ERRATA

In the paper by H. W. Rand, J. F. Bovard and D. E. Minnich (these PROCEEDINGS, 12, no. 9, September, 1926), on page 570, line 4, "adsorption" should read "absorption."

In the paper by Herbert W. Rand and Mildred Ellis (these PROCEEDINGS, 12, no. 9, September, 1926), on page 572, second line from bottom, surface should read surfaces.

AN ACKNOWLEDGMENT

The formula for the distribution of the correlation ratio calculated from random data obtained in my paper in these PROCEEDINGS, 11, no. 10 (October, 1925), pp. 657–662, is equivalent to a result contained in a paper by R. A. Fisher on "The Goodness of Fit of Regression Formulae and the Distribution of Regression Coefficients," J. Roy. Statist. Soc., 85 (1922), pp. 597–612, a fact which unfortunately I overlooked. The credit for the formula belongs to Mr. Fisher.

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tainment of a form normal in relation to the dominant head region. In connection with this inhibitory effect a tissue mass which occupies an abnormal space relation to the dominant head region may undergo a regulatory reduction or "adsorption." The degree of effectiveness, at any given region, of the head-localized formative agencies depends in some way upon the space relations existing between that region and the head. Experimental data strengthening and extending these conclusions will be reported in further papers.


INHIBITION OF REGENERATION IN TWO-HEADED OR TWO-TAILED PLANARIANS

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The experiments to be described in this paper have to do with the question of a form-determining dominance of one part of an organism over another. In terms of C. M. Child’s theory of individuality, organization or physiological unity in protoplasm is the expression of a system of metabolic gradients. This gradient system is the chief factor in the determination of growth and differentiation. It involves relations of dominance and subordination between different parts of the organism. In general, according to Child, a region of higher metabolic rate exerts "physiological dominance" over a region of lower rate. Whether to be interpreted in terms of gradients or otherwise, such experiments as those described below clearly demonstrate the existence of localized form dominance.

Fresh water planarians (especially Planaria maculata) readily regenerate tissue at any cut surface, unless the fragment of the animal is extremely small. They exhibit a strongly marked and persistent polarity. Except under extraordinary conditions a head regenerates at any anterior cut surface and a tail at any posterior cut surface. But the following experiments show that regeneration at a cut surface may be controlled or
inhibited by the presence of appropriate specialized structures in sufficiently close proximity to it.

Double-headed or double-tailed forms may be produced by operations consisting in splitting the appropriate region of the animal in the median plane. By employment of such double forms it may be shown that the presence of the one head (or tail) affects the regenerative behavior at the cut surface produced by removal of the other head (or tail). If one head of a planarian having not only the head but the anterior third or fourth of the body duplicated be excised so that a considerable stump of its branch of the body is left projecting beyond the common posterior part of the body, regeneration of a head at the cut surface will usually take place (although sometimes at a retarded rate) restoring completely the original double-headed condition. If, however, the cut be made close to the common body so that only a very short stump or none at all is left, retardation or inhibition of head formation may result. It may be shown that the delay or the failure to regenerate is specifically due to the presence of a head. The effectiveness of the inhibitory action of the head seems to vary in an inverse relation to the distance between the head and the cut surface. Other factors, however, than this one of distance are concerned. The consideration of these factors must be deferred to a paper reporting further experimental data.

Methods.—The animals were all Planaria maculata. The worms to be operated on were narcotized in chloretone (0.2%). All operations were performed on a clean glass slide under a dissecting microscope. The cutting was done with the point of a very small sharp scalpel or a fragment of a safety razor blade placed in a handle. The stroke was a sudden downward one as the animal, even if narcotized, reacts when touched and immediately discharges mucus. The cuts were made lengthwise, passing as nearly as possible through the middle of the head or tail and varying extents of the body. As soon as a cut was made, concentration of pigment toward the cut edge was observed. This appearance was doubtless due, at least, in part to general contraction of tissues at the wound, but there was some indication also of an actual migration of pigment toward the raw surface. The return of the pigment to a normal distribution was slow and often was not accomplished until new tissue had regenerated along the cut surface.

It was found that if the incision involved only a small proportion of the length of the body, the cut edges very quickly grew together. Very long cuts (more than two-thirds the length of the animal) generally caused the animal to break into two pieces. To obtain the desired double forms, it was usually necessary to keep the wound open by making successive incisions at the same place and at frequent intervals, even repeating the operation two or three times within one day. When the separation between
the two lateral portions of a part of the animal has become well established (by healing of the wound without fusion of the adjacent cut edges) new tissue develops rapidly along the healed edges and in due time either portion regenerates the structures requisite for the perfection of its bilateral symmetry, resulting in the complete duplication of the region of the animal affected by the operation. The animals were not fed.

Experiments.—Of the forty-seven experiments which were carried out, twenty failed for one reason or another to yield results of significance. Twenty-seven offered more or less convincing evidence of the form-determining dominance of one part over another.

Two types of cases may be recognized. In one (in the following description to be designated as a case of type "A") the results, while entirely consistent with the idea of dominance, yet do not afford absolute proof of it. That is, inhibition of the regeneration of the excised head or tail was not necessarily due to the physiological dominance of the head or tail which remained, but might conceivably have been due to the shock of operation or to lack of food or general exhaustion of regenerative energy, or possibly to other causes. In cases of the other type ("B") appropriate secondary control operations were made in such a way as to prove beyond doubt that the failure to regenerate was really an inhibition due to the dominance of the existing head or tail and not a consequence of any of the other conditions suggested above.

The general nature of the results of the experiments will be indicated by describing one of each of the two types of cases of head inhibition and one of each of the two types of tail inhibition.

I. Tail Inhibition, Case A.—A double-tailed animal was produced. The right tail was excised leaving a short stump (Fig. 1). The stump regenerated a new tail. Sixteen days after the first amputation, the regenerated tail, along with the stump bearing it, was excised close to the common anterior part of the body (Fig. 2). No tail was regenerated. A little new tissue developed at the wound region tending to restore the outline of the body of a normal individual.

Case B. From a double-tailed animal, the left tail was excised leaving a short stump (Fig. 3). Regeneration of a tail began. The regenerating tail, together with the original stump, was then excised (Fig. 4). Seven days later there were no indications of regeneration. New tissue had formed at the wound region and the body had acquired a fairly normal outline. The animal was then divided into two parts by a cut shaped like the letter "V" (Fig. 5), the left arm of the "V" passing through the new tissue resulting from the last operation and the right arm of the "V" severing what had been the right portion of the originally bifurcated body. Three days later regeneration was actively in progress at the cut surface of both parts of the worm. Eventually the posterior part developed a
single normal head and the anterior part developed a single symmetrically formed tail. The tissue intersected by the left arm of the V-shaped cut was tissue where, following the earlier operation, regeneration had failed. Yet, after this later operation, regeneration of the tail proceeded at equal rate on the right and left sides.

FIGURES 1-9.

Regenerated regions are indicated by lighter lines. Dotted lines indicate limits between old and regenerated tissue. Broken lines indicate planes of tran-section.

II. Head Inhibition, Case A.—From a double-headed animal, the right head-bearing portion was excised, leaving no projecting stump (Fig. 6). A little new tissue developed at the wound region. No head regenerated. The outline of the right side of the animal gradually straightened out and, sixteen days after the amputation of the right head, the animal had the form of a normal individual.
CASE B.—From a double-headed animal, the left head was excised leaving only a very slight projecting stump (Fig. 7). No head was regenerated and, thirty-one days after the amputation, the animal appeared like a normal individual (Fig. 8). Two days later the remaining (original right) head was excised by a cut extending obliquely across the animal (Fig. 8) so as to intersect on the left side the region where regeneration had formerly failed. Regeneration of a single symmetrical head proceeded without delay and within a week the new head was well established (Fig. 9). On the ninth day following the last operation, this regenerated head was excised (Fig. 9). Again regeneration of a head took place without retardation or abnormality of any sort.

Results.—Splitting operations performed on Planaria maculata result in the duplication either of the head and varying portions of the anterior region of the body, or of the tail and varying portions of the posterior region of the body. Any one of these duplicated regions is the complete morphological equivalent of the corresponding antero-posterior extent of the body of a normal individual. Further, any one of these duplicated regions possesses, within itself, the same capacity for regeneration that the corresponding region of a normal body possesses. If, however, one of these duplicated parts be transected sufficiently close to the single common portion of the body, then (other conditions, not now to be specified in detail, being favorable) the regenerative replacement of that excised duplicate part may exhibit retardation or complete failure. If, following such inhibition, the remaining one of the previously duplicate regions is removed by transection at its base and the cut is carried across through the region which had just failed to regenerate, there will then be regenerated a single normal body region and extremity (head or tail) of appropriate polarity and equivalent to one of the formerly duplicated parts. The tissues in the region which had recently exhibited inhibition participate actively in this regeneration. Further, the literature of planarian regeneration contains experimental data ample to justify the assertion that inherent capacity for regeneration of head or tail ends is present in relation to any such cut surface as those at which, in our experiments, inhibition has been shown.

It is, therefore, proved that the inhibition is not due to shock of operation, pathological condition of tissues or general exhaustion of regenerative capacity, but is specifically due to the presence, in appropriate proximity and relations, of the equivalent of the structures which had been removed. It is thus shown that the regenerative behavior at a cut surface of a planarian is influenced by the presence or absence of structures at a region more or less remote from the wound. There is demonstrated a "dominance"—but an inhibitory dominance—of one part of an organism over another.