc. All of these need not be discussed specifically, as their relations will be evident enough on a moment's thought, but the last two deserve special mention.

The behaviour of planarians on meeting solid bodies in their path in the course of movement is entirely made up of reactions to mechanical stimuli. The behaviour in detail is as follows :—If a gliding specimen meets squarely head-on an obstruction of considerable size, so that it cannot glide over it without changing to some extent the position of its long axis, it will stop an instant, raise the head, let it drop down till it touches the obstruction again, and then glide directly up on to and over the solid body. This behaviour is invariable, so far as my observations go, if the worm meets the obstruction squarely. It is at once seen to be merely a special case of the usual reaction to a weak mechanical stimulus, characterised by the raising of the head. The behaviour is evidently purposeful in the long run, because it will take the organism up on to food material just as well as indifferent bodies. If the gliding worm meets the obstruction obliquely the behaviour depends in large part on the physical nature of the object. If it is food material, or something else of a rather soft and yielding texture—as, for example, another planarian,—the worm will immediately raise the head, turn it towards the object, and crawl up over it. This behaviour is evidently the typical positive reaction to a weak mechanical stimulus. A special and rather curious case of this positive reaction, which I have twice observed, appeared when two specimens gliding along, with the anterior ends slightly raised in the normal manner, met head-on. Both were simultaneously stimulated to the positive reaction and raised the anterior ends, and then let them drop again. As they came down the two ventral surfaces were brought squarely together in the way shown in Fig. 24; then each started gliding up the ventral surface of the other. In a movement as a result of the constantly changing form of the body, the ventral surfaces slipped off from one another and the two worms went on their way. When the obstruction is a hard body, as a piece of glass, the specimen meeting it obliquely usually turns the head away slightly at the first contact (negative reaction), and then glides along parallel to the edge of the body for a distance. If it happens to touch it again with the side of the head, it frequently gives the negative reaction and turns away again. After the solid body has been touched several times, however, the positive reaction is usually given, and the worm passes at once up on to the solid body. This behaviour is shown in Fig. 25. The precise form of the behaviour on meeting obliquely a solid body in the path varies considerably with the general physiological condition of the individual. In case it is much excited, the first touch will induce a strong negative reaction, and the individual will turn away and pass out of the neighbourhood. In the cases where the final positive reaction is preceded by two or three negative ones, it would seem as if repetition of what must be an almost identical stimulus causes it to become in effect weaker. Leaving aside all variations in the exact character of the behaviour on meeting a solid, the important point to be brought out is that all this behaviour is based on the simple reactions to mechanical stimuli. The

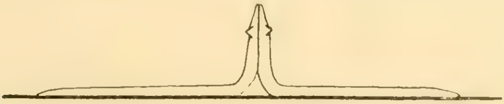

FIG. 24.—Side view of two planarians starting to glide up on the ventral surfaces of each other.

exact behaviour in any given case depends on several different factors. These are the position of the animal with reference to the obstruction, the physical nature of the obstruction, and the physiological condition, whether of greater or less excitation.

So, again, with reference to the habit of the animal of moving about on the surface film, a problem is presented. When a specimen, gliding up the side of a dish, touches its anterior end to the surface film at the point where the latter joins the glass, it immediately gives a characteristic positive reaction, precisely like that in response to any other weak mechanical stimulus. The head is raised and turned towards the side from which the stimulus came, and then dropped again. As a consequence of this reaction, the head end comes to rest on the under side of the surface film at a point some little distance out from the side of the dish. The ventral surface of the anterior end of the body flattens out on the surface film, and the animal glides out on to the film, following the direction determined by the reaction of the anterior end. Thus it is seen that the going on to the surface film is only a special case of a response to a weak mechanical stimulus, i. e. the positive reaction, the film itself acting as the stimulant. The leaving of the surface film and passing down the side of the dish is evidently also due to the same positive reaction.

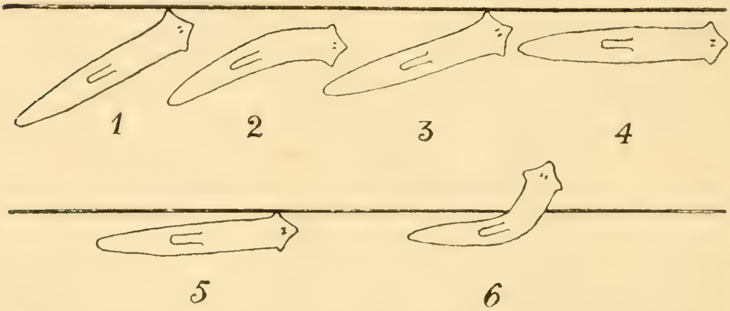

FIG. 25.—1, 2, 3, 4, 5, and 6 are successive stages in the reactions of Planaria on meeting obliquely an obstacle in its path. The heavy straight line represents the obstacle.

There are a number of other points in the general behaviour which are directly related to the reactions to mechanical stimuli, which will be taken up later in connection with the other reactions.

f. Summary.—Before passing on to a discussion of the next subject, it may be well to summarise briefly the chief findings with reference to the effect of mechanical stimuli on planarians.

It has been shown that the planarian responds in a well-nigh perfect manner to the localisation and intensity of mechanical stimuli. It turns away from strong stimuli (in the long run harmful) applied to the side of the body; turns towards weak stimuli (in the long run beneficial, almost never harmful); it crawls rapidly away from strong stimuli applied to the posterior end; backs and turns away from similar strong stimuli applied at the anterior end.

It has been shown, further, that these reactions have all the characteristics of reflex actions, complex, it is true, but still reflexes.

The mechanisms of the reactions to unilateral stimulation are unilateral, and lie in the side stimulated.

Discussion of the implications of these results on mechanical stimulation, with reference to the psychology of the organism and the general theories regarding the reactions of organisms to stimuli, is deferred till the results from other sorts of stimuli are in hand.

II. Reactions to Food and Chemical Stimuli.

Evidently one of the most important factors in the sum total of the activities of any aquatic organism is its reactions to chemical substances. Its ability to receive chemical stimuli and react to them must be of prime importance in its struggle for existence, for in its natural habitat such an aquatic organism must be almost constantly encountering different chemical substances. Some of these may be harmful and some beneficial, and it would seem that if a species is to survive, its individuals must have some sort of reaction whereby they may avoid the harmful and take advantage of the beneficial. In the case of planarians, the reactions to chemicals seem to be of about equal importance with the reactions to contact stimuli in the general activities. Since the reactions to food substances are a special case of the reactions to chemicals in general, they may be discussed first.

a. Food Reactions.—The nature of the things used as food by fresh-water planarians has been discussed already in the section on "Natural History," and hence need not detain us here.

A typical case of the food reactions to a bit of crushed mollusc may first be described, to serve as a basis for the account.[1] If a piece of the body of Physa which has just been extracted from the shell and crushed between the points of a pair of forceps is placed in a small dish containing a number of active planarians, it will result from chance alone that some of the flat-worms must in course of time pass near the food material. For a very short time after the food has

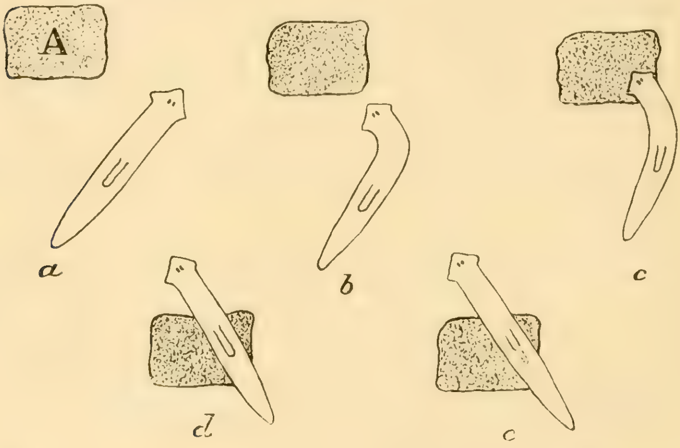

FIG. 26.—Diagram showing the successive stages in the normal food reaction of Planaria. A represents a small bit of meat.

---

[1] The food reactions of Planaria have been briefly described by Bardeen (:01, *a*).

been placed in the dish specimens may pass very near it—within two or three millimetres—without being affected in any way. They simply glide straight by as if there were no food there. After a few minutes have passed, however, it will be found that a worm coming near the food is affected in a very characteristic manner. Its behaviour is as follows:—When within about three or four millimetres of the piece of meat (Fig. 26, *a*) it stops abruptly, raises the head, and turns it towards the food (Fig. 26, *b*). As the head is raised and turned the gliding is resumed, and the head being almost immediately lowered, the movement is directly towards the food. Thus far the reaction is evidently precisely like the positive reaction to weak mechanical stimuli, and so we may speak of it as the positive reaction to food, the reaction being the same in the two cases, though the stimulus differs. When the anterior end of the head touches the food it flattens down upon it, and, if the configuration is such as to make it possible, "grips" it (Fig. 26, *c*). The details of this "gripping" (shown in side view in Fig. 27) are as follows:—The anterior end closes down over the very edge of the piece of food, or over the whole piece provided it is small enough, and then apparently squeezes it by contraction of the longitudinal muscles on the ventral surface of the head. The action is very characteristic, and evidently forms an integral part of the normal food reaction. Its probable function will be brought out later. While it is taking place the worm as a whole stops its progressive movement and remains quiet. After the "gripping" has continued for some time the worm starts gliding ahead up on to the food. It passes forward till the point where the opening for the extrusion of the pharynx is located is approximately over the place pre-

FIG. 27.—Diagrammatic side view of Planaria to show the "gripping" of a bit of food, A.

viously "gripped" (Fig. 26, *d*). Then the pharynx is extruded and feeding begins (Fig. 26, *e*). After a time the worm voluntarily leaves the food and glides off over the bottom.

Having described the typical case of a food reaction, we may take up some of the more important variations from the type, and describe the various phases in the reaction in greater detail.

Starting with the very beginning of the reaction, it may be said that the distance from the food at which any effect on the planarian is produced varies greatly, as is to be expected. This distance, of course, depends on the extent which the juices or chemicals of the food have diffused from it. When a piece of meat is first put into the water specimens will pass very close to it without being stimulated. In fact, if a specimen finds a piece of food within three or four minutes after it is put into the dish, it will usually have done so as a result of accidentally coming in contact with it. As has been brought out above, when a gliding worm touches anything of a rather yielding texture, like food, it immediately gives the positive reaction and passes up over it. This plays an important part in the getting of food, because, as I have found in experiments, unless the food is crushed and pressed with forceps the juices diffuse rather slowly, and for some time specimens will not give the positive reaction unless they actually touch the food. On the other hand, after the food has been in the water for some time, so that diffusion has taken place, the distance at which specimens may be affected becomes quite considerable. I have seen specimens gliding by a small piece of meat at a distance of 1½ cm. from it give the positive reaction and turn towards it. At greater distances than this food is not effective, according to my observations. The distance from food at which a given specimen will give the positive reaction and go towards it depends also on the physiological condition of the individual. Specimens in a state of general excitation will, as I have frequently observed, go closely by a piece of food without turning towards it, while other specimens in a more normal condition will give the positive reaction some distance from it.

After the first specimen has begun feeding on a piece of material the zone of influence of that piece becomes almost immediately widened appreciably. As the number of feeding specimens increases the area in the surrounding water which affects others becomes correspondingly greater. This phenomenon is very striking in many cases, as an illustration will indicate. Several pieces of crushed snail were put in a dish with a number of planarians. In a short time a specimen in gliding about the dish had come near to one of these pieces, had given the positive reaction and begun feeding. At almost the same time another of the pieces of food had "attracted" another specimen. The other bits of food were quite similar in every way to these two, and lay in the dish not far from them. Yet at the end of fifteen minutes the two pieces by which the first two worms had been affected were completely covered with feeding specimens, while the remaining pieces of food, with a single exception,[1] did not have a specimen on them. This increase in the effectiveness of the food as a stimulus must be due to the diffusion of more chemical substance from it. Apparently the increase is due either to some secretion of the feeding animals or to some change which they induce in the food. It is probably due to a combination of these two factors. That a digestive secretion is poured out through the pharynx of the feeding worm is well known, and clearly shown by the appearance of a piece of food on which a specimen has been feeding. The surface of the meat is turned white, and rendered very soft and almost flocculent. It is probable that this digestive secretion acts as a positive chemotactic stimulus to other worms, and that coupled with this there is an increased diffusion of juices from the food itself caused by the changes which it is undergoing.

The reaction which is caused by this chemical stimulus

---

[1] One piece farthest removed from the others had a single specimen on it.

from the food is evidently essentially the same thing as the positive reaction given to weak mechanical stimuli. It consists in a turning of the anterior end of the body towards the source of the stimulus. There is no reason for supposing that its mechanism is in any way different from that of the same reaction to mechanical stimuli, and hence this need not be further discussed here. A question of prime importance with regard to this positive reaction in response to chemical stimuli, which was not taken up before, is—how well localised, with reference to the stimulus, is the reaction? or, in other words, how precisely does the anterior end point towards the source of the stimulus,—in this case food? Have we here a clear-cut orienting response? In answer to this problem it may be said that when the worm is only a short distance from the food the response is very precise. The anterior end is brought by the first positive reaction so as to point exactly towards the meat, and as the worm glides ahead it never misses it. This is true where the specimen is near enough (usually within three quarters of its own length), so that the stimulus which reaches it is a fairly strong one. In case the worm is stimulated near the edge of a large diffusion area when the stimulus is very weak, the first reaction may not suffice to direct the animal straight towards the food. In this case the behaviour is usually like that shown in Fig. 28, in which the line B, B, B, represents the effective margin of the diffusion area of the piece of food A. (By "effective margin" is meant the line outside of which no effect is produced by the food on passing specimens.) The first reaction which the worm gives on reaching this diffusion area (Fig. 28, 1 and 2) is a weak positive one. It then proceeds on the new path into this area, but not directly towards the food. After a short time, however (Fig. 28, 3), it is again stimulated to a positive reaction (4). This time both the stimulus and the reaction are stronger than before, and the worm is directed more nearly towards the centre of diffusion, but still not exactly. When it gets opposite the food again (5) another positive reaction (6) is given, and this time, since the stimulus is a rather strong one, the reaction is a very precise one, and the subsequent movement carries the animal directly to the food (Fig. 28, 7). This behaviour is typical for this sort of stimulation, but may vary in its component phases, depending on the relative strength of the stimulus—the distance from the food when first stimulated.

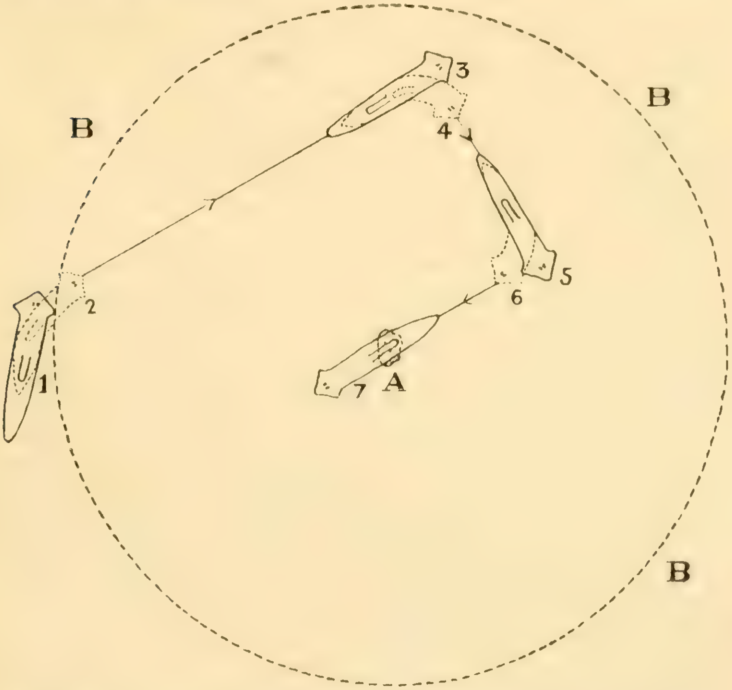

FIG. 28.—Diagram showing the reactions of Planaria to food (A) from which juices have been diffusing into the water for some time. B, B, B, represent the effective margin of the diffusion area of the food A. 1, 2, 3, 4, 5, 6, and 7 are successive positions taken by the organism.

Thus either two or as many as four positive reactions may be necessary to bring the animal to the food. This shows clearly that with reference to chemical stimuli, the precision of localisation of the positive reaction decreases as the intensity of the stimulus diminishes. Indeed, I have observed what is evidently an unlocalised positive reaction, although this seems paradoxical. The behaviour was as follows:—A large diffusion area had been formed, and a specimen was stimulated to a weak positive reaction at a distance of about twice its own length from the food (Fig. 29, 1). It passed into the diffusion area, but did not give another positive reaction when opposite the food, but instead glided by and away from it. When it had gone some distance in this direction it stopped and gave a very clear and characteristic positive reaction, so far as the form of the reaction indicated, but with the turn away from instead of towards the centre of

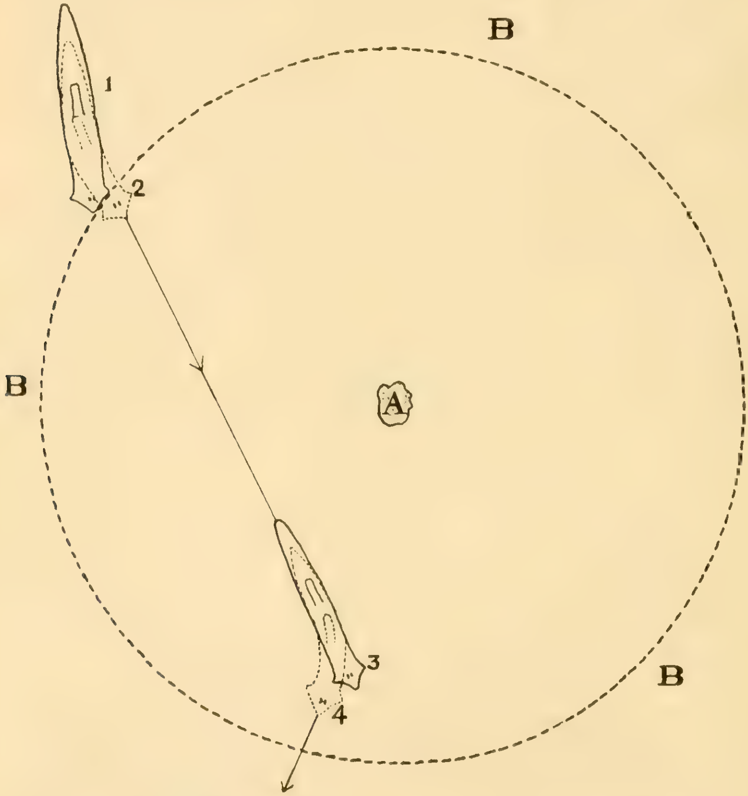

Fig. 29.—Showing the reaction of a planarian to a very weak food stimulus. Letters as in Fig. 28.

diffusion. There was no doubt of the character of the reaction; the head was raised and the body turned in the usual manner of the positive reaction, which one can never mistake after once having become familiar with it. The specimen kept on in the path determined by this last reaction (Fig. 29, 4), and passed entirely out of the region of the food. Evidently in this the worm was stimulated very weakly by a chemical, and the stimulus was nearly as strong on one side of the body as on the other, and when the reflex was set off it was on the wrong side of the body. This is not the usual result of weak stimulation, and has been observed in only two cases, but it serves very well to show the decrease of the power of localisation when the stimulus is very weak.

When, as frequently happens, the worm approaches the food exactly head-on, the reaction usually consists merely of that portion of the reflex expressed in the raising of the head, while the worm keeps on in its straight path till it reaches the food. The head may be waved from side to side slightly, but the general direction of motion is not changed. The action evidently corresponds to the positive reaction following weak mechanical stimulation of the dorsal surface of the head in the middle line, as described above. In some cases, however, I have observed very active and hungry specimens of Dendrocœlum, sp., which were going straight towards the food, give a complete positive reaction and turn to one side and start off in a new direction away from the food. This, however, of course brought the specimen at once into a position where the stimulus was acting unilaterally, and it again gave a positive reaction, this time heading it again for the food, which it usually reached without further reaction. But in some cases I have observed the specimen give so strong a reaction as to be taken almost directly away from the food by the subsequent movement, and, passing out of the area of diffusion, fail to reach it at all. Specimens behaving in this way were "wild" in their general reactions. The responses were very vigorous, but not localised with reference to the stimulus with the usual precision.

The "gripping" of the food substance by the anterior part of the worm is a very characteristic feature of the normal food reaction. Its exact form depends on the configuration of the food or other body "gripped." In its most typical form, where the food material is in the form of a cylinder, or approximately such, the action reminds one of the action of the human hand in grasping a stick. The tip of the head closes over the material in the same way that the fingers do, while the region just behind the auricles bears the same relation as does the proximal part of the palm, just in front of the wrist, in grasping. After the head has been placed over the material in this way it can be seen to contract rather strongly, and thus literally squeeze the food. In case the surface contour of the food does not admit of this reflex being carried out in its typical form, as close an approximation to this is made as possible. To compare again with the human hand, when the surface is flat, or forms the surface of a cylinder of large radius, the ventral surface of the head is pressed closely to it, the tip attempting to dip in, as it were, below the surface, in just the same way that a man "claws" with his finger tips in attempting to obtain a hold on a similarly configured body, too large for complete grasping.

While the "gripping" is in general a very characteristic feature of the food reaction, it may be omitted in rather exceptional cases. The cause for the omission where it occurs, or any laws governing the matter, I have not been able to discover. A necessary accompaniment of the "gripping" of the food is the cessation of the forward movement of the animal as a whole. This pause when the food is first touched by the anterior end and before the worm passes up on to it, occurs in practically every case, whether the gripping accompanies it or not. The length of the pause is, of course, considerably greater when the "gripping" occurs than when it is absent.

The function of the "gripping" of the food material before feeding begins is not immediately apparent, but I am inclined to think its purpose is to intimately test the substance with regard to its availability as food. Some evidence on this point and further discussion regarding it will be introduced later.

After the preliminary pause and "gripping" of the food the worm glides up on to it to begin active feeding. The position taken by the worm brings out a very nice correlation in reflexes. In a very large number of cases (certainly over 75 per cent., so far as my observations have gone) the worm advances over the food until the pharyngeal opening is exactly over the place where the first "gripping" occurred, and there the pharynx is extruded and feeding begins.

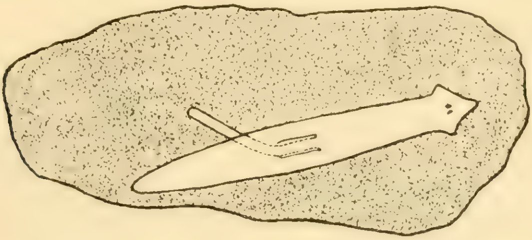

FIG. 30.—Diagram showing great extension of the pharynx. The stippled area represents food substance on which the planarian is resting.

When the worm reaches this position the posterior part of the body relaxes and takes on the appearance characteristic of the resting specimen. The pharynx is thrust out, and becomes attached very quickly. As it passes out through the opening in the body-wall it becomes usually considerably extended, and its diameter becomes correspondingly smaller than when it is in the pharyngeal sac. It may or may not attach to the food directly beneath the body. When conditions are favourable it usually does, and consequently cannot be seen on looking down on the animal from above. On the other hand, I have frequently seen it stretched out and attached some little distance to one side of the body, as shown in Fig. 30. The stimulus, causing the extrusion of the pharynx, is the contact of food or other solid body with the pharyngeal region of the ventral surface, together with an appropriate chemical stimulus. The pharynx is not extruded until the animal gets up on to the food so that the opening of the pharyngeal sac is in direct contact with it. This can be demonstrated by direct observation by the use of a very small piece of food material and a plane mirror placed beneath the glass dish in which the specimen is moving. By lifting gently the posterior end of the body on a needle it can also be seen that the pharynx is not extruded before it is over the food. The most striking illustration of the correlation in the reaction which brings about the extrusion of the pharynx when it is just over the food, is to be seen when a specimen of the nemertean Stichostemma asensoriatum is used as food, and the long axis of the planarian and of the nemertean are at right angles to each other. After first "gripping" the nemertean the planarian glides along over it until the pharyngeal opening is just above it, and then pauses, and the pharynx is extruded and attached (*a* and *b*, Fig. 31). These facts strongly indicate that the effective stimulus for pharyngeal extrusion is received, at least in part, in the pharyngeal region itself. That it is necessary for both contact and chemical stimuli to act to produce the extrusion of the pharynx may be shown by experiments on specimens gliding on the surface film ventral side uppermost. If, with such a specimen, a chemical known to produce under other conditions extrusion of the pharynx, is allowed to come in contact with the pharyngeal region, there is no result. Of course in performing this experiment proper precautions were taken not to disturb the animal by allowing the solution to drop upon it. Another demonstration of the same fact that a chemical stimulus alone does not suffice to cause extrusion

FIG. 31.—Diagrammatic longitudinal section of a planarian feeding on a nemertean (shown in cross-section at ×).

of the pharynx is that specimens immersed in favourable solutions, such as sugar solutions, do not show this phenomenon. That mechanical stimulation alone does not suffice is demonstrated by the fact that planarians pass over and rest on other planarians without extruding the pharynx, although the consistency of their bodies is evidently much the same as that of the animals used as food. In fact, they will be used as food frequently if they are wounded so as to afford the proper chemical stimulus. The stimulation of the anterior end of the body by the food seems also to be necessary before pharyngeal extrusion takes place. The data on this point will be presented later in connection with operation experiments.

The appearance of the body on the food is quite characteristic. As mentioned above, when the pharynx is extruded forward, movement stops, and the posterior part of the body becomes more or less relaxed. The anterior third of the body, however, keeps in movement during a considerable part of the time the specimen is feeding. The head is waved about from side to side, and touched to the food or the bottom of the dish here and there. It keeps its characteristic extended form to a greater or less degree. A favourite position is for the anterior third or half of the body to lie on the bottom and move about, while the posterior part lies up on the food. This is the position most frequently seen in specimens feeding on a rather small piece of meat. When the anterior end gets on the bottom it gives every appearance, in many cases, of attempting to glide away, and being only restrained by the attachment of the pharynx to the food. In other cases, however, the anterior end remains quiet. The importance of the attempted movement will be brought out later. As has been mentioned above, the flatworm is able to move off and drag the food still attached to the extruded pharynx along behind it. In the fastening of the food to the body in this case the sticky slime undoubtedly assists the pharynx.

After the food has been softened by the digestive juices, it is taken into the body through the pharynx.

After the worm has been feeding for a certain length of time it will detach the pharynx and spontaneously move off from the food, the pharynx being withdrawn again into its sac. The length of time after the beginning of the feeding at which this takes place varies very greatly in different cases. I have observed a specimen which fed on a piece of mollusc for as long as an hour and thirty minutes, while in other cases the worm may stay on the food only ten minutes, or even less. Judging from the rate at which food is taken up while the animal is feeding during the day, and from the fact that pieces of meat left in the dish overnight are almost entirely consumed by morning, it would appear that much of the time during the night is spent in feeding when any material available for the purpose is at hand. While the anterior end of the feeding worm retains its normal sensitiveness to stimuli, it nevertheless requires considerable stimulation to induce a feeding worm to leave the food. Shaking of the dish, which would ordinarily set all resting specimens into rapid movement, has little or no effect on feeding specimens. If a worm is suddenly pulled off a piece of meat on which it is feeding a very good view of the extruded pharynx may usually be had, as this organ is retracted somewhat slowly when torn from food in this way.

So far as I have been able to discover, the presence of food in the immediate neighbourhood of a resting planarian has no effect upon it. Apparently the stimulus afforded by crushed meat is not sufficiently strong to produce a response from such an individual. The following experiment copied from my notes will show this.

May 14th, 1901, 3.10 p.m.—A piece of freshly crushed snail was placed 1 mm. distant from the anterior end of a resting specimen. No reaction or other effect produced.

3.30 p.m.—Worm in same position as before.

4.5 p.m.—No change. (At this time the worm was accidentally started into movement and the experiment consequently ended.)

This lack of effect of food on resting specimens may be the reason for the statement of Bardeen (loc. cit., p 522) "that worms which had been kept in pure rain water for a week or two, and were thus in a hungry condition, would remain unmoved by the presence close by their side of a piece of fresh snail, a food much prized by them."

1. Food Reactions of Specimens after Operations.—For the purpose of throwing light on the general mechanism of the food reaction, experiments were tried on specimens cut in different ways. It is unfortunately very different from practical reasons to get many certain results from these experiments. Many of the results are negative, and hence not entirely conclusive. Since, however, some important facts have been brought out by these experiments, they will be described.

The first operation which will be discussed is that of cutting the animal in two transversely. If such a cut is made in the region in front of the pharynx, the anterior resulting piece, after it has recovered somewhat from the shock effect of the operation, will show the following reaction. On coming into the zone of diffusion about a piece of meat it gives the positive reaction just as a normal worm does, and turns towards the food. On reaching the edge of the meat its behaviour is again like that of the normal animal; it stops, usually "grips" the food, and then passes on over it. At this point appears the striking difference between the behaviour of this anterior piece, which, it must be remembered, has no pharynx, and the behaviour of the entire worm. The anterior piece after gripping the food glides up over it, and without the slightest change, even in the rate of gliding, passes down off of it on the other side. There is not the slightest indication of any stopping for the pharynx to be extruded.

If the transverse cut is made farther back, so that the pharynx is included in the anterior piece, this will then behave with reference to food quite as a normal animal does. It will stop on the food and extrude the pharynx.

The posterior pieces resulting from transverse cuts do not give any definite food reaction, so far as I have been able to ascertain, until they have been regenerated to some considerable extent. Posterior pieces from which only the head has been cut will glide by pieces of snail on which other worms are feeding, without giving the slightest reaction.[1] In experiments so arranged that the gliding posterior piece would just touch with its anterior end the edge of a piece of food, it gave no reaction. This same arrangement with a normal worm practically never fails to call forth the positive reaction and bring the worm up on to the food. Posterior pieces placed gently on pieces of food material do not extrude the pharynx and start feeding, but immediately glide down from it and over the bottom of the dish. These experiments with posterior pieces have been tried many times and under varied conditions, in the hope that some sort of positive results might be obtained, but never with success. This is true for three days after the operation. After a new head has been fairly well formed the animal will react to food again. The behaviour of one of these posterior pieces on touching with the anterior end a piece of food is very strikingly different from that of a normal animal. The cut piece, if it touches with the front or sides of the anterior end the smallest shred of food material, or any other substance, gives a well-marked negative reaction, and goes in a new direction away from the obstruction. It does not, as a rule, crawl up over anything which it meets squarely "head-on," but instead turns away.

Thinking that possibly the pharynx might play a more or less independent part in the normal food reaction, i. e., that it might have a set of reflexes of its own, not determined by the rest of the body, I tried experiments with the isolated pharynx removed entire from the body. Such an isolated pharynx will remain alive for a considerable period, and respond to stimulation. When first removed from the body

---

[1] Bardeen (:01, *a*) has shown that if the transverse cut is in the region in front of the eyes the posterior piece (comprising in this case nearly the whole worm) will react normally to food.

it contracts rhythmically in a longitudinal direction for a time, and then comes to rest at about its normal length when in the body. Mechanical stimulation causes merely longitudinal contraction, while the presence of food near it has no effect whatever. Freshly crushed snail meat placed within a millimetre of such an isolated pharynx had no effect upon it in the course of an hour. I have tried laying the isolated pharynx directly on pieces of meat to see if there would be any tendency for the end of the organ to attach itself as it normally does. This was not done, nor was any other definite reaction produced.

These operation experiments show, so far as they go, that—

(1) The presence of the pharynx in the body (i.e., the functional ability to take food) has nothing to do with determining the reaction of the anterior end of the body to food stimuli. The anterior part of the body gives the same reaction to food in every case, without regard to whether so doing actually puts the animal in a position to get food or not. The reaction is only purposive under certain circumstances; when changed conditions make it no longer purposive, no adaptive change in the behaviour of the anterior end occurs. This shows clearly how little basis there is for considering the behaviour towards food as anything of the nature of intelligent behaviour.

(2) The stopping of the worm on the food under normal circumstances is due to the posterior half of the body, not the anterior. The behaviour of the anterior cut piece in gliding directly over the food is what one might be led to expect from the behaviour of the same part of the body under normal circumstances. As described above, it was seen that the anterior end of the normal individual gives every appearance of attempting to continue moving forward while the posterior part is feeding, and is only prevented from doing this by the mechanical hindrance of the attached pharynx. In a sense, we may consider that in a large degree the work of the anterior end of the body with reference to feeding is over when it gets the animal up on to the food.

(3) The reception of the food stimulus is a function of the head. In other words, the head is the only part of the body capable of receiving very weak chemical stimuli.

(4) Decapitated specimens do not extrude the pharynx, so far as my observations go, even though the proper normal stimuli are given the pharyngeal region. Presumably the brain is the necessary organ in this connection, as we have already seen that the sense organs concerned with the act of extrusion are not those of the head, but of the pharyngeal region.

Bardeen (: 01, *a*, p. 178) states that "the simple reflexes of extending the pharynx and of swallowing are preserved after removal of the head. I found, by repeated trials, that one of the headless pieces could usually be made to eat if it was placed on its back on a slide in a small drop of water. Under the conditions mentioned the pharynx is usually protruded, and will engulf bits of food placed in the mouth." Regarding this conclusion, I can only say that in a large number of experiments with decapitated specimens I have never been able to induce extrusion of the pharynx, under conditions approximating as closely as possible to the normal. I do not wish to affirm that the decapitated planarian cannot extrude the pharynx, but merely that it does not when placed in situations which normally produce pharynx extrusion.

(5) The pharynx is not an independent organ in its reactions, since, when separated from the body, it does not react with reference to the localisation of the stimulus, as it does when normally connected with the remainder of the body.[1]

2. Summary of Food Reactions.—It is shown above that planarians have a very definite and characteristic set of reactions to food substances which enable them to become aware of the presence of food, and find it. The importance of these reactions in the life of the individual can hardly be over-estimated. While planarians, like many other lower organisms, can live for a considerable time without food, yet in the long run they must, of course, have it. The question

---

[1] Evidence on this latter point will be brought forward in connection with the reaction to chemicals.

of how a lower organism gets its food, taking advantage of the good and rejecting the bad, and thus apparently choosing one thing from several, is one of the most interesting and important in comparative psychology.

The food reaction of planarians consists of an extremely well co-ordinated set of reflexes, which may be set into action by stimuli of two sorts,—first, chemical; and second, mechanical. Both sorts of stimuli are, of course, given by the food. The first and most important of all the reflexes in the food reaction is the turning of the head towards the source of stimulation, followed by movement in that direction. This is the reaction which enables the animal to find food. Evidently it is the same thing exactly as what has been described as the positive reaction to mechanical stimuli; or, in other words, the positive reaction to mechanical stimuli is only a special case of the general food reaction. Its primary function is evidently the getting of food, whatever the stimulus which calls it forth. The reason for a food response following mechanical stimulation is to be found in the fact that it most frequently happens that many things (e. g., whole animals) which are available for food are not emitting chemical substances into the water in sufficient quantity to cause an effective stimulus. If the planarian did not give a positive reaction after contact with such bodies they would be missed, and no advantage taken of them as food. By reacting positively to weak mechanical stimuli the animal is in a position to take advantage of the presence of food of all sorts, whether it is in condition such as to diffuse chemical substances through the water or not. This fact that the animals react to food substances as a result of mechanical stimulation affords a possible explanation of the "gripping" phase of the general response. The purpose of this "gripping" may be to bring the sense organs of the head, which are sensitive to chemical stimuli, into very close contact with the substance in order to determine whether it possesses the chemical characteristics of food. In other words, this reaction is a "tasting" reaction, which is made necessary by the fact that the organism turns toward all bodies of a certain physical texture under most circumstances. The active squeezing of the material in the "gripping" undoubtedly helps to press out to the surface any juices which may be in the material.

In closing the section on food reactions it may be well to give a sort of general picture of the whole behaviour of fresh-water planarians towards food. The method by which the planarian finds material suitable for food is as follows:

1. Chemical substances diffusing from food come in contact with the sensitive head region of the planarian; or—

The moving animal touches with the head some soft substance, and as a result of either of these two sorts of stimulation—

2. The organism gives a positive reaction, i. e. turns towards the source of the stimulus. This reaction is very precisely localised in most cases, and is the most essential part of the whole food behaviour. Its mechanism has been previously described (v. sup., p. 619).

3. When the anterior end squarely touches the food as a result of this reaction it typically closes tightly over it, giving what I have called the "gripping" reaction. This reaction is evidently a very much specialised feeling movement for the purpose of closely testing the chemical nature of material. It is produced by a contraction of the ventral longitudinal muscles of the head region. While it is taking place progressive motion ceases.

4. After this pause the worm glides over the piece of food till the opening of the pharyngeal sac lies over or nearly over the place "gripped," and there the posterior part stops and the pharynx is extruded and attached to the food. The factors determining the place where the pharynx shall be extruded are (*a*) the stimulation of the ventral surface of the body in the pharyngeal region of the food (pure reflex factor), and (*b*) the presence of the brain, which probably acts as a co-ordinating centre for this reaction.

5. A digestive fluid is poured out through the pharynx, and the food is partly digested before being taken up.

6. The softened food is taken into the body through the pharynx.

7. The animal spontaneously stops feeding after a certain time.

The question now arises, if the normal process of getting food is at bottom in the majority of cases a reaction to a chemical stimulus, what is the nature of the chemical substance causing it? Can the same response be induced by the use of different inorganic and organic chemicals? Is there any relation between chemical composition and the intensity or form of the reaction? To answer these and a number of other questions arising out of them recourse must be had to experiments in which the nature and concentration of the chemicals affecting the organisms may be controlled. All the experiments of this kind I will group together under the heading—

b. Reactions to Chemical Stimuli—Chemotaxis.

1. Reactions to Localised Chemical Stimuli.—This particular phase of the general subject of the effects of chemicals may be considered first, since it is most closely related to what has preceded on the food reactions. The plan of the experiments was to try the effect of a series of substances when applied to restricted areas of the body. A sufficiently large number of chemicals were used to include representatives from each of the main groups of substances which have been found to have marked effects on organisms.

a. Methods.—The method which was found to give the most satisfactory results in the application of localised chemical stimuli was the use of a capillary tube filled with the solution whose effects it was desired to test. The form of the tube used is shown in Fig. 32. The tubes were 10 to 15 cm. long, and were made from glass tubing of about 2·5 mm. internal diameter. Each end was drawn to capillary fineness, and then broken off so as to give an opening of the desired size. The opening at the upper end was made slightly larger than that at the lower, which was used in giving the stimulus. The tube was filled with solution by suction. The rate of diffusion can be regulated by changing the sizes of the openings, and can be determined for each tube from the rate at which the fluid sinks at the upper end of the tube. Considerable experimenting is necessary in order to get the best rate of diffusion for work on planarians. Since the animal is moving rather rapidly while the stimulus is being applied it is necessary to have reasonably rapid diffusion or the worm will not react at all, or not for so long a time after the stimulation has begun that one cannot be certain of the results. It is easily possible to get the capillary so fine that no results can be obtained. On the other hand, when it is too large the solution affects too large a portion of the body at one time, and furthermore, as will be shown later, may cause a rheotactic reaction of the organism. This, of course, introduces a possible source of serious error. It can be avoided by frequent and proper control experiments.

FIG. 32.—Glass tube used in giving localised chemical stimuli.

It will be well to describe in advance the conduct of a typical experiment and the precautions taken, so that it may not be necessary to repeat these details in the account of each experiment. Six to ten normal active planarians were taken from the aquarium dish and put in a Petri dish of about 10 cm. diameter, in freshly drawn, filtered tap water. Enough water was put in the dish to give a depth of about 1 cm. Two or three of the capillary tubes with different sized openings were filled with the test solution. These tubes were all tested before a final experimental series was begun, and usually only one which had been found to allow diffusion at the satisfactory rate was used. In some cases, however, varying degrees of sensitiveness among the different specimens made it necessary to use for some individuals capillaries of faster or slower rates than what may be called the standard. After preliminary experiments to determine the relative sensitiveness of the different parts of the body to chemicals, attention was devoted almost entirely to stimulation of the head region, and consequently in the experiments which will be reported first the stimulus was applied only to the head, unless otherwise stated. The method of applying the stimulus was to place the point of the capillary tube a short distance (about 2 mm.) from the place on the body to be stimulated. The animal was stimulated as it was gliding along in the normal way, and hence it was necessary to move the capillary tube at the same rate the animal moved in order to keep it opposite the same point in case the reaction was not given at the instant the capillary was put into place, which, of course, almost never happens. With a little practice one can move the tube along as the worm glides so as to keep the relative position of the two almost identically the same. Just as soon as a reaction had been obtained with a given specimen the capillary tube was removed from the water, so as to permit as little as possible of the chemical to get into the water surrounding the organism. After a series with any substance, the worms were transferred at once to a dish of fresh water before beginning another series. Further, in any long series, when for any reason it might be supposed that the water was becoming contaminated with the chemical to an extent sufficient to affect the results, the worms were transferred to another dish of fresh water. All through the course of an experiment frequent control tests were made by trying the effect on the worms of the water surrounding them when diffusing out from the same tube used previously for the chemical. After each experiment the tubes were thoroughly rinsed by drawing distilled water back and forth through them many times. The tubes were also frequently discarded and new ones substituted.

The following substances were used in the experiments :

Mineral acids . .	Nitric Hydrochloric Sulphuric
Organic acids . .	Oxalic Citric Formic
Alkalies . .	Sodium hydrate Sodium carbonate
Salts of heavy metals	Copper sulphate Zinc sulphate
Other salts . .	Sodium chloride Sodium bromide Potassium chloride Magnesium chloride

Cane-sugar.
Distilled water.

Since distilled water was found to have a decided effect in producing a reaction, the solutions were prepared in both distilled water and in filtered tap water. In case of any doubt, as with very dilute solutions, the effects of the solutions prepared in each sort of water were tested and compared.

Since only qualitative results were desired, and for the practical reason of greater convenience, percentage rather than molecular solutions were used.

β. Results.—The results are, in a way, so remarkable that they will be presented in some detail.

Mineral Acids.

Nitric (sp. gr. 1·42), $\frac{1}{5}$ per cent.—This solution causes strong negative reaction. If applied to the head region the animal turns away from the side stimulated immediately, and strongly. If the stimulus is long continued the animal writhes and twists about violently.

Stimulation of the posterior region causes the part where the solution strikes to contract very violently, and the whole animal to start crawling ahead rapidly. This concentration is very injurious, and if its action is continued, quickly kills the individual. It will be noted that its effects are the same essentially as those of strong mechanical stimuli applied to the same parts of the body.

$\frac{1}{10}$ per cent. and $\frac{1}{20}$ per cent.—Results the same as in $\frac{1}{5}$ per cent. The animal is not as quickly and extensively injured by these solutions as by the former. It is to be noted that with these comparatively strong solutions the reaction time after stimulation of the posterior end of the body is so slow that this part of the body is permanently injured or destroyed before the animal gets away.

$\frac{1}{40}$ per cent.—In some cases a well-marked positive reaction was caused by stimulation of the head region with this solution. The head would turn towards the mouth of the pipette in the characteristic fashion of the food reaction, or the reaction to weak mechanical stimuli. In other individuals the reaction given was weakly negative, while still other specimens were indifferent. In cases where there was an indifferent reaction there was a local contraction of the side of the head stimulated.

$\frac{1}{80}$ per cent.—Clearly marked positive reaction in large majority of cases after the stimulus has acted for some time. This solution never caused the negative reaction. Some individuals were, in a few cases, indifferent to this solution. This solution is too weak to start a resting specimen into movement.

$\frac{1}{160}$ per cent. and weaker.—Indifferent reactions or weak positive.

This acid appears to be a very strong stimulus for the negative reaction in concentrations down to $\frac{1}{40}$ per cent., while below that it is a rather ineffective stimulus, and the reaction when induced is positive.

Hydrochloric, $\frac{1}{10}$ per cent.—Strong negative reaction. There is noticeable in some cases a tendency for some individuals to turn very slightly towards the source of stimulation before giving the strong negative reaction. Stimulation of the anterior end of a decapitated specimen caused a slow negative reaction with long reaction time. This solution causes the change from the glide to the crawl when applied to the posterior end of a normal worm.

$\frac{1}{20}$ per cent.—Negative reaction; rather weaker than with preceding solution. With this solution one specimen would turn towards the source of the stimulus until the head came into the strong acid near the mouth of the pipette, and then give the sharp negative reaction.

$\frac{1}{40}$ per cent.—Specimen A gave positive reaction in every case; specimen B in about 50 per cent. of all cases, while in the remainder of trials gave weak negative. Other specimens negative reaction.

$\frac{1}{80}$ per cent.—Specimen A as in preceding case. Specimen B gave positive reaction in about 90 per cent. of all trials. Other specimens weakly negative reactions.

$\frac{1}{160}$ per cent.—All specimens give well-marked positive reaction. They glide up to the end of the capillary and "grip" it with the anterior end as in the food reaction. After holding on for a moment they let go and give a sharp negative reaction, indicating that the stimulus is still too strong when continued. This behaviour will indicate the machine-like character of the positive reaction.

$\frac{1}{320}$ per cent.—In the majority of cases indifferent reaction. Remainder positive.

To give an idea of the dependence of the reactions to chemicals on the physiological condition of the organism, the following series of experiments with HCl in solutions of $\frac{1}{160}$ per cent. and weaker concentrations may be described. It is to be understood that these experiments were carried out on different animals from those just given.

$\frac{1}{160}$ per cent.—No sharp positive reaction. Specimens will give a weak negative reaction if the opening of the capillary is held very near the head. In most cases reactions are indifferent.

$\frac{1}{320}$ per cent.—One specimen gives positive reaction and goes through whole food reaction on the end of tube. The remainder still give weak negative reactions.

$\frac{1}{640}$ per cent.—Reactions essentially the same as in $\frac{1}{320}$ per cent.

At this point this series was discontinued. It shows that any absolute concentration for a chemical solution which will cause all planarians to give the positive reaction cannot be assigned. How a given individual will react to a given concentration of chemical depends almost, if not quite as much, on the individual as it does upon the solution.

Sulphuric, $\frac{1}{10}$ per cent. and $\frac{1}{20}$ per cent.—Caused immediate and violent reaction. Decapitated worm reacts like normal. This is evidently a very strong stimulus.

$\frac{1}{40}$ per cent.—Caused strong negative reaction in majority of cases. One specimen reacted as follows:—the capillary tube being held some distance away from the head, it first gave a well-marked positive reaction. On coming into the stronger solution near the mouth of the tube it began strong convulsive contractions (evidently on account of too strong stimulation). It remained, however, at the same spot, and after a few minutes extruded the pharynx and swept it about over the bottom. The specimen remained this way for some time. The tube was, of course, removed immediately after the first positive reaction was given. A decapitated specimen in one case gave a very distinct positive reaction to this solution, the tube being held some distance away from the specimen.

$\frac{1}{80}$ per cent.—Negative reaction. Decapitated specimen gave positive reaction once. This solution, applied to the posterior end of the body, induces the crawling movement.

$\frac{1}{160}$ per cent.—Negative reaction. Isolated pharynx contracts into a ball when stimulated with this solution.

$\frac{1}{320}$ per cent.—Positive reaction in one case. Remainder negative. Same result with pharynx as in $\frac{1}{160}$ per cent.

$\frac{1}{640}$ per cent., $\frac{1}{1280}$ per cent., and $\frac{1}{2560}$ per cent.—With these solutions the reactions were for the most part negative.

In a few cases positive responses were produced, but not regularly.

$\frac{1}{5120}$ per cent. — Positive reaction in all cases. The whole food response was produced in case the end of the tube was left in position. The worms "gripped" it, glided up on to it, and extruded the pharynx, in many cases running the latter up into the lumen of the tube. Anterior piece, resulting from cutting animal in two transversely, acts like whole worm (positive reaction), but less strongly. Decapitated worm gave no response. In order to make sure that in this case it was the extremely diluted acid which was producing the result, numerous controls with distilled water and culture water and fresh tap water were tried on the same specimens, in alternation with trials with the acid. With tap water and culture water the specimens were indifferent; but with the acid solution ($\frac{1}{5120}$ per cent.) mixed in either tap water or distilled water they gave a well-marked positive reaction. This showed clearly that the results were due to the acid.

Summary.—With the three mineral acids tested it was found that to concentrations above a certain point the specimens always gave the negative reaction, while to concentrations below this point the positive reaction was given. The absolute value of this "critical point" varies widely with different individuals. The behaviour is essentially the same as that in response to mechanical stimulation, viz. to strong stimuli the negative reaction is given, to weak the positive.

Organic Acids.

Oxalic, $\frac{1}{5}$ per cent. and $\frac{1}{10}$ per cent.—Sharp negative reaction. This solution affords a very strong stimulus and quickly kills the specimen. The negative reaction is very violent when once induced, but several specimens were killed before they turned away. There was noticeable a slight tendency to turn towards the stimulus the instant it was perceived, and before this could be replaced by the negative reaction the specimens were nearly or quite killed.

$\frac{1}{20}$ per cent.—Convulsive negative reaction in the great majority of cases. In one case stimulation was followed by sharp positive reaction, succeeded by extrusion of the pharynx.

$\frac{1}{40}$ per cent. and $\frac{1}{80}$ per cent.—A few specimens on some trials give positive reaction, and then go into convulsive twisting movements as they get into stronger solution. Remainder negative.

$\frac{1}{160}$ per cent. and $\frac{1}{320}$ per cent.—Positive and weak negative reactions about equally divided.

$\frac{1}{640}$ per cent. and $\frac{1}{1280}$ per cent.—Positive reactions becoming proportionately more numerous. Negative reactions are very weak when given in response to these solutions. In the cases where there is a positive reaction the full response is not given; the specimens go up to the mouth of the tube, but do not grip it nor extrude the pharynx.

$\frac{1}{2560}$ per cent.—With this solution all but one specimen give the positive reaction. Specimens will follow the end of the pipette about the dish if it is moved slowly. This is done by a series of positive reactions. Specimens will give the complete food reaction on the end of the tube.

Citric, 2 per cent.—Strong negative reactions.

1 per cent.—Less marked negative reactions. Tendency to positive in some cases.

$\frac{4}{10}$ per cent.—Positive reactions in nearly all cases. Remainder indifferent.

$\frac{2}{10}$ per cent.—Indifferent.

Citric acid in weak solutions seems to be a very ineffective sort of stimulus, not causing pronounced reactions of any kind.

Formic, $\frac{1}{5}$ per cent. and $\frac{1}{10}$ per cent.—Prompt and decided negative reaction. Causes a resting worm to give a weak negative reaction of the anterior end, but does not start the whole animal into movement, provided the tube is withdrawn after the first reaction is obtained.

$\frac{1}{20}$ per cent.—Negative reaction, but decidedly less pronounced than with preceding concentrations. Does not cause any movement whatever in resting specimen.

$\frac{1}{40}$ per cent.—Negative reaction, less strong than in previous cases. In some cases positive reaction. Noticeable tendency to give slight positive reaction just before the definite negative response.

$\frac{1}{80}$ per cent.—Well-marked positive response.

Summary.—The same conclusions are to be drawn from the experiments on organic acids as from those on mineral acids, viz. that to strong concentrations of a given substance the negative reaction is given, while weak concentrations cause a positive response. Oxalic acid is rather peculiar in that it appears to furnish in all concentrations a stimulus of the proper quality to induce the positive response, but is at the same time excessively harmful in any above the weakest solutions.

Alkalies.

Sodium Hydrate, $\frac{1}{5}$ per cent., $\frac{1}{10}$ per cent.,and $\frac{1}{20}$ per cent. — Immediate strong negative response. Specimens turn away very sharply. In $\frac{1}{20}$ per cent. the reaction is slightly weaker than in the other two.

$\frac{1}{40}$ per cent.—Negative reaction. Stimulus applied to posterior end of body is sufficiently strong to cause crawling movement.

$\frac{1}{80}$ per cent. — Weaker negative reaction. Sufficiently strong to start resting animal into movement.

$\frac{1}{160}$ per cent.—Weak negative reaction. Ineffective on resting worm and on posterior end of body of moving specimen.

$\frac{1}{320}$ per cent.—Very weak negative response. In one specimen sharp positive reaction; performs whole food reaction on the end of the tube.

$\frac{1}{640}$ per cent.—Positive reactions from all specimens. The complete food reaction is given.

To solutions below this concentration the organisms are either indifferent or, in a few cases, weakly positive.

Sodium Carbonate, $\frac{1}{5}$ per cent.—Rather weak negative reaction.

$\frac{1}{10}$ per cent.—Majority of all reactions positive. Remainder weakly negative.

$\frac{1}{20}$ per cent.—Well-marked positive reaction in all cases. The specimens can be led around the dish by moving the tube slowly.

Below this concentration the reactions were either indifferent or weakly positive.

Summary.—A caustic alkali (NaOH) and a salt of strong alkaline reaction (Na_2CO_3) produce essentially the same results as the acids. In strong solutions they cause negative reactions; in weak, positive.

Salts of Heavy Metals.

Copper Sulphate, $\frac{1}{10}$ per cent.—At the very first trials the animals all turned sharply and immediately towards the stimulus (positive reaction), but the solution was so strong as to throw the animal into convulsions, when the head came very near the mouth of the tube. Subsequent trials produced the negative response.

$\frac{1}{20}$ and $\frac{1}{40}$ per cent.—All specimens give positive reaction. The head is brought up to the tube, and the worm glides up over the latter.

With all concentrations of $CuSO_4$ there is a very well-marked local contraction of that part of the body which is stimulated.

In another series of experiments with this same substance, the strongest concentration which would produce the positive reaction in all cases was $\frac{1}{640}$ per cent.

Zinc Sulphate, $\frac{1}{5}$ and $\frac{1}{10}$ per cent.—Sharp and immediate negative reaction.

$\frac{1}{20}$ per cent.—Negative reaction, but less pronounced than in former cases.

$\frac{1}{40}$ and $\frac{1}{80}$ per cent.—Specimens stop when stimulated, and wave the anterior end about in the water, first away from and then towards the source of stimulation. As the head comes nearer to the end of the tube, where the solution is strongest, it is more strongly stimulated, and gives a definite negative reaction. As it gets out into the weaker zone again it is stimulated to a positive reaction once more. If the tube is now removed the specimen will, in some cases, after a short time turn sharply towards the place where it was, and move in that direction. In other cases the negative reaction finally predominates. It not infrequently happens that in the earlier part of this reaction the anterior end only moves very slightly towards, or very slightly away from the stimulus, so that the body seems, at first sight, to be fixed in one position. The planarian, in this strenuous reaction, probably comes as near to the hypothecated behaviour of the famous "Buridan's ass" as anything is ever likely to in actual practice.

$\frac{1}{160}$ per cent.—One specimen gave clearly marked positive reaction in every case. Others as in the preceding solutions ($\frac{1}{40}$ per cent. and $\frac{1}{80}$ per cent.).

$\frac{1}{320}$ per cent.—Well-marked positive reaction. Specimens give complete typical food reaction.

In one case, with a small worm, I was able to produce crawling in a backward direction by continuous stimulation of the anterior end in the middle line of the body with $\frac{1}{80}$ per cent. $ZnSO_4$.

Summary.—The results from solutions of salts of two heavy metals are in accord with those obtained with other chemicals.

Other Salts.

Sodium Chloride, $\frac{1}{5}$ per cent. and $\frac{1}{10}$ per cent.—Negative reaction; distinct, but not as strongly marked as the negative reaction to strong acids.

$\frac{1}{20}$ per cent.—Weak negative reactions and weak positive reactions in about equal numbers. Many of the trials produce no response whatever.

$\frac{1}{40}$ per cent.—Weak positive reactions in nearly every case. No negative reactions. The typical, complete food reflex I have not been able to induce with sodium chloride.

Concentrations below this do not produce any definite reaction.

In general, NaCl is a very ineffective stimulus to planarians, either to the positive or the negative reaction. Distilled water is a considerably stronger stimulus to the positive reaction.

Sodium Bromide, 2 per cent.—Weak but distinct negative reaction in all cases.

$\frac{2}{5}$ per cent.—Well-marked positive reaction in all cases. Complete normal food reaction is produced.

Potassium Chloride, 2 per cent.—The animals usually react in a peculiar way to this and stronger solutions of KCl. When stimulated they stop, turn the anterior end either slightly towards or slightly away from the source of stimulation, and then stay in the same place and squirm and twist the body. In some cases there is a well-marked negative reaction.

$\frac{1}{5}$ per cent.—Some specimens give negative reactions in the first few trials; afterwards give definite positive responses, as do other specimens in all cases. In one case the specimen gave marked positive reaction, and after the head was turned towards the stimulus, remained quiet in the same position as long as the chemical acted.

$\frac{1}{10}$ per cent.—All specimens give positive reaction or are indifferent. The whole food reaction took place on the end of the tube. In this experiment it could be clearly demonstrated that the pharynx is positively chemotactic to this substance. It is probably positively chemotactic to all substances which induce the preceding portions of the feeding reaction. If, after the pharynx had been extruded, the tube was turned about so that the ventral surface of the animal could be seen, and the posterior part of the body was moved with a needle, so as to change the position of the pharynx with reference to the mouth of the tube, it could be seen that this organ bent directly towards the mouth of the capillary. The pharynx oriented itself with reference to the issuing chemical.

The cases in which specimens were "indifferent" to this solution (i. e. did not give either the positive or negative reaction) were evidently not due to the fact that the animal was not stimulated, but, on the contrary, that it was stimulated about equally to negative and positive responses. This was indicated by their restless behaviour when "indifferent." While the animal as a whole moves in a straight line, the head constantly moves slightly towards and away from the stimulus. Evidently the solution is not quite strong enough to induce a definite negative reaction, nor quite weak enough to cause a clear positive response.

$\frac{1}{20}$ per cent., $\frac{1}{40}$ per cent., and $\frac{1}{80}$ per cent.—Distinct positive reaction in all cases.

$\frac{1}{160}$ per cent.—Positive reactions in some cases, mainly indifferent. The "indifference" is now due to lack of stimulation.

Below $\frac{1}{160}$ per cent. I have been unable to get definite responses of any sort with KCl.

Magnesium Chloride, $\frac{1}{5}$ per cent.—Usually sharp negative reaction. In some cases a slight turn towards the stimulus preceded the negative response, and in some few other trials the animal was indifferent.

$\frac{1}{10}$ per cent.—Weaker negative reaction. In one case clear positive reaction. No local contraction of the region stimulated is caused by this chemical.

$\frac{1}{20}$ per cent.—Positive reaction in all cases. Complete food reaction could be induced.

$\frac{1}{40}$ per cent.—Weak positive reaction or indifferent.

Summary.—To the salts NaCl, NaBr, KCl, and $MgCl_2$ the planarians react as to other chemicals, by giving the negative response to strong concentrations and the positive to weak.

Cane-sugar.—Sugar solutions, in all concentrations above $\frac{1}{10}$ per cent., so far as I have been able to discover, cause well-marked positive reactions in all cases. This is the only chemical which I have found that causes only one of the reactions.

Distilled Water.—To distilled water applied by the capillary method the organisms give a well-marked positive reaction in all cases. That the reactions to very dilute solutions of chemicals were not due to the distilled water in cases where this was used as the solvent, rather than to the chemical itself, was proven in the following way :—Parallel experiments were performed, using tap water as a solvent, and in every case the same reaction was given to the tap-water solution as to that in distilled water. At the same time the specimens would not react to clear tap water applied in the same way by the same tube.

2. General Summary.—Putting all the results on the effects of localised chemical stimuli together, we are forced to the somewhat remarkable conclusion that practically all substances are both "attractive" and "repellent" to planarians. Evidently, then, the chemical composition of a substance is not of the first importance in determining how the individuals shall react to it; but, on the contrary, its concentration is the important matter. To weak solutions of any chemical the animals give positive responses, while to strong solutions they give negative.

Between the behaviour towards chemical stimuli and towards mechanical stimuli there is a very close parallelism, or, perhaps better, identity, which is evidently something of fundamental importance. In order to bring this out more clearly it may be well to arrange in tabular form the results of the study of the reactions to these two stimuli.

	Mechanical Stimuli.		Chemical Stimuli.	
	Strong.	Weak.	Strong.	Weak.
Unilateral stimulation of head region	Negative reaction	Positive reaction	Negative reaction	Positive reaction.
Stimulation of head region on median line	Either a very strong negative reaction, or crawling backwards	Positive reaction	Strong negative reaction, or crawling backwards	Positive reaction.
Stimulation of middle region of body	Essentially the same as for stimulation of the head		The same as for stimulation of the head, except that the sensitivity is much less, and diminishes more rapidly posteriorly than in case of mechanical stimuli.	
Stimulation of posterior region of body	Crawling ahead	Local contraction	Crawling ahead	No effect, or slight local contraction.

From this close parallelism we must conclude, I think, that in the behaviour of planarians the qualitative character of a stimulus is of little importance in comparison with its quantitative relations. Or, to express it differently, to all stimuli which are of low intensity the flat-worm gives the positive reaction, while to stimuli which are of high intensity it gives a negative response. This sort of behaviour will at once be seen to be, in the long run, purposive, and is, further, of a kind which might very well have been developed by the action of natural selection. In the long run the planarian's reactions will take it away from injurious substances and into favourable surroundings.

These results on chemicals are interesting in connection with the work so much done in recent times on the specific effects of ions and the conclusions based on very fine quantitative results with chemicals. Two such series of experiments as those quoted above from HCl and $CuSO_4$ indicate what would be the worth of the assignment of an absolute value for the concentration of either of these two substances which would produce the positive reaction in planarians. Such instances might be multiplied, and they serve to bring out the fact, apparently so frequently lost sight of, that what an organism will do when stimulated is quite as much a function of the physiological condition of the organism itself at the time as it is of the stimulus.

A comparison of these results with those of Yerkes (: 02) on the reactions of Gonionemus is of much interest. This author finds that though there is a well-marked and characteristic food reaction, which is given in response to food substances, whether in solid or liquid form, yet this reaction cannot be induced by other chemicals. It is stated that a number of chemicals were tried in all concentrations for the special purpose of determining whether the food reaction might not depend upon intensity rather than quality of stimulus. This was not found to be the case. We must, then, conclude that Gonionemus is a stage farther along in its psychic development than is the flat-worm, for the medusa reacts with reference to the quality as well as to the intensity and location of the stimulus, while with the flat-worm the intensity and location of the stimulus are by far the most important factors. It is necessary in the case of the flat-worm, to be sure, that there be mechanical and chemical stimuli acting together in order to produce the complex of reflexes forming the complete food reaction, thus indicating some relation to quality of stimulus. But for the production of what is, in one sense, the most important phase of the reaction, the turning towards the source of stimulation, the quality of the stimulus is not significant.

With an understanding of the method of reaction to localised chemical stimuli, a number of interesting special problems present themselves. While it will not be possible to take up all of them in this paper, a few of the specially important ones may be considered.

One such important general question which arises is the problem of orientation to diffusing chemicals. Do planarians orient themselves along radial lines of diffusion and proceed towards the centre of diffusion? It would seem that in the case of such a perfectly bilaterally symmetrical organism as Planaria, if anywhere, Loeb's theory of orientation ought to hold good. This theory accounts for orientation by supposing that when an organism is stimulated unilaterally its motor organs are caused to act either more strongly or more weakly, as the case may be, on that side than on the other. This results in bringing the long axis of the body parallel with the lines of action of the stimulus; and then, since symmetrical points on either side of the body must be equally stimulated, the organism moves in a straight line towards or away from the stimulus. Jennings has shown (: 01) that for most stimuli this theory of orientation does not hold in the case of the Infusoria.

From the account of the reactions of planarians to chemical stimuli which has been given, it will be at once seen that there is in this case, to some degree at least, an orienting reaction. With weak chemical stimuli the head turns towards the stimulus in such a way as to point the anterior end very directly towards the source of stimulation. It might be thought that this marked a pure orientation, but it must be remembered that the organisms turn the head just as precisely towards the point from which a weak mechanical stimulus comes. The two reactions are evidently exactly the same thing. However, a single mechanical stimulus can hardly be considered a directive stimulus of the sort which induces an orientation, such as, for example, the electric current. The orientation of unicellular organisms to the constant current is the purest type of an orienting response, however, and the most characteristic thing about it is that the organism, after having the anterior end turned towards one of the poles, keeps the long axis of the body parallel to the lines of action of the stimulus. This movement of the animal in a constant relation to a constantly acting stimulus is, as I understand it, the fundamental criterion of an orientation according to the theory above mentioned. Now if we find, as has been shown above to be the case, that the organism gives precisely the same reaction to a chemical unilaterally applied as it does to a single weak mechanical stimulus similarly applied, it seems doubtful whether we can consider that there is such an orientation in the case of the chemical, even though the head is directed very precisely towards it. On the contrary, it seems apparent that we are dealing here with a well coördinated motor reflex only—such as, for example, the reflex of a frog's hind leg, which brings its foot very exactly to the point stimulated on the side of the body.

A crucial test of this point may be obtained by submitting the animals to the action of some chemical to which they are known to give the positive reaction when it is applied locally, only arranging the experiment so that it is diffusing over a large area. Under these conditions, if the organism shows positive orientation, it ought to move along the lines of diffusion straight up to the source of diffusion. To test this matter I constructed a trough of the form shown in Fig. 33, I. On a plate of glass A was fastened the trough B, which was cut from a block of paraffin. The internal dimensions of this trough were 50 mm. × 50 mm. × 5 mm. Only the sides were of paraffin, the glass plate serving as the bottom. A hollow was cut in one end of the trough, and a glass tube D, about 4 cm. long, was fastened into it in an upright position. Then from the point x on the inside of the trough a fine needle was thrust through the paraffin till it came out into the hollow previously cut in the wall. A sectional view of this part of the device is shown in Fig. 33, II. When it was desired to use the apparatus the trough was filled with filtered tap water and a number of planarians placed in it. Then into the tube D was introduced a certain amount of the solution whose effects were to be tested. By varying the amount of the solution introduced, the rate of its diffusion through x into the water could be very nicely controlled. This matter was thoroughly tested, and the apparatus in a sense calibrated by the use of coloured solutions before the actual experiments were begun.

A considerable number of experiments were tried with this diffusion trough, with the following results:—In no case was there any observable orientation of the organisms. A typical experiment will illustrate what actually took place. A $\frac{1}{20}$ per cent. solution of Na_2CO_3, which by the capillary method always produces a sharp positive reaction, was put into the tube D in sufficient quantity to give a diffusion of moderate rate. After it had been diffusing for some time (by test with coloured solutions long enough to reach the middle of the trough) specimens were introduced at the end C. They started gliding about in random directions at once. Some passed diagonally up to the end D; others remained nearer the end C; while still others went up on the paraffin sides to the end D. None went straight towards x after they had come into the region where the chemical had diffused. No reaction of any sort was given in the course of the passage

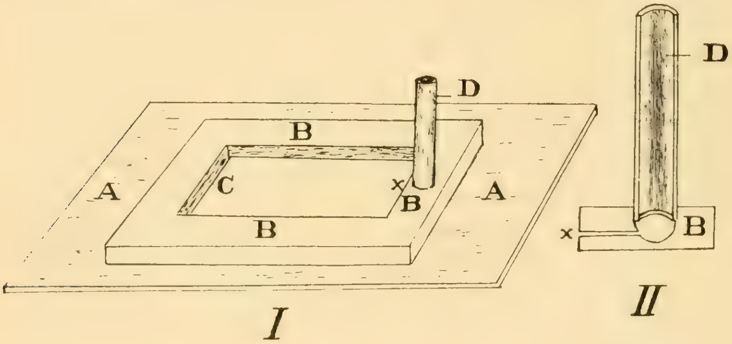

Fig. 33.—I. Diffusion trough used for testing the reactions of planarians to diffusing chemicals. A, A. Glass base plate. B, B, B. Paraffin trough. x. Point of opening of diffusion tube. C. Cavity of trough in which the specimens are placed. D. Tube in which the solution to be tested is placed. II. Enlarged sectional view of the end of the trough bearing the diffusion tube. Lettering as in I.

towards the end D in the majority of cases. In some few instances an individual would give a weak positive reaction (i. e. turn slightly towards *x*) at some point in its course, but this was so small in amount that it did not in most cases turn the animal directly towards *x*. Further, the direction of movement was frequently changed considerably, and turned away from *x* after this weak positive response. In other words, the animals moved about in the trough practically at random, giving only slight reactions in a few cases while in the area of diffusion. Many of the individuals, after reaching end D of the trough, turned around and went back to the other end again, just as they would have done provided no chemical had been present. Other specimens would glide across the trough on the paraffin of the end D. Only these specimens showed any definite response to the chemical. When they came within the length of their own bodies from the opening *x* they gave a well-marked positive reaction and went to *x*. Having arrived there, they explored and "gripped" the edge of the hole with the head, and then extruded the pharynx. The pharynx was usually stretched up into the diffusion opening, and the worm proceeded to feed for a time on Na_2CO_3.

These experiments were repeated many times with a variety of chemicals of various concentrations, and diffusing at various rates. It was very certain in all cases that there was no definite orientation along lines of diffusing ions. When the organism by chance came near the diffusion opening *x*, it would give a positive reaction if the solution was of the proper concentration, and then proceed to give the complete food reaction over the hole, but there was no continued orientation.

There was a similar absence of a negative orienting response when strong solutions of acids were used. In this case the animals stayed at end C of the trough, but this was because when, in the course of their random movements, they struck the diffusing chemical where it was of sufficient concentration, they gave the usual negative reaction, turning the anterior ends about 30° away, and starting off on the courses so defined. If they came in contact with the strong solution again they repeated the reaction. In no case did they turn squarely around with their heads directly away from x and the long axis parallel to the lines of diffusion.

It would be unprofitable to further multiply accounts of these experiments, since all led to the same result. No definite orientation occurred, but only the positive and negative motor reflexes coupled with random movements. Whether, as some maintain, we have in these positive and negative reactions the "Dinge an sich" of orientations is a question for the metaphysician rather than the physiologist to decide. The objective reality of the matter is that in the behaviour of planarians towards chemicals there is no orientation in the lines of diffusing ions, i. e. no phenomenon like the orientation of Paramecium to the electric current.

Another problem of importance in connection with the reactions of the organisms to chemicals has to do with the formation of collections of individuals. Are collections formed in certain chemicals, as is the case with certain of the Infusoria as described by Jennings? As this author has set forth, Paramecia will form dense aggregations in drops of various chemicals, particularly weak acids, introduced into the culture water. The method by which this is done is as follows:—Individuals swimming about at random strike the drop of acid by chance and pass into it without giving any reaction; when, however, they come to the opposite side of the drop, and start to pass from it to the water again, they are stimulated and give their characteristic motor reaction (jerk back and turn towards the aboral side). This reaction turns them back into the drop, which forms, as it were, a trap for all that enter it. In a short time a dense aggregation is formed. This is almost the only method of active reaction, known aside from orientation, which will produce collections of organisms in chemicals. Its essential feature is not the getting of the organisms into the chemical, this being purely a matter of chance, but the holding of them in the chemical after they have entered it, by what amounts to a negative reaction to the surrounding water. The question, then, is, can we get any such formation of collections by the retention of those specimens which have entered an area by chance in the case of Planaria?

This problem was attacked in a number of different ways, but the clearest results could be obtained by the "two-drop" method of Massart. Two drops of fluid of equal size are placed near each other on a slide, and a narrow connecting band is made between the two by drawing some of the fluid across with a needle. One of them was usually of culture water, while the other was of the solution to be tested. Now evidently, if the animals form collections by the "motor reflex" method, they ought to pass into the drop of solution without any reaction, but when they attempt to pass back into the water drop they should be stimulated to a negative reaction and thus turned back.

An experiment with a solution to which the animal gives a sharp positive reaction may first be reported. One of the drops was tap water, and the other was 1 per cent. sugar solution, to which the specimens gave a strong positive reaction. Several small planarians were put into the water drop. They glided rapidly about this drop, and soon one came up to the bridge connecting the water with the sugar. It was headed straight for the sugar drop, and passed over into it without any reaction whatever. Up to this point the behaviour is like that of the Infusoria towards the acid drop. This specimen circled about in the sugar drop, and after a time became directed towards the connection between the sugar and water, and passed back into the water drop without giving the faintest trace of a reaction of any sort. All the specimens passed back and forth between the two drops without giving any reaction, except in some cases a weak positive one. The conditions under which a positive reaction is given are that a specimen should come more or less transversely across one end of the connecting bridge, as shown in Fig. 34. It then usually gives a weak positive reaction and turns slightly towards the other drop. It may do this on passing either from the water to the sugar or vice versâ. When in sugar solution it gives a positive reaction to tap water, whether applied by the capillary tube method or as just described. It is evident, from this experiment, that collections are not formed by planarians in the same way that they are by Infusoria. The animals are not negative to the surrounding water after they have been in the solution. To test and verify this conclusion the experiment was repeated with solutions of different substances. It was found that in case of all substances in concentrations to which the animals gave a positive response when stimulated by the capillary method, the specimens would pass back and forth from water to solution and vice versâ, indifferently. If solutions were used in concentrations to which a negative reaction was given when stimulation was by the capillary method, the specimens merely stayed in the water drop. When they came to the boundary line of the strong solution they gave the negative reaction, and hence stayed in the water. This immediately raises the question, why would there not be a permanent collection of the planarians formed in a drop of a substance to which they give the positive reaction, provided they were first put in a drop of some substance to which they were strongly negative? There is evidently no theoretical reason why this should not take place, but there is an important practical one. This is that any solution which would cause a negative reaction, under these circumstances, will, so far as I have found, also seriously modify the animals' movements, if

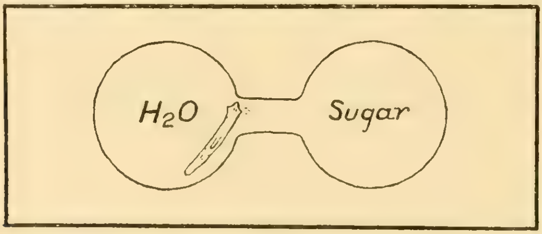

FIG. 34.—Diagram showing the arrangement of "two-drop" experiment with chemicals.

they are immersed in it. They will simply squirm about and make no progressive movements, and hence not get into the drop of substance to which they are positive. But it is quite possible that by making a long enough series of experiments on this point, one might get a solution just strong enough to cause a negative reaction, and in which the organisms would still move well. We would then get a collection in the positive drop. The important thing, however, is that to the water in which they live the animals do not, under any circumstances, give a negative reaction, and hence under normal conditions no collections can be found by a "motor reflex" method.

It may be well, before leaving this subject, to point out the fundamental physiological difference between the Infusoria and the planarians, on which the difference in the behaviour towards chemicals is based. It is that in the case of the Infusoria there is but one form of reaction (the "motor reflex" turn towards a structurally defined side) regardless of whether the stimulus is strong or weak, while in the case of the planarian there is a qualitatively different reaction to strong stimuli from that which is given to weak. When the infusorian passes into the drop of acid it is apparently not stimulated at all (for what reason we do not know). When it attempts to pass from acid to water it is given a stimulus which must be in the nature of things a rather weak one, yet it responds with the only reaction it has, and is, as a consequence, kept in the acid. With the planarian any slight change in environmental conditions gives a weak stimulus, and the specimen turns towards the source of stimulation. This serves, together with random movements, to get it into the drop of solution; but when it strikes again the water, which again must furnish a weak stimulus, it gives the same positive reaction and passes out into the water. The ability to differentiate in the reactions between the strong and weak stimuli gives the organism a far greater range in its activities.

Another problem which is of interest in connection with food and chemical reactions is the relation of the condition of the organism as regards hunger to its reactions to stimuli. It might be supposed that an individual which had not had food for some time would be more apt to give the positive reaction to a given stimulus than one which had just fed.

To test this point parallel experiments were instituted with specimens allowed to feed till they left the food spontaneously about three hours before the experiments, and specimens which had been kept for three weeks in a dish of clear water. NaBr was used as the stimulating solution, and was applied by the capillary method. The specimens chosen were of the same species, P. dorotocephala, and as nearly as possible of the same size. The only difference which could be detected between the fed and the unfed animals in their behaviour towards a $\frac{2}{5}$ per cent. solution of NaBr was that the unfed animals gave the whole food reaction on the end of the capillary tube, while the recently fed specimens only went so far as to give the positive reaction, and touched the end of the tube with the anterior end of the head. They did not "grip" it and pass up on to it, as did the others. In the main point at which I was working, namely, the giving of the definite positive reaction, there was no discoverable difference between the fed and unfed specimens. One set gave the reaction just as promptly and decidedly as did the other. Next a weaker solution, $\frac{1}{10}$ per cent., was tried. With this solution about 50 per cent. of the specimens in ordinary condition give a weak positive reaction, and 50 per cent. are indifferent. This concentration, being about on the border line between that which affords no stimulus at all and that which is a definite stimulus for the positive reaction, ought to bring out any differences which may exist between fed and unfed individuals in the sensitivity to stimuli for the positive reaction. As a matter of fact, no difference in the behaviour of the two sets was to be observed. One gave a well-marked positive reaction in as many cases as did the other. In some instances the reaction time of the fed specimens seemed to be slightly greater than that of the unfed, but this was neither marked nor of general occurrence. This experiment was afterwards repeated with other specimens, and with sugar as the stimulus, with essentially the same results. I have also repeatedly tried stimulating with various solutions specimens which had just ceased feeding, and in these cases found no certain difference between their behaviour and that of specimens which had not been fed for some time, with regard to the giving of the positive reaction. It would appear, then, that so far as the giving of the positive response to weak stimuli is concerned, the amount of food the animal has previously had is of very little consequence. The failure of fully fed specimens to give the full feeding reaction on the end of the capillary tube indicates that the physiological changes induced by recent feeding affect the performance of the food-taking rather than the food-seeking reflexes.

3. Unlocalised Action of Chemicals.—An extensive series of experiments on the effects of immersing planarians in various solutions was performed, but as the results threw but comparatively little light on the general nature of the behaviour, they will be reported only briefly. Immersion in any strong solution causes marked changes in the movements. The gliding is made very much slower or entirely disappears. In 10 per cent. NaCl a peculiar form of crawling appears. Very pronounced contraction waves pass over the body longitudinally, giving it the appearance shown in Fig. 35. In 2 per cent. $CuSO_4$ the animals make no progressive movements, but wave the head violently from side to side. In strong solutions of acids the worms squirm violently without making any effective progressive movements. In all these strong solutions the sensitiveness to all stimuli is

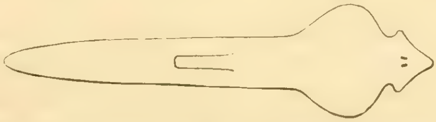

FIG. 35.—Diagram showing the form of crawling movement exhibited by Planaria when placed in 10 per cent. NaCl.

greatly diminished. This can best be shown with mechanical stimulation. In strong solutions of NaCl (10 per cent.) the animals make no attempt to right themselves if placed with their dorsal surfaces down. Another peculiar effect of strong solutions of NaCl is to cause the extrusion of the pharynx. This organ is thrust out of the body and extended to a much greater length than is usual. Immersion of the animal in weak solutions that cause the positive reaction—as, for example, 1 per cent. sugar—has no definite effect on the movements, but when in these solutions the animals will give the positive reaction to tap water when the latter is applied by the capillary tube method. Under such circumstances contact with water is a slight environmental change, and acts as a weak stimulus.

III. Thigmotaxis and the Righting Reaction.

a. Thigmotaxis.—If a specimen of Planaria is turned over and placed dorsal side down on the bottom, it will immediately right itself. This is done by a very characteristic reaction, and is one of the first things to attract the attention of one studying the behaviour of the organism. Loeb ('94, pp. 251—252) held that the righting reaction in the polyclad Thysanozoon was due to the negative and positive thigmotaxis ("stereotropism") of the dorsal and ventral surfaces respectively. The evidence offered for this view was that when the thigmotactic relations of these two surfaces were reversed, the animal reacted strongly, and that this result could not be due to any effect of gravitation, since the animal assumed all possible relations to gravity, and kept them for considerable periods of time. It seemed to me desirable to get, if possible, some further evidence on this subject, and to work out the mechanism of the righting reaction.

That the dorsal surface of the animal is negatively thigmotactic is certain, and can be shown in other ways than by laying the animal on its dorsal surface. For example, if a piece of cover-glass be gently laid on the dorsal surface of either a resting or a moving specimen, it will very promptly move out from under it. Further, if crevices are arranged of this form () by supporting cover-glasses at two corners, and letting the two opposite corners rest on the bottom of the dish, specimens will not go into them. The moment the dorsal surface touches the cover-glass above, the worm begins to react violently, changing its direction of movement, and goes out from under the cover.

With the existence of an apparent negative thigmotaxis of the dorsal surface established, however, there still arises the question as to whether this is the sole cause which induces the inverted animal to right itself. The following experiment throws light on this point:—A specimen is placed ventral side up on a dry spatula in the air, and then the spatula is placed just beneath the surface of the water in a tall jar or large test-tube and quickly pulled out from under the worm, so that the latter starts falling through the water in an inverted position. Another way in which the worm may be started falling ventral side up is by holding it on a scalpel point above the water, and then dropping it beneath the surface in the desired position. Before the worm has dropped any great distance it will give the characteristic righting reaction, and turn itself over so as to bring the ventral side down again. This is done in precisely the same way as when the animal is inverted on the bottom (to be described later). After the falling animal has thus righted itself it may again give the same reaction, and thus turn itself over so that the dorsal side is down again. In a few cases I have seen a worm after righting itself the first time keep right side up during the remainder of the fall. The most usual behaviour is for the animal to keep giving the righting reaction all the time that it is falling, although this does not, of course, keep it all the time with the same side uppermost. I have performed a large number of these dropping experiments in which the animals were started in both upright and inverted positions, and in all cases they gave the righting reacting one or more (usually more) times before reaching the bottom, provided the distance through which the drop was made was greater than 7—10 cm. This result seems to indicate that there is something more concerned in the righting reaction than the negative thigmotaxis of the dorsal surface for the following reasons:—(1) the dorsal surface is not in contact with any solid of this experiment; (2) it is in contact with water only, just as is normally the case when the animal is right side up. It may be objected that the experiment is not conclusive, because, as a result of the falling, there is an increased water-pressure on the dorsal surface, and this may act as a thigmotactic stimulus. This objection is met by two different facts. First, the animal gives the righting response in some cases while falling ventral side down, under which circumstances there can be no increased pressure on the dorsal surface. Second, if a stream of water from a pipette is directly squarely against the dorsal surface of a worm normally gliding about on the bottom the righting reaction is not induced, regardless of the force of the stream. Evidently this stream of water against the dorsal surface produces a pressure on the dorsal surface similar to that when the animal is falling, and if the righting reaction in the falling is due to increase of pressure on the dorsal surface, we might suppose that some indication of it would be produced in this case. As a matter of fact it is not. We must conclude, then, that the righting reaction is due, at least in very large part, to some other cause than the negative thigmotaxis of the dorsal surface. This is indicated also by the fact that when solid bodies are laid on the back of a specimen in its normal position, the reaction which is caused is not the righting action, as would be expected if the latter were due solely to the negative thigmotaxis of the dorsal surface. The righting reaction is clearly not due to gravitation, since the flat-worms move on the surface film with the dorsal surface downward. This leaves, as the only factor to which the reaction can be due, the positive thigmotaxis of the ventral surface. I am convinced that it is to this factor that the reaction is chiefly due. While the negative thigmotaxis of the dorsal surface plays some part in the reaction, it is, as the experiments described above show, a comparatively unimportant factor. The specific relation of these two factors to the definite righting reaction will be brought out in the next section, in which the form and mechanism of this reaction will be set forth.

b. The Righting Reaction.—The righting reaction is a very characteristic piece of behaviour, and can best be described in a single phrase by saying that when the animal is placed on its back it throws itself into a spiral in such a way that the ventral surface of the head comes into contact with the bottom. This ventral surface then attaches itself to the bottom by means of the mucous secretion, and starts gliding ahead. As it goes forward it unwinds the remainder of the spiral, as each successive posterior part of the ventral surface comes into full contact with the bottom. The form of this spiral just after the ventral surface of the head has come into contact with the bottom is shown in Fig. 36. The spiral is thrown very quickly after the dorsal surface touches the bottom, and usually includes the whole length of the body at once. However, by observing a specimen in which it takes place a little more slowly than usual, it can be seen that the movement is started at the anterior end. Beginning with, for example, the right side of the head, this is turned under, while at the same time the left side is raised. This, of course, brings the ventral surface of the head region down, and at the same time makes a twist in the body, just back of the head. In some cases this is the only twist that is made, while in others another similar twist is thrown in the body farther back. As the anterior end after it is righted glides

FIG. 36.—Showing the form taken by Planaria in the righting reaction.

ahead, the spiral is unwound by the raised edge of each twist dropping down and attaching to the bottom as soon as it is in a position where this is possible. Thus, of course, when the animal has traversed a distance equal to its own length it will have come entirely into the normal position again. The reaction is really a rotation of the body on its long axis through 180°. The mechanism of the turning is such that only a part of the body rotates at a time,—first the anterior end, then the portion next behind that, and so on, till the whole animal has turned over. This rotation by sections, as it were, causes the spiral form which the animal takes on in the reaction.

The number of turns into which the body is thrown in forming the spiral varies with the length of the individual, and apparently to some extent with its physiological condition. There may be only a half-turn in the whole body, or there may be one complete turn; or, again, one and a half turns; or, finally, as many as two complete turns in the body. One complete or nearly complete turn, as shown in Fig. 36, is the usual form of the reaction. In large individuals more twisting is frequently seen. Evidently all the twisting that is absolutely essential for the righting of the specimen is the half-turn given by the turning of the anterior end ventral side down.

The determination of the direction in which the spiral is thrown, or, in other words, the side of the body towards which the anterior end turns in order to get right side up, was for some time a very puzzling problem. A collection of statistics on the matter showed that the anterior end twisted towards the right and towards the left[1] in an approximately number of cases. This is precisely the result which would be expected if the matter were due to chance only, but the reaction did not give the appearance of being a chance matter. Finally, the determining factor was found to be the relation of the dorsal surface to the bottom. A cross-section

---

[1] In the figure (Fig. 36) the worm is represented with the spiral thrown towards the left.

of the body of Planaria has the form shown in Fig. 37. It is convex in outline on the dorsal side, and nearly straight on the ventral. As a consequence of this shape of the dorsal surface the animal when placed in an inverted position very seldom lies exactly on the mid-dorsal line, and if it does at first it almost immediately tips over to one side or the other, so that its cross-section has the relation to the bottom shown in Fig. 37, B and C. It is then found that the side of the body which is in contact with the bottom determines in which direction the spiral shall be thrown. If the right side of the dorsal surface is down the right side of the head will turn under towards the left and the left side will be raised up over towards the right, or, in other words, the head as a whole will rotate from right to left, i. e. in a counter-clockwise direction. If the left side of the dorsal surface of the body is down at the beginning, the head will rotate from left to right. This relation may be made out easily by direct observation in all cases where the reaction is not too rapid.

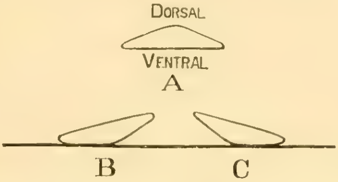

FIG. 37.—Diagrammatic cross-section of Planaria to show the contact relations of the dorsal surface of the body to the substrate in the case of a specimen in an inverted position.

The righting reaction is a fairly rapid one. The head is turned over and the spiral thrown in the case of a normal individual almost immediately when the dorsal surface touches the solid. The length of time which it takes a specimen to get completely righted evidently depends on the length of the body, because the longer spiral which must be unwound, the more the time which must be taken. The following figures will bring out this relation between the size of the individual and the time taken in righting. In ten trials with an active but large specimen (about 12 mm. long) of P. dorotocephala the average time taken to regain completely the normal position after being inverted was 8·68 seconds. With a small specimen (5·5 mm. long) the average time taken in righting in ten trials was 5·22 seconds. The time taken in the reaction also depends, of course, on the general physiological condition of the animal. Thus in ten trials with a sluggish specimen, approximately 9 mm. long (thus shorter than the first specimen mentioned), the average time taken in regaining the normal position was 10·90 seconds.

The thigmotactic irritability may be modified or reduced in several ways, and, as a consequence, the righting reaction will disappear entirely or in part. One of these cases has been mentioned above (p. 670) where it was shown that a specimen placed on its back in a 10 per cent. solution of NaCl makes no attempt to right itself. Similarly a specimen put in an inverted position on a dry surface, care being taken that no water surrounds the animal, will not give the righting reaction. In both of these cases the specimens are able to move.

The Mechanism of the Reaction.—It is a very difficult matter to determine exactly the muscular mechanism of this righting reaction, since it is such a complicated movement, and is ordinarily done in its most essential feature—the formation of the spiral—so very quickly. Furthermore, as will appear from the operation experiments to be described, it is almost impossible to devise crucial experiments of a character which will demonstrate what the mechanism is. What I shall do, then, will be to present a tentative explanation of the mechanism of the reaction, together with the evidence for it which I have been able to obtain. I may say that the view to be presented is the result of a long and careful study of the phenomena both in normal and operated worms, and I believe that it is a correct explanation.

The mechanism of the righting reaction is probably as follows:—The half of the body of an inverted specimen which is in contact with the bottom extends (by the mechanism previously described, pp. 556, 557) in response to the stimulus given by the contact of the dorsal surface of that side of the body with the bottom. At the same time the opposite half of the body, by active muscular contraction, keeps its length the same. Thus any bending of the body away from the side stimulated as in the ordinary negative reaction is prevented, or, in other words, the long axis is kept straight by the opposite side maintaining actively its normal length. Now the necessary mechanical result of keeping one side of a flexible system at a constant length while the other side lengthens must be that the lengthening side will be thrown into a series of waves. In other words, it is mechanically impossible for the lengthening side to keep its whole edge in the same plane. Furthermore, if in such a system it is possible for rotation about a longitudinal axis to occur, the system will be thrown into a spiral of the form which the planarian takes in the righting reaction. Again, as soon as one side of such a system under elongating stress changes its level with reference to the remainder of the system, and thus starts the formation of the spiral, the long axis of the system (i. e. the centre of the spiral) will keep itself straight. Any further force elongating one side will merely throw the spiral into tighter coils without having any tendency to bend its long axis. This fact is of importance in the case of the planarian where the maintenance of the initial straightness of the long axis is done by the opposite side of the body. Of course, a symmetrical spiral cannot be formed unless the two edges are of equal length, but the moment the spiral of the planarian is started all necessity for one side keeping a constant length ceases. It must be kept in mind, however, as has been indicated above, that the force which produces the spiral must act on one side only, and hence the side of the planarian opposite that initiating the movement must be moved passively by the other in the spiral formation after this has once begun. The direction in which the spiral shall turn will evidently not be determined by the mere lengthening of one side of the body. The determinant of this is evidently a difference of tension on the upper and lower sides, the spiral turning towards the side of greatest tension.[1] This greatest tension is evidently, then, in the normal reaction on the dorsal surface, as we should expect on a priori grounds, since that is the part directly stimulated.

To sum up, the spiral righting reaction of the planarian, as I have worked it out, is due to an elongation of that side of the body whose dorsal surface is in contact with the solid, while the opposite side of the body actively maintains its original length. As the elongation occurs the various parts of the body rotate freely about its long axis, and hence the whole worm takes on the spiral form. The spiral turns towards the dorsal surface in every case (i. e. so as to bring the ventral surface of the head down), as a result of the greater tension of the dorsal musculature on the elongating side.

The reaction is thus seen to be of almost the same character as the ordinary negative reaction to strong mechanical stimuli, in that the primary reaction is an extension of the side stimulated. The difference between the two is that in one case there is a bending of the longitudinal axis of the body, while in the other there is a rotation about this axis. On the view just given of the mechanism of the righting reaction the specific parts played by the positive and negative thigmotaxis of the ventral and dorsal surfaces are evident. The positive thigmotaxis of the ventral surface is the primary cause of the whole reaction, and is evidently the stronger factor of the two, as shown by the experiments of laying solid bodies on the dorsal surface of the animal when in a normal position. It will be recalled that such treatment does not call forth the specific righting reaction. Further evidence of this same thing is found in the fact that speci-

---

[1] The statements as to the mechanical principles of a spiral have been verified with different sorts of models, including plastic clay, rubber bands, etc. Lack of space will not permit the enumeration of these experiments in detail, but anyone can verify for himself the various statements with very little trouble.

mens will remain in the normal position on the bottom of a dish when there is a layer of plant débris a half-centimetre in thickness above them, and necessarily in contact with the dorsal surface. The negative thigmotaxis of the dorsal surface plays its part in the righting reaction in determining in which direction the turning shall take place.

It has so far been shown that the view of the mechanism of the righting reaction presented is in accord with all the mechanical principles necessary to produce the observed results. The attention may now be turned to an examination of the evidence that this mechanism is the one which actually brings about the reaction. This evidence is obtained from experiments with worms on which operations have been performed. Obviously, if the mechanism described is the one by which the reaction is produced, any operation which destroys or throws out of working order any essential part of the mechanism will cause the typical reaction to disappear, or be greatly modified.

We may first consider the reactions of the pieces resulting from cutting the animal in two transversely in the middle of the body. It is found that each of the pieces resulting from such a cut will perform the righting reaction in the typical manner. The spiral is formed, but there is usually only one half-turn of the body, i. e. just enough to bring the anterior end ventral side down. This then attaches itself to the bottom and starts gliding, unwinding the spiral just as under normal circumstances. There is observable the same relation between the side of the body, which is in contact with the bottom and the direction of the turn as in the normal individual. The only striking difference in the behaviour of the anterior and posterior pieces is that the reaction time of the former is much shorter than that of the latter. The anterior piece rights itself practically as quickly as does the normal animal, while the posterior piece took in one series of experiments 1 minute and 38·1 seconds (average of ten trials) for complete righting. This slower righting reaction is another expression of the generally lowered tonus of such posterior pieces. By varying the position of the cuts, segments of the body of various lengths may be obtained. All of these, which are about 1½ mm. in length, will usually right themselves by as close an approximation to the typical spiral reaction as is possible under the circumstances. The side of the body which is lowest can be seen to elongate in these very short pieces, and just enough of a twist is found to bring the ventral surface of one corner of the anterior end into contact with the bottom. Of course, no complete spiral can be found in such short pieces. Their reaction time is very slow.

Next, experiments were tried with the pieces resulting from splitting longitudinally anterior halves of worms in the middle line. These pieces had the form shown in Fig. 38. Evidently such pieces have only a half of the mechanism necessary for the performance of the spiral righting reaction, according to the view given above, and therefore should not be able to give the typical response. They have one complete side which may elongate, but they have no other side to keep the middle line straight, and so make the elongation effective in forming a spiral. Such pieces, when placed with the dorsal surface down, reacted immediately by bending strongly towards the cut side, i. e., so that the concavity was on the cut side. This was kept up for a time, the animal squirming about violently, but it was finally replaced by another reaction. The ventral longitudinal muscles contracted strongly, and raised the anterior end of the piece well up from the bottom (shown in side view in Fig. 39, *a*). After a strong raising contraction the piece would extend and settle back again. Then after a time the raising was repeated, and it soon became noticeable that the piece was rising higher each time and

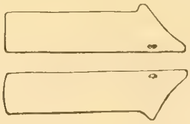

FIG. 38.—Operation diagram (see text).

settling back less after each trial. Successive stages of this rising are shown in Fig. 39, *b*, *c*, *d*. Finally, it worked up till it stood directly on the posterior end (*e*), and then the next contraction caused it to fall over of its own weight and come down right side up (*f*). The sticky mucous secretion at the posterior end was undoubtedly what held the piece up after each successive trial. This behaviour, as described, was uniform in all the trials.

The behaviour of these pieces brings out several points of importance. First, it is to be noticed that no trace of the typical spiral righting reaction is to be seen; yet, on the other hand, we find the pieces bending strongly towards the cut side when first inverted, which is just the effect which would be produced by the lengthening of the stimulated side in the normal righting reaction, provided, as actually obtains in this case, there was no opposite side to keep the long axis of the piece straight. Thus we get precisely the result which would be expected if the view given of the mechanism of the reaction is the correct one. Another fact that is brought out by this experiment is the apparent adaptation shown. When the animal is unable to give the usual reaction for righting itself it very quickly reacts in an entirely different way, but attains the same end result.

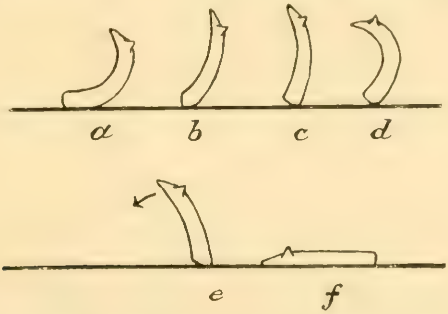

FIG. 39.—Diagram showing the method of righting adopted by one of the pieces shown in Fig. 38.

A worm was cut so as to give a piece of the form shown at A in Fig. 40. This piece was placed in an inverted position and its reactions observed. Evidently, so far as injury of the mechanism by the operation is concerned, such a piece is in essentially the same condition as the pieces described in the previous experiment. It has only one complete side of the body. The piece when inverted squirmed about considerably at first, but gave no indication whatever of the normal spiral reaction. In a short time the violent movements ceased, and a notch was noticed in about the middle of the uncut edge (cf. Fig. 40, *b*). This soon grew larger, and extended more and more towards the ends of the piece, as shown in *c* and *d*. By close observation the cause of this appearance was found to be that the thin mobile edge was folding under and attaching its ventral surface along the bottom. A cross-section through the worm at this stage had the outline shown in *e*. As soon as a considerable portion of the edge had so folded under and become attached, the piece gave a series of strong contractions and literally "flopped" over the attached edge and came down right side up. A stage in this process is shown in cross-section in *f*. This behaviour was so peculiar, and at the same time precise, that the

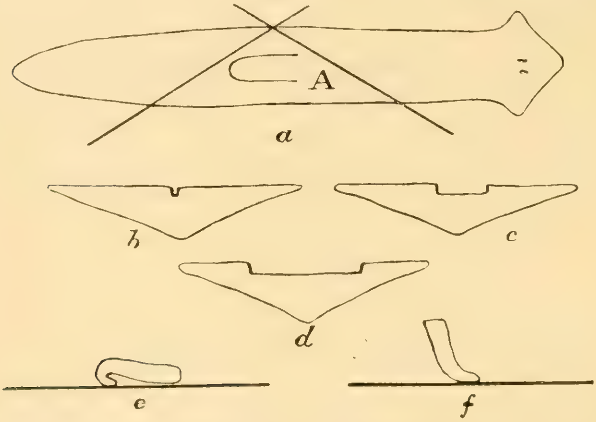

FIG. 40.—*a*. Operation diagram. Heavy lines indicate the cuts. *b*, *c*, and *d*. Successive stages in the righting reaction of the piece A of diagram *a*. *e* and *f*. Cross-sections through A at two successive stages in the righting process. See text for further explanation.

experiment was repeated many times on this piece and on others cut in the same way. The same method of righting was always observed. After the first few times the turn is made in this way; it is done more quickly at each successive trial.

This experiment leads to the same conclusion regarding the mechanism of the righting reaction as did the previous one. It affords another and more striking example of regulation in reactions. The piece attains the end (normal position) by a reaction which it undoubtedly never had occasion to practise before.

Isolated longitudinal halves of the body react in the same way as did the piece described in the preceding experiment. They right themselves by folding under the edge, and then, by violent contraction, drawing the rest of the body up over it. There is no trace of the spiral righting reaction.

A specimen cut in the manner shown in Fig. 41 shows a very peculiar righting reaction. When placed dorsal side down the portion posterior to the median longitudinal slit immediately gives the spiral righting reaction, and drags the two passive anterior pieces over. The process is slow but very characteristic, so that there is no doubt of the nature of the reaction. This shows that in that part of a single piece of a worm where the necessary mechanism is present we get the spiral righting reaction, while in other parts it does not appear.

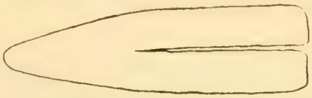

FIG. 41.—Operation diagram (see text).

The same point can be brought out by splitting a worm longitudinally from the posterior end up to a point near the head. The complete anterior part of such specimens gives the normal spiral reaction, while the posterior parts remain passive so far as this reaction is concerned.

A considerable number of different experiments were performed for the purpose of testing the righting reactions after operations, but since none of them bring out anything different in principle from the results already given, they will not be reported here. But it may be said in general, that all the experiments gave the same results with reference to the mechanism of the reaction, namely, that so long as the mechanism described above was intact the typical spiral reaction was given; when this mechanism was destroyed or injured the reaction was not given, but the animal, if it righted itself at all, did it by a different method.

When the animal falls freely in the water the righting reaction is induced because the ventral surface is no longer in contact with a solid. There is no reason for thinking that the mechanism of the reaction in this case is any different from what it is when the animal is placed in an inverted position on the bottom. The direction in which the spiral is thrown in the case of the falling animal is probably determined by slight differences of pressure on the two sides of the body.

c. Summary.—The flat-worm is positively thigmotactic on its ventral surface, and negatively thigmotactic on its dorsal surface. As a result of this it gives a characteristic righting reaction whenever the normal relations of either surface are changed. This righting reaction consists in throwing the body into a spiral in such a way as to bring the ventral surface of the anterior end down into contact with a solid (in all cases except when the animal is dropped into free water). The anterior end starts gliding and unwinds the spiral, thus righting the whole body. The thigmotactic reaction may be modified by chemical and other stimuli. All the evidence shows that the spiral righting reaction is due to a lengthening of the side whose dorsal surface is in contact with a solid, while the other side of the body keeps the long axis straight. The direction of the turn in the spiral is determined by the side of the body which is in contact with the solid. This reaction is thus seen to be closely related to the negative reaction to mechanical and chemical stimuli, so far as mechanism is concerned. Cut pieces, in which the normal mechanism for the righting reaction has been destroyed, right themselves in various ways, thus showing a sort of regulation in reactions.

IV. Electrotaxis.

In view of the sharp and precise reactions of planarians to other stimuli, it was thought that they would furnish excellent objects for the study of electrotaxis, but unfortunately this is not the case. Their reactions to the constant current are not clear-cut, since the specimens become wholly or partially paralysed in a very short time after the current begins to act, and as a consequence the reactions become feeble and indistinct. For the sake of completeness, however, and since some facts of importance are brought out, the experiments on this subject will be briefly reported.

a. Methods.—The following methods were used:—The constant current used was obtained from the general lighting circuit of the University, and reduced to the proper intensity by interposed resistance. This apparatus for getting the current I have described fully elsewhere (: 00, : 01), so that it need not detain us here. In the circuit a rheostat was inserted for regulating the strength of the current. Ordinary unpolarisable brush electrodes were used. The specimens were placed either in a trough with clay ends, to serve as poles, and with paraffin sides of 5 mm. depth, or else on a slide under a cover supported by several layers of moistened filter-paper. These filter-paper ends then serve as the poles of the preparation, the brushes of the electrodes being laid upon them. The layer of water in which the specimens were in this sort of a preparation was approximately 2·5 mm. in thickness. Identical results were obtained by both the trough and the filter-paper method, but since the latter is the neater and generally more satisfactory method, it was used almost entirely in preference to the trough.

b. Results.—The typical result of the action of the current on specimens in such a position that the long axis of the body is approximately at right angles to the direction of the current, may be described first. If a number of specimens are gliding about at the normal rate, and a current of from weak to medium intensity is made through the preparation, the first reaction of all the specimens is to stop their forward motion, turn towards the kathode, and start crawling very slowly towards this pole. The orientation towards the kathode is at the first trial usually rather precise. The whole animal gets squarely into line with the current and moves slowly towards this pole. While the current is acting the anode end of the body, in this case the posterior end, remains rather strongly contracted, presenting the same appearance as when mechanically stimulated. Movement occurs only for a short time after the current begins acting. The worm soon comes to rest, and further stimulation serves only to cause contraction of various parts of the body without producing any progressive movement. The successive stages of the first typical reaction to the constant current are shown in Fig. 42.

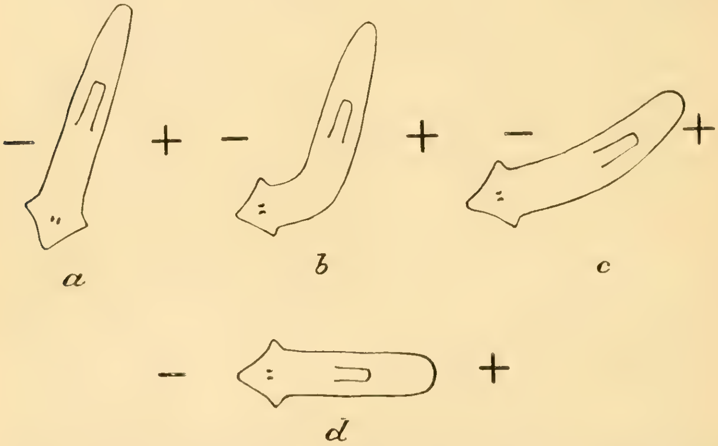

Fig. 42.—Diagram showing the typical electrotactic reaction of Planaria. *a*. Position at the moment of making the current. *b*, *c*, and *d*. Successive phases of the reaction.

In succeeding experiments on a given individual, and in many cases with the very first experiment, the reaction is much less pronounced. The animal in the transverse position, at the moment of making the current, will simply turn the anterior part of the body somewhat toward the kathode and then stop. Reversal of the current causes the head to swing a short distance towards the new kathode, and then stop again. The orientation becomes less and less precise the longer the current acts. The position most frequently taken by a specimen after it has been submitted to the action of the current for a short time is shown in Fig. 43, where it is seen that the orientation of even the anterior end is not very precise. In all such cases the specimen remains perfectly quiet after the first turn towards the kathode until the current is reversed or broken.

The behaviour described is that which is typical for currents of medium to fairly weak intensities. With very weak currents no striking effect is produced. With a current which is just stong enough to cause a general movement of Paramœcium towards the kathode, the only effect on a planarian gliding at right angles to the current is to cause in some cases a very slight turn of the head towards the kathode at the moment of making. The specimen does not stop the gliding movement, and is not forced into any orientation, but may give a slight turning reaction, which changes its course from one squarely at right angles to the current to one turned a little diagonally towards the kathode. In many cases such a current produces no effect whatever. With very strong currents the planarian stops at the moment of making, jerks the anterior end around towards the kathode more or less, and then curls up into the form shown in Fig. 44, as a result of very strong contraction of the ventral longitudinal

FIG. 43.—Diagram showing partial orientation of Planaria to the constant current.

musculature, and dies. I have never been able to produce disintegration on the anode side with any current strength at my disposal except in a single case, where disintegration began in the region just behind the pharynx in a specimen strongly curled up in the way described.

In case the long axis of the planarian is parallel with the direction of the current, and the head is towards the kathode at the moment of making, with a perfectly fresh specimen the effect is to cause a cessation of the gliding movement and a change to a very slow crawling. The direction of the movement is not changed. There is a well-marked contraction of the anode (posterior) end of the body. The reaction of the animal in this position is shown in Fig. 45, *b*. Very weak currents have either no effect on a specimen in this position or else may cause a very slight contraction of the ventral longitudinal fibres mentioned above.

FIG. 44.—Diagrammatic side view of a planarian subjected to the action of a very strong constant current.

When the long axis of the body is parallel to the direction of the current, and the head is towards the anode at the moment of making, the effect of a current of medium intensity is to cause the gliding movement to stop. At the same time there is a very definite contraction of the anode (head) end of the body. As the current continues to act the specimen begins to squirm about, and very soon gets out of line with the current. Then the anterior end is turned towards the

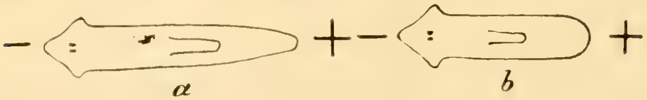

FIG. 45.—Diagram showing the electrotactic reaction of Planaria when the long axis of the body is in line with the current direction, and the head is towards the kathode. Contracted portions are indicated by heavy lines.

kathode slowly, and this process may be continued until complete reversal is brought about and the animal comes to lie again in line with the current, but with the anterior end now directed towards the kathode. This reversal into the usual orientation is the typical reaction for fresh specimens at the first trials of the current; it is shown in Fig. 46. In case the specimens have been under the action of the current for some time, there is no reversal of the position. The specimen simply remains in the same position and contracts strongly at the anode (head) end of the body.

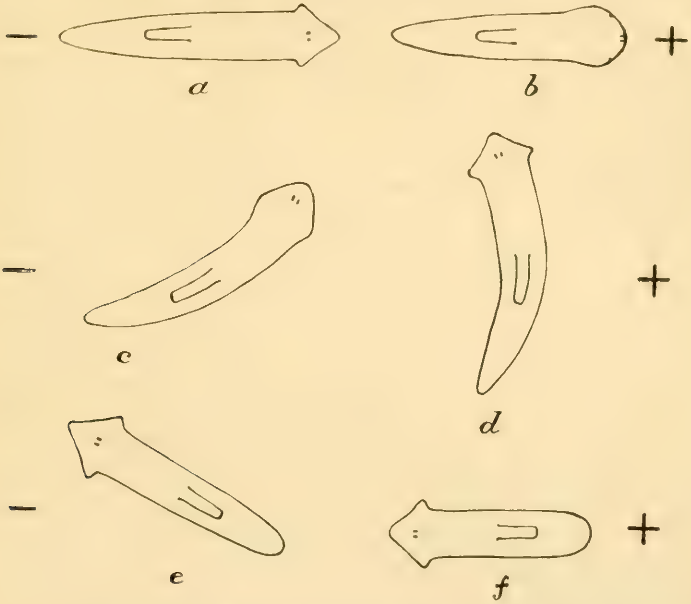

FIG. 46.—Diagram showing the electrotactic reaction of *Planaria* when the long axis of the body is in line with the current direction, and the head is towards the anode. Contracted portions are indicated by heavy lines.

Strong currents have the same effect as described in the preceding experiment. Very weak currents either have no definite effort, or else cause a slight jerking back of the head, and turning a little to one side at the moment of making.

After the animals have become partially paralysed by the action of the current, the nature of the contractions and relaxations of different parts of the body can be very clearly seen, and since these are the most significant features of the animal's reactions to the electric current, they may be described a little more fully. These reactions for the three chief positions are shown in Fig. 47. The essential features are contraction of the anode end of the body when in line with the current, and convexity on the anode side when at right angles. Besides this there seems to be some slight expansion at the kathode end of specimens in line with the current, but this appearance is not constant. Reversal of the current in these paralysed specimens causes contraction at the new anode end or bending towards the new kathode. On breaking the current the contracted portions relax.

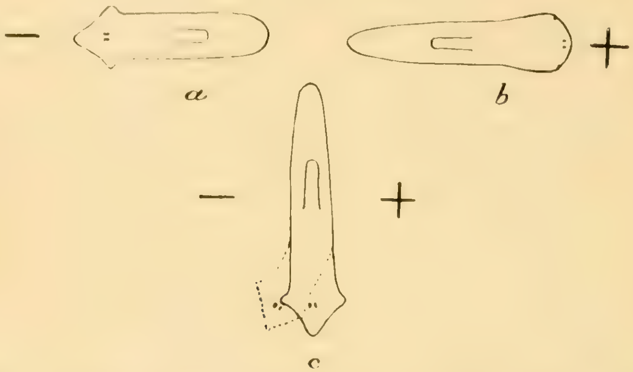

Fig. 47.—Diagram showing the contractions caused by the current with the body in the three principal positions.

c. Mechanism of the Reactions.—It will be seen from the figures, and the account which has been given of the responses to the electric current, that there is an apparent anomaly in the behaviour. The specimen contracts always at the anode end of the body, but apparently not on the anode side of the body. I believe that the explanation for this apparent difference in behaviour is to be found in the structure of the animal, and in a peculiarity in the action of the constant current which has been noted in another case. When the animal is in line with the current the contraction observed at the anode end is, as shown by the form taken by the part reacting, a contraction of the longitudinal muscle-fibres, while the fibres of the circular and transverse system are relaxed. In other words, the current only affects those fibres which bear a definite orientation with relation to direction of its flow, viz. those which are parallel with it. Now it has been shown in an earlier part of this paper that in the ordinary negative reaction the turning away from the stimulus is produced by a contraction of the circular, transverse, and dorso-ventral fibres (principally the circular) on the side stimulated. Evidently when the animal is at right angles to the direction of the flow of the current the only muscle-fibres in the body whose longitudinal axes are in line with the current are the fibres of the circular and transverse systems. Unless it is assumed that the current acts differently in one case from in another there is no apparent reason why, when the animal is in the transverse position, the fibres which are in line with the direction of the current on the anode side of the body should not contract. If the fibres fulfilling these conditions as to location and orientation (the circular system) do contract, they will cause the anterior end to be turned towards the kathode and the anode side to become convex,—in other words, produce the actually observed result. The fibres of the longitudinal system should not be affected, and there is no evidence that they are. This explanation assumes that the current produces its effect by directly causing the contraction of properly oriented muscle-fibres, possibly, or even probably, without relation to the stimulation of any sense-organs of the animal. Or, to put it in another way, the responses according to this view might not necessarily be reactions of the organism at all, in the sense of being something that the animal does after receiving and transforming a stimulus, but are direct effects of the stimulus acting on the motor organs. It has doubtless occurred to the reader that another explanation is possible for these reactions, namely, that they are in no way essentially different from what would be produced if the animal were given strong mechanical stimuli on those parts of the body which are nearest the anode in the several positions. In other words, the constant current, from the standpoint of the planarian, produces the same effect on the anode side or end of the body that a strong mechanical stimulus applied in the same place would.

Which of these two views is the correct one the planarian does not show clearly. Yet there is some inferential evidence which makes it seem probable that the first view as to the cause of the reaction is the correct one, viz. that the current produces direct contractions of muscle-fibres oriented in line with its direction. The evidence for this view is as follows:— (1) In the case of specimens which have been for some time under the action of the current, and are, as has been mentioned, almost completely paralysed, the essential features of contraction on the anode side or end can still be produced by a fairly weak current. At the same time it takes a very strong mechanical stimulus to get any reaction from these pieces, indicating that their sense-organs are almost completely paralysed, and their general sensitivity gone. If the current acts merely as a stimulus qualitatively like others which produce the same reactions, it is not apparent why it should be effective in weak intensities when another stimulus fails in strong intensity. If it acts directly on the muscles we should expect that it would be capable of producing an effect after the general sensory functions had been lost. (2) The contractions produced by the current are sharply localised, i. e. they involve only a certain definite part of the body whether the current is strong or weak (within certain limits); whereas mechanical stimuli applied to the same places with an intensity sufficient to cause the same definitive reaction will also cause a marked general response of the whole organism. This is just what would be expected if the current affects only the muscles oriented in line with it and lying at the anode pole of the worm. (3) By analogy with other forms—for example, the Protozoa—it would be expected that the current would produce some other effect than that of an ordinary stimulus applied at the same point. In the case of the Infusoria the current causes an entirely different reaction from that produced by any other known stimulus.

For these reasons, then, I am inclined to think that in the case of the flat-worm the current affects certain definitely oriented muscle-fibres directly, and by this means produces in the main the characteristic reactions. That the current does not also stimulate the sense-organs, and so act like other stimuli applied to the same places, I am not prepared to say, but it seems probable that the phenomena observed are not primarily caused by such action.

It has been brought out by inference that the cilia play no part in the electrotactic reaction of planarians. This is the true state of the case. The current in any intensity sufficient to cause the definite reactions stops immediately, so far as I have been able to observe, all ciliary movement. The evidence for this is twofold. First, all gliding movement stops in effective currents; and second, by direct observation of specimens crawling ventral side up on the surface film no ciliary currents can be observed while the electric current acts. This result is of interest in connection with the reactions of the rhabdocœle Stenostoma leucops, O. Schm. This form, which normally moves freely through the water by the activity of its cilia, reacts to the electric current in essentially the same way as do the Infusoria (cf. Pearl, : 00). That is to say, the cilia on the kathode half of the body take a reverse position when the current is made, and their effective stroke is towards the anterior end. The different relations of the cilia in different positions of the body are shown in Fig. 48. This relation of the ciliary beat, coupled with the form of the body, causes, as a mechanical necessity (cf. Ludloff, '95), the animal to orient with the anterior end towards the kathode. This method of reaction of Stenostoma I worked out by precisely the same methods as I used in a previous study of the electrotaxis of the Infusoria (: 00). This reversal of the position of the cilia as a result of the action of the current has hitherto been observed only in the Infusoria, and to find the same thing in a multicellular organism is a matter of considerable interest. It is outside the scope of the present paper to discuss the relation of this result to current theories of electrotaxis, as I hope to be able to do in a later paper, but it may be said that this furnishes another strong piece of evidence that in the case of these lower organisms the current does not cause the observed reactions in any way comparable to that in which a mechanical stimulus causes a reaction, i. e. by furnishing a certain "sensation." On the contrary, the current acts as a physical force on a structure organised in a certain way.

Experiments on the electrotactic reaction of cut pieces of planarians have been tried in considerable numbers, but with, on the whole, unsatisfactory results. Anterior pieces resulting from transverse cuts are the only ones from which I have been able to obtain any constant results. Such pieces react like the normal animal in every way. Posterior pieces from transverse cuts show the contractions on the anode side and ends in a slight degree, but there is no constant production of orientation. Specimens slit longitudinally in the middle line from the posterior end nearly to the head react essentially like a normal specimen, although much more weakly. I have observed in one case fairly precise orientations of such a specimen. From specimens slit longitudinally

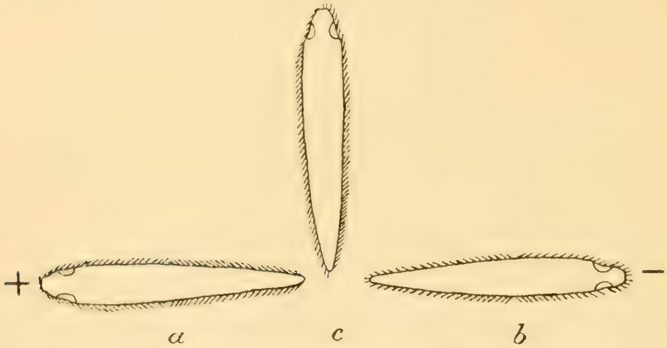

FIG. 48.—Diagram showing the electrotactic reaction of the rhabdocele, *Stenostoma leucops*, O. Schm.

in the middle line from in front backwards I have never been able to obtain any definite results. They simply squirm about in an aimless way for a moment when the current is made and then become quiet, and remain so while the current passes. The direction in which the current is flowing makes no difference in their behaviour. All operated specimens become very quickly paralysed by the current.

d. Summary.—The constant current very quickly paralyses planarians. Its specific effect is to cause a contraction of the anode side or end of the body. This produces in the case of fresh specimens a well-defined orientation, with the anterior end towards the kathode. All progressive movement after the making of an effective current is by the crawling method, the cilia being stopped or very greatly slowed in their beat. The electrotactic reaction, so far as the attainment of orientation is concerned, is essentially the same as the negative reaction to mechanical stimuli. In the rhabdocœle Stenostoma leucops there is found to occur a reversal of the cilia on the kathode half of the body, such as occurs in the case of the Infusoria.

V. Reaction to Desiccation.

A series of experiments was performed to determine the reactions of the animal on drying. This is an environmental condition which planarians probably have had to meet with relative frequency in the course of their history as a species, and it is a matter of interest to determine whether they have any method of reacting which protects them from it.

Experiments were first performed in the following manner:—Specimens were taken from the aquarium dish on the point of a scalpel or a spatula, and lightly touched to a filter-paper for a moment to remove any adherent water, and then laid upon a dry surface—either glass or paper. The behaviour was usually as follows:—The worm would curl up closely and thrust the head under the body, as shown in Fig. 49. The purpose of their behaviour seems to be to get the body into as small space as possible, and especially to keep the head from drying. At fairly frequent intervals the animal straightens out and extends the head in front as far as possible, and makes "feeling" movements. It is then withdrawn, and the animal curls up again. After the drying has proceeded for some time the most characteristic feature of the whole reaction appears. This is a lengthening of the posterior part of the body to its fullest extent. The posterior end then attaches itself to the surface, and strong waves of contraction, like those in the crawling movement, pass over the body from the posterior end forward. No progressive movement is made, but backward crawling is evidently attempted, and is only prevented by the dry surface which the animal is on. There may be considerable variation in the first part of the reaction with regard to the curling up; this may appear or may not, but the attempted backward crawling movement of the posterior part of the body I have found to be a constant feature in the experiments which I have performed. When the dorsal surface of the worm becomes dry all movement ceases. If quickly put back into the water the worm will usually recover completely, even though all movement has ceased in the air.

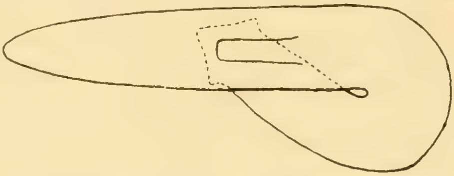

FIG. 49.—Diagram showing the reaction of Planaria to desiccation.

If the worm is put on a slide in the centre of a small area which has been wet, but on which there is no standing water, it will squirm about and extend the head frequently, as in the last experiment. If the head goes outside the wet area it is very quickly jerked back, and the specimen gives the negative reaction, i. e. turns away from the side stimulated. The attempted backward crawling occurs in this case just as in the others, a short time before the dorsal surface dries off.

It is to be noted that there is never any actual progressive movement of a specimen in the air. If a specimen is placed on very wet filter-paper it is not able to progress unless water is kept constantly dropping on it from above, so that it is at any time surrounded by a layer of water. On account of this lack of ability to move when out of water, there is no true hydrotaxis in the sense of movement towards water.

As has been mentioned before, specimens placed on a dry surface dorsal side down do not show the righting reaction.

To sum up, it is found that planarians, when removed from the water and subjected to a process of drying, are unable to make progressive movements. At a certain stage in the drying process they attempt to crawl backwards—a form of movement which, under certain circumstances, might get the animal back into water. On meeting a dry surface with the anterior end the animals give a well-marked negative reaction. The animal does not give the righting reaction on being inverted on a dry surface.

On the whole, the general behaviour when subjected to drying is purposeful; that is, it would tend to prevent the animal ever becoming dried up under natural conditions. There is nothing in the behaviour of planarians to indicate how the change from aquatic to terrestrial life could be brought about. The fresh-water Triclads, so far as I have observed them, never leave the water and crawl up into the air above the surface film as some other forms do.

VI. Rheotaxis.

A large number of experiments were performed early in the course of the work with various sorts of devices to determine whether the animal showed any distinct reaction to currents in the water, but without success. Streams of water from a pipette, currents made by filling the tube of the diffusion apparatus described above (pp. 661, 662) with water and blowing into it, and other methods gave no results. If the currents were made with sufficient force to threaten dislodgment of the animal from its hold on the bottom it would stop moving and contract longitudinally, and thus attach itself more firmly to the substrate. Weaker currents caused no effect whatever. I was inclined to believe that the longitudinal contraction and the gripping of the bottom were the only rheotactic reactions which the organism exhibited. It was found later, however, that there was a very precise rheotactic reaction of a different character. In the course of the experiments on reactions to localised chemical stimuli by the capillary tube method, it was discovered that by using a tube with a relatively large opening (from $\frac{1}{4}$ to $\frac{1}{2}$ mm. in diameter) and letting the ordinary tap-water in which the animals were flow out of it, by its own weight, a current of just the right intensity to cause a positive reaction could be produced. The animals would turn very sharply towards the source of such a current, the reaction being evidently the same as that given to other weak stimuli (chemical and mechanical). This reaction is localised in the same way as the usual positive reaction. It is given only when the current is directed against the head or anterior part of the body.

It is thus seen that the planarian is positively rheotactic to very weak currents, the form of the reaction being precisely the same as that given to other weak stimuli. It seems very doubtful if this reaction is of any importance in the normal activity of the animal.

G. GENERAL SUMMARY AND DISCUSSION OF RESULTS.

As was stated earlier in the paper, the problem with which this study deals is the analysis of the behaviour of the common fresh-water planarian. The movements and reactions to all the more important stimuli, with the exception of light and heat, have been described and analysed into their component factors in the body of the paper. It is believed that it is of the greatest importance to have as complete and detailed an account of the various activities as possible, and as a consequence full details have been given in the case of each subject treated. Since this method of treatment necessarily makes the account of considerable length, it has a tendency to obscure the general and significant results in a mass of detail. It is desirable, then, to state clearly at the end the important general facts which have been brought out by this study, and to discuss to some extent their significance. In this place I shall state the results in a categorical manner, making no attempt to indicate the evidence on which the conclusions are based. This will avoid needless repetition.

1. The locomotor movements of Planaria are of two sorts, gliding and crawling. The gliding movement is produced by the beating of the cilia on the ventral surface of the organism. It is by far the most usual method of locomotion. For its production it is necessary that there be a layer of sticky, mucous slime between the ventral surface of the body and the substrate. In this slimy secretion the cilia beat and so propel the animal (cf. pp. 544 and 545). The organism never moves freely through the water without some sort of mechanical support. The rate of the gliding is changed by the action of various agents, such as light, chemicals, electricity, etc. Its direction is always forward.

The crawling movement is produced by strong longitudinal waves of muscular contraction passing over the body from the anterior to the posterior end. It is more rapid in rate than the gliding. It appears only after strong stimulation of the organism, and its purpose is evidently to get the animal quickly away from harmful stimuli. Its direction may be either forward or backward.

Periods of movement alternate with periods of rest in the course of the animal's daily activity. When at rest the flatworm is in a condition of relaxation and generally lowered tonus, corresponding to the condition of a higher organism in sleep. The causes which induce the coming to rest are—(*a*) a more or less fatigued condition of the organism. This is the primary cause; without it the other causes are ineffective. (*b*) A relatively low intensity of light. (*c*) Roughness of the substrate. This brings the body into a position such that its different parts form angles with one another, and causes the animal to come to rest as the result of a reaction which I have called goniotaxis (p. 562). (*d*) Certain chemical conditions. As a result of the action of some one or all of these above-mentioned factors, collections or groups of planarians are frequently formed.

Planarians which have been injured by operative procedure move comparatively little during the course of regeneration, thus showing a sort of regulation or correlation between behaviour and morphogenetic processes (pp. 573, 574).

2. There are two principal qualitatively different reactions to stimuli, the positive and negative reactions.

The negative reaction is given in response to strong unilateral stimulation of the anterior portion of the body. It consists essentially in a turning of the head away from the side stimulated. It is brought about by the extension of the body on the side stimulated. This extension is produced by a contraction of the circular, dorso-ventral, and transverse systems of muscle-fibres. The purpose of the negative reaction is evidently to get the organism away from harmful stimuli.

The positive reaction is given only in response to weak unilateral stimulation of the anterior portion of the body. It is essentially a turning of the head towards the source of the stimulus. This reaction is one of considerable precision, bringing the anterior end into such a position that it points in most cases exactly towards the source of the stimulus. The turning is brought about by the contraction of the longitudinal muscle-fibres of the side stimulated. The evident purpose of the positive reaction is to get the animal into regions of beneficial stimuli.

3. Whether the negative or the positive reaction shall be given in response to a particular stimulus depends primarily on the intensity of the stimulus, and secondarily on its location. Neither reaction is given unless some part of the body in front of the pharyngeal region is stimulated. The negative reaction is given only in response to stimuli above a certain intensity (strong stimuli). This relation between intensity of stimulus and form of reaction holds for both mechanical and chemical stimuli.

4. The reactions of Planaria to a variety of chemicals, including representatives of several of the most important chemical groups, were studied. It was found that to a weak solution of any substance, regardless of its chemical composition, the organism gave a positive reaction identical with the positive reaction to mechanical stimuli. To strong solutions of the same substances (with a single exception, see p. 657) the organisms responded by a negative reaction identical with that caused by strong mechanical stimuli.

Planaria does not orient itself to a diffusing chemical in such a way that the longitudinal axis of the body is parallel to the lines of diffusing ions. Its reactions to chemicals are motor reflexes identical with those to mechanical stimuli. The positive reaction is an orienting reaction in the sense that it directs the anterior end of the body towards the source of the stimulus with considerable precision, but it does not bring about an orientation of the sort defined above.

5. Several important features in the normal behaviour of the flat-worm are found upon analysis to have their explanation in the positive and negative reactions to mechanical and chemical stimuli.

The method by which the organism gets its food is simply a special case of the positive reaction. From substances which serve as food for the planarians, various juices diffuse into the surrounding water. When the planarian meets any of these diffusing substances it gives the positive reaction,—that is, turns in the direction from which the stimulus comes. The food substance acts as a weak chemical stimulus, to which the animal reacts in the same way as to all other weak chemicals.

The direction of the planarian's movement, and its behaviour with reference to obstacles in its path, are usually determined by its reactions to mechanical stimuli.

The behaviour of the organism with reference to the surface film is determined by its reactions to mechanical stimuli.

6. Strong stimulation—either mechanical or chemical—of

the posterior portions of the body induces the crawling movement. This is to be regarded as the specific reaction of this portion of the body. Weak stimulation of the same region causes local contraction at the point stimulated in the case of mechanical stimuli, while weak chemical stimuli applied to this region are ineffective.

7. The ventral surface of the body of Planaria is strongly positively thigmotactic, and the dorsal surface is negatively thigmotactic.

8. When the organism is placed in an inverted position it performs the righting reaction. This reaction consists in a turning of successive parts of the body about the longitudinal axis through 180°. During the process the animal takes the form of a spiral. The anterior end is brought into the upright position first. On analysis the righting reaction is found to be a special case of the reaction to strong stimuli (the negative reaction). It is brought about by an extension of one side of the body, while the other side maintains its original length (pp. 676—679). The reaction is given whenever the ventral surface is removed from a solid or the surface film of the water.

9. To the constant electric current Planaria reacts by turning the anterior end towards the kathode. Complete orientation and movement towards the kathode may occur. The turning towards the kathode is brought about by an extension of the anode side of the body. The current causes a contraction of muscular elements whose long axes are parallel to the direction of the current (pp. 690—693). The current very quickly paralyses planarians on which it acts.

The rhabdocœle Stenostoma leucops orients to the current with the anterior end towards the kathode, and moves towards this pole. This orientation is brought about by changes in the positions and consequent effective beat of the cilia, exactly like those which occur in the case of the ciliate Infusoria. Cilia, on the portions of the body directed towards the kathode pole, take on reversed positions.

10. All the normal reactions to stimuli are of the nature of

reflexes, more or less complex. What the animal will do after a given stimulus, or in a given situation, can be predicted with reasonable certainty. There is, however, some variation in the behaviour, depending on the physiological or tonic condition of the individual at the time of stimulation. Thus a stimulus sufficiently weak to induce the positive reaction in one specimen may cause the negative reaction in another; or at different times the same individual may show different reactions—either the positive or negative—to the same stimulus.

11. Psychological Position of Planaria.—The objective psychological position of any organism is evidently determined by the relative simplicity or complexity of what it does. With a view of determining what the position of Planaria in the psychological scale is, it may be well to make a catalogue of the things which it does in the course of its ordinary existence.

The animal performs the following acts:

a. It moves progressively by two methods, a ciliary motion and a muscular motion.

b. It turns, by a complex of simple reflex acts, towards all weak stimuli investigated.

c. It turns, by another set of simple reflex acts, away from all strong stimuli investigated.

d. It comes to rest in certain definite environmental situations.

e. When stimulated in a certain way it extends the pharynx and feeds.

f. When its ventral surface is removed from contact with a solid body (or the surface film), a reflex of essentially the same character as that of *c* brings this surface again into contact with the solid.

From these essential factors is composed a behaviour whose complexity one has only to study to realise.

The behaviour is thus seen to be, in the main, what may be characterised as reflex. It is very simple to say that an animal's activity is composed of a series of invariable reflex acts in response to stimuli, but I doubt whether the full significance of such a condition is always realised. It implies that the animal as an individual "does" nothing in the sense that a man "does" things. It is moved about from place to place by its locomotor organs; it is put into certain definite and invariable relations to its surroundings by its reflex mechanisms. Considered as a whole, such an organism is a sort of shell to hold a series of mechanisms, each of which is independently capable of doing a certain thing, and in the doing produces some effect on the shell as a whole. We may perhaps get a clearer picture of what such a reflex existence means by considering for a moment what would be the effect if all a man's activities were composed of invariable reflexes, to be set off by the appropriate stimuli. Under such circumstances, whenever a man saw or smelled food he would have to go to it and eat it. Whenever anything touched him he would have to move in a new direction very closely related to the position of the object which touched him. Whenever he touched water he would have to take a bath, or perhaps drink till he could hold no more. During the day he would have to move always in a definite direction with reference to the sun, and so on ad infinitum. All he did would be definitely fixed and, in a sense, predetermined by the things about him.

It is apparent that the behaviour of Planaria is not thus entirely and purely reflex, because there is a certain amount of variation in it. As has been brought out in several places in the body of the paper, and in paragraph 10 of these conclusions, this variation in the behaviour is the result of the physiological condition of the individual. To put this in a more concrete form, we may say that a fatigued animal or an animal in a state of great excitation does not always react to a certain stimulus by the same set of reflexes as that by which a normal animal would react. Furthermore, there is a variation in the intensity of the negative reaction dependent upon the intensity of the stimulus producing it.

Another point in which the reactions of Planaria differ from what would obtain in the case of an organism whose behaviour was composed of invariable reflexes is found in the behaviour following repeated strong stimuli applied to the anterior end (vide pp. 580, 581). In this case the organism shows an evident modifiability in reaction, for after giving for some time the ordinary negative reaction, and not thereby getting away from the stimulus, it finally turns directly towards the source of the stimulus. Again, in the righting reactions of pieces of the body we see entirely new forms of reaction appearing (pp. 680—683).

In order to give a concrete idea of the psychological position of Planaria it may be well to present in parallel columns the principal factors which make for simplicity in the behaviour on the one hand, and for complexity on the other hand.

Factors which tend to make the Behaviour Simple.	Factors which tend to make the Behaviour Complex.
A. Essential reflex character at the basis of all the reactions.	A′. Comparatively large number of qualitatively different general reactions.
B. General lack of modifiability of reactions.	B′. Marked qualitatively different reactions to differing intensities of stimulus.
C. Comparatively small number of qualitatively different reflexes composing the general reactions.	C′. Definite relations of reactions to location of stimulus.
	D′. Rather close dependence of reactions on the physiological condition of the individual. This brings about variation in the reactions.

The behaviour of Planaria is evidently much more complex than that of the Infusoria, as described by Jennings (loc. cit.). In the case of the Infusoria, all the factors A′, B′, C′, D′, which make the behaviour of Planaria so complicated, are nearly or quite absent; and in respect to C these organisms are at a much lower stage than Planaria. The Infusoria have practically but one purely reflex reaction to nearly all stimuli, and this reaction is not localised with reference to the location of the stimulus. Again, the Infusoria do not show qualitatively different reactions to differing intensities of stimuli, as does Planaria to a marked degree. We thus see that Planaria stands considerably higher in the psychological scale than the Infusoria, and that the development is taking place along two main lines: (*a*) the higher organism reacts differentially with reference to the location and intensity of the stimulus; and (*b*) the physiological balance in the higher organism is much more delicately adjusted than in the lower, and as a consequence we see much more variation in the physiological condition. These variations in the physiological condition bring about variability in the reactions.

In the case of the ctenophore Mnemiopsis Leidyi we have an intermediate stage between the Infusoria and Planaria. Here the animal reacts with reference to the position, but not the intensity of the stimulus. This condition, in which an organism reacts with relation to the position of a stimulus, and not to its intensity, must be for the individual a precarious one, because the animal must either go towards or away from all stimuli alike, whether good or harmful. Chances are theoretically equal that after each stimulus it may get a toothsome morsel of food, or, on the contrary, serve in that capacity itself. Further development beyond the point in the behaviour series where Planaria stands must be in the line of further differential reactions with reference to quality of stimulus. A beginning along this line is made by the planarian, and the process is carried a step farther in the case of Gonionemus, as recently described by Yerkes (loc. cit.).

12. Relation of Behaviour and Structure.—The reactions of organisms are evidently, in any case, very closely dependent on the structural relations of the given organism, and on the conditions under which it lives, i. e. its environment in the broadest sense. Thus we find the asymmetrical Infusoria, which live freely in the water and move about by means of cilia, all reacting in the same way, and the determinative

factor in the reaction is the asymmetry of the body (cf. Jennings, :00). Now Jennings has further found[1] that certain rotifers, which live freely in the water and move about by the activity of cilia in a similar way, and furthermore are asymmetrical in fundamentally the same way that the Infusoria are, react in essentially the same manner as do the Infusoria. Similarly, I believe that the general reactions method of the planarians may be found to be in the main the method by which all organisms presenting the same general structural relations and mode of life react. Only one example on which this conviction is based may be given here. In the case of such fresh-water molluscs as Physa it is apparent that the actual locomotor and sensory organisation is symmetrical in form, and furthermore these forms live in fresh water on the surface of solid bodies just as do planarians. Now I have found, in a series of observations not yet published, that in the case of several of these molluscs the fundamental scheme of reaction is like that in the planarian. They react in the same way with reference to the location and intensity of the stimulus, and these are the fundamental things. In fact, the general behaviour is strikingly alike in the two widely separated groups.

13. Purposive Character of Reflexes.—A fact which is strongly impressed on one working on the behaviour of an organism whose activities are largely reflex is the purposive character of these reflexes. They are so adjusted that in the long run they keep the animal out of danger, and get it into favourable conditions. In the flat-worm these two things are very well done in general by the negative and positive reactions. Of these two reactions it is easy to see that the positive is the more highly developed, in particular in the fact that it is much more precisely localised with reference to the position of the stimulus. We can see a reason for this in the fact that under the conditions of the planarian's life the

---

[1] Complete observations not yet published. For preliminary account see 'Science,' N. S., vol. xv, pp. 524 and 525; and Jennings, :01, in bibliography at the end of this paper.

getting of food is of far more importance in the struggle for existence than the avoidance of danger. This point has, however, been discussed earlier in the paper, and need not detain us here. The real problem is presented in the attempt to discover how any of the purposive reflex acts in the organisms arose. I see no reason for denying that many of them—such as, for example, the positive reaction which gets the animal its food—were developed by natural selection. There are other evidently purposeful reactions, however, with whose development it hardly seems as if natural selection could have had anything to do, since they cannot themselves be of selective value. This point has been well brought out in a recent paper by Morgan (:02, p. 281). I think a possible explanation of some of these may be found in their analysis into component factors, when it may appear that only a very few simple reflexes had to be formed by natural selection, and then all the reactions are built up from these. An example will make my meaning clearer. In the righting reaction of the planarian we have a fairly complex reaction which is evidently immediately purposeful. Yet we find on analysis that this reaction is at bottom nothing but a slight modification of the ordinary negative reaction, which might very well have been developed by natural selection. And thus it is with other reactions and pieces of behaviour. They are for the most part built up from a very few simple purposive reflexes. If we can get them subdivided and spread out, as it were, so that we can see what goes to compose them, we may find that our problem has diminished very much, and we shall have to deal with only a few factors where before there appeared to be many.

A difficult problem in purposeful behaviour presents itself when we find that new methods of reaction appear at once if the usual reaction is prevented. The best examples of this are found in the righting reaction of cut pieces of planarians. Here we find pieces of the body, in which the normal mechanism of the reaction has been destroyed, immediately reaching a certain end (the righting) by a method differing entirely from any that planarians ever used before to attain the same end, so far as we have evidence. These phenomena have a considerable resemblance to such phenomena as the well-known regeneration of the lens from the iris in some Amphibia. It is not easy to see how such behaviour comes about, and natural selection helps us very little. The matter belongs apparently to the same class of phenomena as morphological regulations, and probably has ultimately the same explanation. What this explanation is we do not know.

14. Functions of the Nervous System.—The most important function of the brain is the preservation of the tonus of the organism. After its removal the general tonus rapidly diminishes, and on this account the positive reaction—which depends rather closely on the physiological condition—can be obtained only with great difficulty in such decapitated specimens. There is no evidence of the presence of special centres in the brain. The nervous system, as a whole, has its main function in the rapid conduction of impulses.

15. Subjective Psychic Attributes.—One of the principal questions which forever recurs with regard to work on animal behaviour is, does the animal possess consciousness? Now although it has been shown what the component parts of the activities of the planarian are, yet it cannot be said, as it seems to me, that the planarian does not, or, on the other hand, that it does, possess consciousness. All that any such an organism ever has done in the past, or ever will do in the future, cannot tell us whether it was conscious in the doing or not. Any "objective criterion" of consciousness does not exist. Furthermore, whether consciousness is or is not present in any given case is not, in any event, the greatest concern of the physiologist, who rests content with the objective explanation of how results are brought about, regardless of what the animal is thinking about the matter. On this subject Claparède (: 01, p. 24), in concluding an interesting and valuable discussion, has said, "À la question; les animaux sont-ils conscients? la physiologie—et même la psychologie en tant que cette science est explicative—doivent

donc répondre non seulement, 'Je l'ignore,' mais encore, 'Peu m'importe'!" With this standpoint I am in thorough accord.

H. List of Literature.

BARDEEN, C. R. :01.—"On the Physiology of the Planaria maculata, with Especial Reference to the Phenomena of Regeneration," 'Amer. Journ. Physiol.,' vol. v, pp. 1—55.

BARDEEN, C. R. :01, *a*.—"The Function of the Brain in Planaria maculata," ibid., vol. v, pp. 175—179.

CHICHKOFF, G. D. '92.—"Recherches sur les Dendrocœles d'eau douce (Triclades)," 'Arch. de Biol.,' t. xii, pp. 435—568, pls. xv—xx.

CHILD, C. M. :01.—"The Habits and Natural History of Stichostemma," 'Amer. Nat.,' vol. xxxv, pp. 975—1006.

CLAPARÈDE, E. :01.—"Les Animaux sont-ils Conscients?" 'Rev. Philos.,' t. li, pp. 481—498.

DUYNE, J. VAN. '96.—"Ueber die Heteromorphose bei Planarien," 'Arch. f. d. ges. Physiol.,' Bd. lxiv, pp. 569—574, pl. x.

FRANDSEN, P. :01.—"Studies on the Reactions of Limax maximus to Directive Stimuli," 'Proc. Amer. Acad. Arts and Sci.,' vol. xxxvii, pp. 185—227.

GAMBLE, F. W. '93.—"Contributions to a Knowledge of British Marine Turbellaria," 'Quart. Journ. Micr. Sci.,' vol. xxxiv, pp. 433—528, pls. xxxix—xli.

HESSE, R. '97.—"Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren: II, Die Augen der Plathelminthen, insonderheit der tricladen Turbellarien," 'Zeitschr. f. wiss. Zool.,' Bd. lxii, pp. 527—582, Taf. xxvii and xxviii.

JENNINGS, H. S. '97.—"Studies on Reactions to Stimuli in Unicellular Organisms: I, Reactions to Chemical, Osmotic, and Mechanical Stimuli in the Ciliate Infusoria," 'Journ. Physiol.,' vol. xxi, pp. 259—322.

JENNINGS, H. S. '99.—"Studies on Reactions to Stimuli in Unicellular Organisms: II, The Mechanism of the Motor Reactions of Paramecium," 'Amer. Journ. Physiol.,' vol. ii, pp. 311—341.

JENNINGS, H. S. '99, *a*.—"Studies on Reactions to Stimuli in Unicellular Organisms: III, Reactions to Localised Stimuli in Spirostomum and Stentor," 'Amer. Nat.,' vol. xxxiii, pp. 373—389.

JENNINGS, H. S. '99, *b*.—"Studies on Reactions to Stimuli in Unicellular Organisms: IV, Laws of Chemotaxis in Paramecium," 'Amer. Journ. Physiol.,' vol. ii, pp. 355—379.

JENNINGS, H. S. '99, *c.*—"The Psychology of a Protozoan," 'Amer. Journ. Psychol.,' vol. x, pp. 503—515.

JENNINGS, H. S. :00.—"Studies on Reactions to Stimuli in Unicellular Organisms: V, On the Movements and Motor Reflexes of the Flagellata and Ciliata," 'Amer. Journ. Physiol.,' vol. iii, pp. 229—260.

JENNINGS, H. S. :00, *a.*—"The Behaviour of Unicellular Organisms," 'Woods Holl Lectures for 1899,' pp. 93—112.

JENNINGS, H. S. :00, *b.*—"Studies on Reactions to Stimuli in Unicellular Organisms: VI, On the Reactions of Chilomonas to Organic Acids," 'Amer. Journ. Physiol.,' vol. iii, pp. 397—403.

JENNINGS, H. S. :00, *c.*—"Reactions of Infusoria to Chemicals: a Criticism," 'Amer. Nat.,' vol. xxxiv, pp. 259—265.

JENNINGS, H. S. :01.—"On the Significance of the Spiral Swimming of Organisms," ibid., vol. xxxv, pp. 369—378.

JENNINGS, H. S., AND MOORE, E. M. :02.—"Studies on Reactions to Stimuli in Unicellular Organisms: VIII, On the Reactions of Infusoria to Carbonic and other Acids, with Especial Reference to the Cause of the Gatherings spontaneously formed," 'Amer. Journ. Physiol.,' vol. vi, pp. 233—250.

JIJIMA, J. '84.—"Untersuchungen über den Bau und die Entwicklungsgeschichte der Süsswasser Dendrocoelen (Tricladen)," 'Zeitschr. f. wiss. Zool.,' Bd. xl, pp. 359—464, Taf. xx—xxiii.

JORDAN, H. :01.—"Die Physiologie der Locomotion bei Aplysia limacina," 'Inaug. Diss. Bonn,' 1901 (Druck von Oldenbourg, München), p. 51, Taf. i. Also in 'Zeitschr. f. Biol,' Bd. xli, pp. 196—238, Taf. ii.

KENNEL, J. VON. '88.—"Untersuchungen an neuen Turbellarien," 'Zool. Jahrb.,' Abth. Anat. und Ont., Bd. iii, pp. 447—486, Taf. xviii, xix.

LANG, A. '81.—"Untersuchungen zur vergleichenden Anatomie und Histologie des Nervensystems der Plathelminthen: IV, Das Nervensystem der Tricladen," 'Mitth. a. d. Zool. Stat. Neapel,' Bd. iii, pp. 53—76, Taf. v, vi.

LANG, A. '81, *a.*—"Untersuchungen zur vergleichenden Anatomie und Histologie des Nervensystems der Plathelminthen: V, Vergleichende Anatomie des Nervensystems der Plathelminthen," 'Mitth. a. d. Zool. Stat. Neapel,' Bd. iii, pp. 76—95.

LANG, A. '84.—"Die Polycladen (Seeplanarien) des Golfes von Neapel und der angrenzende Meeresabschnitte," 'Fauna u. Flora d. Golfes von Neapel,' XI Monographie (Leipzig, Engelmann), pp. x and 688, Taf. xxxix.

LEHNERT, G. H. '91.—"Beobachtungen an Landplanarien," 'Inaug.-Diss.,' Leipzig (Berlin), pp. 1—47. Also in 'Arch. f. Naturgesch.,' 57th Jahrg., pp. 306—350.

LILLIE, F. R. :00.—"Some Notes on Regeneration and Regulation in Planarians: I, The Source of Material of New Parts and Limits of Size," 'Amer. Nat.,' vol. xxxiv, pp. 173—177.

LILLIE, F. R. :01.—"Notes on Regeneration and Regulation in Planarians," 'Amer. Journ. Physiol.,' vol. vi, pp. 129—141.

LOEB, J. '93.—"Ueber künstliche Unwandlung positiv heliotropischer Thiere in negativ heliotropische und umgekehrt," 'Arch. f. d. ges. Physiol.,' Bd. liv, pp. 81—107.

LOEB, J. '94.—"Beiträge zur Gehirnphysiologie der Würmer," ibid., Bd. lxi, pp. 247—269.

LOEB, J. :00.—'Comparative Physiology of the Brain and Comparative Psychology,' New York (G. P. Putnam's Sons), 1900, pp. x and 309.

LOEB, J., AND MAXWELL, S. S. '96.—"Zur Theorie des Galvanotropismus," 'Arch. f. d. ges. Physiol.,' Bd. lxiii, pp. 121—144, Taf. i.

LUDLOFF, K. '95.—"Untersuchungen über den Galvanotropismus," 'Arch. f. d. ges. Physiol.,' Bd. lix, pp. 525—554.

MITSUKURI, K. :01.—"Negative Phototaxis and other Properties of Littorina as Factors in determining its Habitat," 'Annot. Zool. Japon.,' vol. iv, pp. 1—18.

MORGAN, T. H. '98—"Experimental Studies of the Regeneration of Planaria maculata," 'Arch. f. Entwickelungsmechanik,' Bd. vii, pp. 364—397.

MORGAN, T. H. :00.—"Regeneration in Planarians," ibid., Bd. x, pp 58—119.

MORGAN, T. H. :01.—"Growth and Regeneration in Planaria lugubris," ibid., Bd. xiii, pp. 179—212.

MORGAN, T. H. :02.—"The Reflexes connected with Autotomy in the Hermit Crab," 'Amer. Journ. Physiol.,' vol. vi, pp. 278—282.

MOSELEY, H. N. '74.—"On the Anatomy and Histology of the Land Planarians of Ceylon; with some Account of their Habits, and a Description of Two New Species, and with Notes on the Anatomy of some European Aquatic Species," 'Phil. Trans. Roy. Soc. London,' 1874, pp. 105—171, pls. x—xv.

MOSELEY, H. N. '77.—"Notes on the Structure of Several Forms of Land Planarians, with a Description of Two New Genera and Several New Species, and a List of all Species at Present known," 'Quart. Journ. Micr. Sci.,' N.S., vol. xvii, pp. 273—292.

NORMAN, W. W. :00.—"Do the Reactions of the Lower Animals against Injury indicate Pain Sensations?" 'Amer. Journ. Physiol.,' vol. iii, pp. 271—284.

PARKER, G. H., AND BURNETT, F. L. :00.—"The Reactions of Planarians, with and without Eyes, to Light," ibid., vol. iv, pp. 373—385.

PATTEN, W. '96.—"Variations in the Development of Limulus polyphemus," 'Journ. Morph.,' vol. xii, pp. 17—148, pls. ii—xl.

PEARL, R. :00.—"Studies on Electrotaxis: I, On the Reactions of certain Infusoria to the Electric Current," 'Amer. Journ. Physiol., vol. iv, pp. 96—123.

PEARL, R. :01.—"Studies on the Effects of Electricity on Organisms: II, The Reactions of Hydra to the Constant Current," ibid., vol. v, pp. 301—320.

PREYER, W. '86.—"Über die Bewegungen der Seesterne: ein vergleichend physiologisch-psychologische Untersuchung," Erste Hälfte, 'Mitth. a. d. Zool. Stat. zu Neapel,' Bd. vii, pp. 27—127.

PREYER, W. '87.—"Über die Bewegungen der Seesterne: ein vergleichend physiologisch-psychologische Untersuchung," Zweite Hälfte, ibid., Bd. vii, pp. 191—233, Taf. vii.

RASPAIL, X. '93.—"Note preliminaire sur une Planaire, sp.?" 'Bull. Soc. Zool. France,' t. xviii, pp. 49, 50.

SCOURFIELD, D. J. '94.—"Entomostraca and the Surface Film of Water," 'Journ. Linn. Soc. Zool.,' vol. xxv, pp. 1—19.

SCOURFIELD, D. J. :00.—"Note on Scapholeberis mucronata and the Surface Film of Water," 'Journ. Quekett Micr. Club,' Series 2, vol. vii, pp. 309—312.

SCOURFIELD, D. J. :01.—"Hydra and the Surface Film of Water," ibid., Series 2, vol. viii, pp. 137—142, pl. viii.

STEINER, J. '98.—'Die Functionen des Centralnervensystems und ihre Phylogenese: Dritte Abth.,' "Die wirbellosen Thiere," Braunschweig (Vieweg und Sohn), 1898, pp. x and 154, Taf. i.

UEXKÜLL, J. VON. '96.—"Ueber Reflexe bei den Seeigeln," 'Zeitschr. f. Biol.,' Bd. xxxiv, pp. 298—318.

UEXKÜLL, J. VON. '96, *a*.—"Vergleichende sinnesphysiologische Untersuchungen: II, Die Schatten als Reiz für Centrostephanus longispinus," 'Zeitschr. f. Biol.,' Bd. xxxiv, pp. 319—339, Taf. i—iii.

UEXKÜLL, J. VON. '99.—"Die Physiologie der Pedicellarien," ibid., Bd. xxxvii, pp. 334—403, Taf. iv, v.

UEXKÜLL, J. VON. :00.—"Die Physiologie des Seeigelstachels," ibid., Bd. xxxix, pp. 73—112.

Uexküll, J. von. :00, *a*.—"Die Wirkung von Licht und Schatten auf die Seeigel," ibid., Bd. xl, pp. 446—476, Taf. i.

Verworn, M. '89.—'Psychophysiologische Protistenstudien,' Jena (Fisher), 1889, pp. viii and 218, Taf. i—vi.

Whitman, C. O. '99.—"Animal Behaviour," 'Woods Holl Lectures for 1898,' pp. 285—338.

Willey, A., '97.—"On Heteroplana, a New Genus of Planarians," 'Quart. Journ. Micr. Sci.,' N. S., vol. xl, pp. 203—205.

Wilson, C. B. :00.—"The Habits and Early Development of Cerebratulus lacteus (Verrill): a Contribution to Physiological Morphology," 'Quart. Journ. Micr. Sci.,' N. S., vol. xliii, pp. 97—198, pls. ix—xi.

Woodworth, W. McM. '91.—"Contributions to the Morphology of the Turbellaria: I, On the Structure of Phagocata gracilis, Leidy," 'Bull. Mus. Comp. Zool.,' Harvard College, vol. xxi, No. 1, pp. 1—42, pls. i—iv.

Woodworth, W. McM. '97.—"Contributions to the Morphology of the Turbellaria: II, On some Turbellaria from Illinois," ibid., vol. xxxi, pp. 1—16, pl. i.

Yerkes, R. M. :02.—"A Contribution to the Physiology of the Nervous System of the Medusa Gonionemus Murbachii: Part I, The Sensory Reactions of Gonionemus," 'Amer. Journ. Physiol.,' vol. vi, pp. 434—449.

Zacharias, O. '88.—"Landplanarien auf Pilzen," 'Biol. Centralb.,' Bd. viii, pp. 542, 543.