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[*Classics* Editor's note: Morgan used square brackets a number of points within the original text. All such insertions are his except for page numbers and the few [*sic*]s I have inserted. Also, Morgan used the term "adaption" himself, but quotes others as using the more common modern term "adaptation."]

Up to a date still comparatively recent, the transmission to offspring, in greater or less degree, of those modifications of habit or structure which the parents had acquired in the course of their individual lifetime, was generally accepted. Lamarck is regarded as the intellectual father of the transmissionists. In his 'Histoire Naturelle' he said: "The development of organs and their power of action are continually determined by the use of these organs." This is known as his third law. In the fourth he insisted on the hereditary nature of the effects of such use. "All that has been acquired, begun or changed," he said, "in the course of their life is preserved in reproduction and transmitted to the new individuals which spring from those which have experienced the changes."

accepted such transmission as subordinate to natural selection, and attempted to account for it by his theory of pangenesis. According to that hypothesis all the component cells of an organism throw off minute gemmules, and these and their like, collecting in the reproductive cells, are the parental germs from which all the cells of the offspring of that organism are developed. This theory, here given in briefest outline, came in for its full share of [p. 734] criticism. The problems of heredity were recognized as being of supreme biological importance and were warmly discussed. Meanwhile a different view of the relation between the organism and its reproductive cells came into prominence. With it the names of Francis Galton, in , and August Weismann, in , are inseparably connected. Of late years it has gained the approval of many, though by no means all, of our foremost biologists. This view, again given in briefest possible outline, is as follows: The fertilized egg of any many-celled organism gives origin to all the cells of which that organism is composed. In some of these, the reproductive cells, germinal substance is set aside for the future continuance of the race; the rest give rise to all the other cells of the body, those which constitute or give rise to muscle, nerve, bone, gland

and so forth. Thus we have a division into germ-substance and body-substance. Germ gives origin to germ plus body; but the body takes no share, according to Prof. Weismann, in giving origin to -- though it ministers to, protects, and may exercise an influence on -- the germinal substance of the reproductive cells.

The logical development of this theory led Prof. Weismann to doubt the inheritance of characters acquired by the bodily substance in the course of individual life, and to examine anew the supposed evidence in its favor. For if brain substance, for example, contributes nothing to the reproductive cells, any modification it acquires during individual life can only reach the germ through some indirect mode of influence. But does it-does any modification of the body substance -- so affect the germ as to become hereditary? Prof. Weismann answers this question by asserting that the evidence for the direct transmission of acquired characters is wholly insufficient, and by contending that, until· satisfactory evidence is forthcoming, we may not accept transmission as a factor in evolution.

How, then, is progress possible if none of the modifications which the body suffers is transmitted from parent to offspring? To this question we must reply that though modification is, on this view, excluded from taking any direct share in race-progress, yet there is still variation. By modifications I mean those changes which are in some way wrought in the body-structure, and by variations those differences which are of germinal origin. That variation of germinal origin is a fact in *organic* nature is admitted on all hands, and that some variations are adaptive is also unquestioned. Transmissionists contend that modification in a particular direction in one generation is, through the transmission of the change in some way from the bodily tissues to the germinal cells, a source of variation in the same direction in the next generation. Selectionists, on the other hand, exclude this source of variation, contending that the supposed evidence in its favor is insufficient or unsatisfactory. But their whole theory depends on the occurrence of variations, of which those that are in unfavorable directions are weeded out, while those that are useful and adaptive remain in possession of the held. How these variations originate in the germ we need not here discuss. Let us assume that variations of germinal origin in a great number of directions do as a matter of fact occur.

This, then, is how the matter stands. All acknowledge the existence of variations and admit that their proximate source is in the fertilized ovum. All admit that the individual is, through its plasticity, in greater or less degree capable of adaptive modification. Transmissionists contend that the effects of modification are somehow transferred to the germinal substance there to give origin to variations. Selectionists deny this transmission and contend that adaptive [p. 735] variations are independent of adaptive modifications.

Now, what is natural selection, at any rate as understood by the master -- Darwin? It is a process whereby, in the struggle for existence, individuals possessed of favorable and adaptive variations survive and hand on their good seed, while individuals possessed of unfavorable variations succumb, are sooner or later eliminated, standing therefore a less chance of begetting offspring. This is the natural selection of . But it is clear that to make the difference between survival and elimination the favorableness of the variation must reach a certain amount-varying with the keenness of the struggle. This was termed by Romanes 'selection value.' And one of the difficulties which critics of natural selection have felt is that the little more or the little less of variation must often be too small in amount to be of selection value so as to determine survival. This difficulty is admitted by Prof. Weismann as a real one. "The Lamarckians were right," he says, "when they maintained that the factor for which hitherto the name of natural selection had been exclusively reserved, viz., personal selection [*i.e.,* the selection of individuals, was insufficient for the explanation of the phenomena."[2] And again : [3] "Something is still wanting to the selection of Darwin and Wallace, which it is obligatory on us to discover, if we possibly can."

The additional factor which Dr. Weismann suggests is what he terms germinal selection. This, briefly stated, is as follows: There is a competition for nutriment among those parts of the germ from which the several organs or groups of organs are developed. These he names determinants; in this competition the stronger determinants get the best of it, and are further developed at the expense of the weaker determinants, which are starved and tend to dwindle and eventually disappear. The suggestion is an interesting one, but one well-nigh impossible to put to the test of observation. It must at present be placed among the 'may-bes' of biology. If accepted as a factor, it would serve to account for the existence of determinate variations, that is to say, variations along special or particular lines of adaption.

Such determinate variations are, however, explicable on the theory of natural selection -- a term which, in my opinion, should be reserved for that process of individual survival and elimination to which it was applied by . Writing in 1892 I put the matter thus:[4] "Take the case of an organism which has in some way reached harmony with its environment. Slight variations occur in many directions, but these are bred out by intercrossing. It is as if a hundred pendulums were swinging just a little in many directions, but were at once damped down. Now, place such an organism in changed conditions. The swing of one or two of the pendulums is found advantageous; the organisms in which these two pendulums are swinging are selected; they mate together and in their offspring, while these two pendulums are by congenital inheritance kept a-swinging, the other 98 pendulums are rapidly damped down as before.

"Let us suppose, then, that the variation in tooth structure, in a certain mechanically advantageous direction, be such a selected pendulum swing. That particular pendulum, swinging in that particular direction, will be the subject of selection. The other pendulums will still be damped down as before, and in that particular pendulum variations from the particular direction will be similarly damped down. It will wobble a little, but its wobbling will be as nothing compared with the swing that is [p. 736] fostered by selection. In this case, then, selection will choose between the little more complexity that is advantageous and the little less complexity that is disadvantageous. The little less complexity will be eliminated, the little more complexity will survive. The little less and the little more are, however, in the same line of developmental swing. Hence, the variations discoverable in fossil mammals in which tooth development along special lines is in progress, will, on the hypothesis of selection, be plus and minus along a given line; in other words, the variations will be determinate, and in the direction of special adaptation."

Prof. Weismann adopts a similar position in his recent paper on germinal selection.[5] "By the selection alone," he says, "of the plus or minus variations of a character is the constant modification of that character in the plus or minus direction determined. *** We may assert therefore, in general terms, that a definitely directed progressive variation of a, given part is produced by continued selection in that definite direction. This is no hypothesis, but a direct inference from the facts and may also be expressed as follows: By selection of the kind referred to, the germ is progressively modified in a manner corresponding with the production of a definitely directed progressive variation of the part."

In his Romanes Lecture, Prof. Weismann makes another suggestion which is valuable and helpful and which, I think, may be further developed and extended. He is there dealing with what he terms 'intraselection,' or that individual plasticity to which I have frequently made reference. One of the examples that he adduces is the structure of bone. "Herman Meyer," he says,[6] "seems to have been the first to call attention to the adaptiveness as regards minute structure in animal tissues, which is most strikingly exhibited in the structure of the spongy substance of the long bones in the higher vertebrates. This substance is arranged on a similar mechanical principle to that of arched structures in general; it is composed of numerous fine bony plates so arranged as to withstand the greatest amount of tension and pressure, and to give the utmost firmness with a minimum expenditure of material. But the direction, position and strength of these long bony plates are by no means congenital or determined in advance; they depend on circumstances. If the bone is broken and heals out of the straight, the plates of the spongy tissue become rearranged so as to be in the new direction of greatest tension and pressure; thus they can adapt themselves to changed circumstances."

Then, after referring to the explanation, by Wilhelm Roux, of the cause of these wonderfully fine adaptations by applying the principle of selection to the parts of the organism in which, it is assumed, there is a struggle for existence among each other, Prof. Weismann proceeds to show[7] that "it is not the particular adaptive structures themselves that are transmitted, but only the quality of the material from which intra-selection forms these structures anew in each individual life. *** It is not the particular spongy plates which are transmitted, but a cell mass, that from the germ onwards so reacts to tension and pressure that the spongy structure necessarily results." In other words it is not the more or less definite congenital adaptation that is handed on through heredity, but an innate plasticity which renders possible adaptive modification in the individual.

This individual plasticity is undoubtedly of great advantage in race progress. The adapted individual will escape elimination [p. 737] in the life-struggle, and it matters not whether the adaptation as reached through individual modification of the bodily tissues, or through racial variation of germinal origin. So long as the adaptation is there -- no matter how it originated -- that is sufficient to secure survival. Prof. Weismann applies this conception to one of those difficulties which have been urged by critics of natural selection. "Let us take," he says,[8] "the well-known instance of the gradual increase in development of the deers'[*sic*] antlers, in consequence of which the head, in the course of generations, has become more and more heavily loaded. The question has been asked as to how it is possible for the parts of the body which have to support and move this weight to very simultaneously and harmoniously if there is no such thing as the transmission of the effects of use or disuse, and if the changes have resulted from processes of selection only. This is the question put by Herbert Spencer as to '*co-adaptation*,' and the answer is to be found in connection with the process of intra-selection. It is by no means necessary that all the parts concerned-skull, muscles and ligaments of the neck, cervical vertebra, bones of the fore-limbs, etc -- should simultaneously adapt themselves *by variation of the germ* to the increase of the size of the antlers, for in each separate individual the necessary adaptation will be temporarily accomplished by intra-selection," that is, by individual modification due to the innate plasticity of the parts concerned. "The improvement of the parts in question," Prof. Weismann urges, "when so acquired, will certainly not be transmitted, but yet the primary variation is not lost. Thus when an advantageous increase in the size bf the antlers has taken place, it does not lead to the destruction of the animal in consequence of other parts being unable to suit themselves to it. All parts of the organism are in a certain degree variable [*i.e.*, modifiable] and capable of being determined by the strength and nature of the influences that affect them; and this capacity to respond conformably to functional stimulus must be regarded as the means which make possible the maintenance of a harmonious co-adaptation of parts in the course of the phyletic metamorphosis of a species. *** As the primary variations in the phyletic metamorphosis occurred little by little, the secondary adaptations would as a rule be able to keep pace with them."

So far Prof. Weismann. According to his conception, variations of germinal origin occur from time to time. By its innate plasticity the several parts of an organism implicated by their association with the varying part are modified in individual life in such away that their modifications cooperate with the germinal variation in producing an adaption of double origin, partly congenital, partly acquired. The organism then waits, so to speak, for a further congenital variation, when a like process of adaptation again occurs; and thus race-progress is effected by a series of successive variational steps, assisted by a series of cooperating individual modifications.

If now it would be shown that, although on selectionist principles there is no transmission of modification due to individual plasticity, yet these modifications afford the conditions under which variations of like nature are afforded an opportunity of occuring[*sic*] and of making themselves felt in race-progress, a further step would be taken towards a reconciliation of opposing views. Such it appears to me, may well be the case.

To explain the connection which may exist between modifications of the bodily tissues due to innate plasticity (intra-selection) and variations of germinal origin in similar adaptive directions, we may revert [p. 738] to the pendulum analogy which was adduced a few pages back. Assuming that variations do tend to occur in a great number of divergent directions we may liken each to a pendulum which tends to swing; nay, which is swinging through a small arc. The organism, so far as variation is concerned, is a complex aggregate of such pendulums. Suppose then that it has reached congenital harmony with its environment. The pendulums are all swinging through the small arc implied by the slight variations which occur even among the offspring of the same parents. No pendulum can materially increase its swing; for since the organism has reached congenital harmony with its environment, any marked variation will be out of harmony and the individual in which it occurs will be eliminated. Natural selection, then, will ensure the damping down of the swing of all the pendulums within comparatively narrow limits.

But now suppose that the conditions of the environment somewhat rapidly change. Congenital variations will not be equal to the occasion. The swing of the pendulums concerned cannot be rapidly augmented. Here individual plasticity steps in to save some of the members of the race from extinction. They adapt themselves to the changed conditions through a modification of the bodily tissues. If no members of the race have sufficient plasticity to effect this accommodation the race will become extinct, as has indeed occurred again and again in the course of geological history. The stereotyped races have succumbed; the plastic races have survived. Let us grant, then, that certain organisms accommodate themselves to the new conditions by plastic modification of the bodily tissues, say by the adaptive strengthening of some bony structure. What is the effect on congenital variations? Whereas all the other pendulums are still damped down by natural selection as before, the oscillation of the pendulum, which represents a variation in this bony structure, is no longer checked. It is free to swing as much as it can. Congenital variations in the direction of adaptive modification will be so much to the good of the individual concerned. They will constitute a congenital predisposition to that strengthening of the part which is essential for survival. Variations in the opposite direction, tending to thwart the adaptive modification, will be disadvantageous and will be eliminated. Thus, if the conditions remain constant for many generations, congenital variation will gradually render hereditary the same strengthening of bone structure that was provisionally attained by plastic modification. The effects are precisely the same as they would be if the modification in question were directly transmitted in a slight but cumulatively increasing degree. They are reached, however, in a manner which involves no such transmission.

To take a particular case: Let us grant that, in the evolution of the horse tribe, it was of advantage to this line of vertebrate life that the middle digit of each foot should be largely developed and the lateral digits reduced in size; and let us grant that this took its rise in adaptive modification through the increased use of the middle digit and the relative disuse of the lateral digits. Variations in these digits are no longer suppressed and eliminated. Any congenital predisposition to increased development of the middle digit and decreased size in the lateral digits will tend to assist the adaptive modification and to supplement its deficiencies. Any congenital predisposition in the contrary direction will tend to thwart the adaptive modification and to render it less efficient. The former will let adaptive modification start at a higher level, so to speak, and thus enable it to be carried A step further. The latter [p. 739] will force it to start at a lower level, and will prevent its going so far. If natural selection take place at all, we may well believe that it would do a under such circumstances.[9] And it would work along the lines laid down for it in adaptive modification. Modification would lead; variation follow in its wake. It is not surprising that for long we believed that modification was transmitted as hereditary variation. Such an interpretation of the facts is the simpler and more obvious. But simple and obvious interpretations are not always correct. And if, on closer examination, in the light of fuller knowledge, they are found to present grave difficulties, a less simple and less obvious interpretation may claim our provisional acceptance.

In his recent paper on Germinal Selection Prof. Weismann says:[10]· "I am fain to relinquish myself to the hope that now, after another explanation has been found, a reconciliation and unification of the hostile views is not so very distant, and that then we can continue our work together on the newly laid foundations." As one to whom Prof. Weismann alludes as having expressed the opinion that the Lamarckian principle must be admitted as a working hypothesis, I am now ready to relinquish myself also to the same hope. Germinal Selection does not convince me, though I regard it as a suggestive hypothesis; and assuredly I am not convinced by the argument that because in certain cases, such as the changes in the chitinous parts of the skeleton of insects and crustacea, and in the teeth of mammals, use and disuse can have played no part, therefore in no other cases has use-inheritance prevailed.

Even Homer sometimes nods, and Prof. Weismann's logical acumen seems to have deserted him here. But it appears to me that on the lines I have sketched out, it is open to us to accept the facts adduced by the transmissionists and at the same time interpret them on selectionist principles.

It may be well now briefly to summarize the line of argument in a series of numbered paragraphs.

1. In addition to what is congenitally definite in structure or mode of response, an organism inherits a certain amount of innate modifiability or plasticity,

2. Natural selection secures:

(*a*) such congenital definiteness as is advantageous.

(*b*) such innate plasticity as is advantageous.

3. Both *a* and *b* are commonly present; but uniformity of conditions tends to emphasize the former variable conditions of life, the latter.

4. The organism is subject to:

(*a*) variation of germinal origin.'

(*b*) modification of environmental origin, affecting the soma or body tissues.

5. Transmissionists contend that somatic modification in a given direction in one generation is transmitted to the reproductive cells to constitute a source of germinal variation in the same direction in the next generation.

6. It is here suggested that persistent modification through many generations, though not transmitted to the germ, nevertheless affords the opportunity for the occurrence of germinal variation of like nature.

7. Under constant conditions of life, though variations in many directions are occurring in the organisms which have reached harmonious adjustment: to these conditions, yet natural selection eliminates all those which are of such amount as to be disadvantageous, and thus acts as a check on all variations, repressing them to within narrow limits. [p. 740]

8. Let ns suppose, however, that a group of organisms belonging to a plastic species is placed under new conditions of environment.

9. Those whose innate somatic plasticity is equal to the occasion survive. They are modified. Those whose innate plasticity is not equal to the occasion are eliminated.

10. Such modification takes place generation after generation, but, as such, is not inherited. There is no transmission of the effects of modification to the germinal substance.

11. But variations in the same direction as the somatic modification are now no longer repressed and are allowed full scope.

12. Any congenital variations antagonistic in direction to these modifications will tend to thwart them and to render the organism in which they occur liable to elimination.

13. Any congenital variations similar in direction to these modifications will tend to support them and to favor the individuals in which they occur.

14. Thus will arise a congenital predisposition to the modifications in question.

15. The longer this process continues, the more marked will be the predisposition and the greater the tendency of the congenital variations to conform in all respects to the persistent plastic modifications; while

16. The plasticity continuing the operation, the modifications become yet further adaptive.

17. Thus plastic modification leads and germinal variation follows; the one paves the way for the other.

18. Natural selection will tend to foster variability in given advantageous lines when once initiated, for (*a*) the constant elimination of variations leads to the survival of the relatively invariable; but (*b*) the perpetuation of variations in any given direction leads to the survival of the variable in that direction. Lamarckian paleontologists are apt to overlook this fact that natural selection produces determinate variation.

19. The transmissionist, fixing his attention first on the modification, and secondly the fact that organic effects similar to those produced by the modification gradually become congenitally stereotyped, assumes that the modification *as such* is inherited.

20. It is here suggested that the modification *as such,* is not inherited, but is the condition under which congenital variations are favored and given time to get a hold on the organism, and are thus enabled by degrees to reach the fully adaptive level.

When we remember that plastic modification and germinal variation have been working together all along the line of organic evolution, to reach the common goal of adaptation, it is difficult to believe that they have been all along wholly independent of each other. If the direct dependence advocated by the transmissionists be rejected, perhaps the indirect dependence here suggested may be found worthy of consideration.

Footnotes

[1] Being a chapter [XIV] from a forthcoming work on *Habit and Instinct* communicated at the request of Prof. Henry F. Osborn.

[2] *Germinal Selection,* Monist Jan., 1896, p. 290.

[3] *Op. cit.* p. 264.

[4] *Natural Science,* Vol. I., April, 1892, pp. 100-101.

[5] *Monist,* Jan., 1896, p. 268.

[6] Romanes Lecture on *The Effect of External Influences on Development,* pp. 11, 12.

[7] Romanes Lecture, p. 15.

[8] Romanes Lecture, pp. 18, 19.

[9] Prof. Weismann's 'Germinal Selection' if a *vera causa* would be a cooperating factor and assist in producing the requisite variations.

[10] *Monist, loc cit,* p. 290.