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THE PHYSIOLOGY OF FEATHER PATTERN

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I. INTRODUCTION

In coöperation with colleagues, whose work will be discussed in the following pages, I have been engaged during the last ten years in studying the manifestations and control of sexual characteristics in the Brown Leghorn fowl chiefly. The characters of the highly dimorphic plumage have engaged our attention from the start, and the readiness of control of plumage sex-characteristics led us to make a special study of the mechanisms concerned. This resulted in the discovery that differences of rate of growth of different feather tracts are highly determinative for the threshold of reaction to the female sex hormone (Juhn and Gustavson, 1930; Juhn, Faulkner, and Gustavson, 1931). The idea then occurred to me that differences in the rates of growth of parts of the individual feather might similarly be an important factor in the determination of its pattern, whether sexual or not; and an extended analysis of development and growth of feathers confirmed this

theory (Lillie and Juhn, 1932). It has been suggested to me that the principles involved should be of general interest to ornithologists.

It should be stated at the start that the range of physiological determination (by hormones, other physiological conditions of the organism, and environment) is limited by genetic determiners, which include, in my opinion, not only the general genetic make-up of the organism, but also the skin mosaic factors responsible for the formation of different feather types in different tracts, as for instance in the saddle and breast of male Leghorns or capons. Nevertheless, the range of physiological determination of feather structure and pattern is very considerable. The analysis of experimentally determined variations may be expected to throw some light also upon the principles determining natural feather pattern.

In the experiments the female sex hormone and crystalline thyroxin were used. Injections of these produce specific effects on feathers, showing wide quantitative ranges dependent on concentration. Males or capons of the Brown Leghorn fowl were used exclusively for the experiments. The female sex hormone was prepared by our coöperating biochemist, Dr. R. G. Gustavson, from placenta or human pregnancy urine. It should be recalled in this connection that male hormone is without noticeable effect on the plumage of this breed of fowl, and that the plumage of the capon or poularde is the same as the male in all major aspects. The effect of the female hormone is to induce the female form, structure and pattern, specific for each feather tract, in all regenerating feathers, so long as its concentration is above the threshold of reaction. Thyroxin, "in physiological doses", produces definite pattern effects, more especially in the "lacy" feathers of the saddle, back, and neck.

These hormones are administered by subcutaneous injections. There is, therefore, always a period of absorption during which the concentration of the substance is rising in the blood to a maximum, dependent on the dose, and a period of excretion during which the concentration of the substance in the blood is sinking. An "intensity curve" can be used to picture these conditions (see Fig. 52). If the maximum is above the "threshold of reaction", a definite effect is produced, the quantity of which is dependent on the duration of threshold-concentration. The effect begins to manifest itself after a variable latent period, if concentration in the blood is above the minimum for reaction (threshold); and increases as concentration rises to the maximum, then decreasing again to disappearance. The result of

this is to establish a symmetrical mark in the vane of the feather. Accurately measured amounts of hormone were always used.

It is obvious that by suitably repeated injections the level of concentration of hormone in the blood may be kept constant, or caused to fluctuate up or down as desired. A great variety of patterns may thus be produced.

For the interpretation of the results knowledge of the *mechanics* of development of the feather is necessary. As this was substantially unknown, a detailed study of the development of the feather was necessary (Lillie and Juhn, 1932).

In all of the studies summarized here regenerating feathers of males or capons were used. Feathers regenerate promptly at any season of the year at constant rates. In order to obtain any desired stage for study of hormone effects, definite feathers are plucked at known periods of time before beginning any experiment, and preserved for comparison with the experimental regenerating feathers. The results can thus be compared with the predecessor feather, from the same follicle if desired. The record is completed after regeneration by preserving the experimental feathers also.

We may divide our review into two parts, the first dealing with plumage areas, the second with the individual feathers.

II. PLUMAGE AREAS

We shall discuss this subject briefly, and only with reference to areal gynandromorphism; but it deserves attention because the principle of relationship between rate of growth and threshold of reaction was first discovered here. Domm (1927) observed that in the reversion from male type plumage, which follows sinistral ovariectomy, to female type, which develops more or less completely at a later time, feathers of the back and saddle may be first affected; however, no special attention was given to this phenomenon. Juhn and Gustavson (1930) found in their experiments of injection of female hormone into capons, that, when a series of daily injections was interrupted for a day, the regenerating breast feathers recorded the interruption by temporary reversion to male type, while the regenerating saddle feathers remained pure female in type. They interpreted this to mean that excretion of the female hormone during the interruption had reduced the concentration in the blood below the threshold of reaction for the breast feathers, but not below the threshold for the saddle feathers; in other words, that the breast feathers had a higher threshold of reaction than the saddle feathers. They found also that it was possible to induce

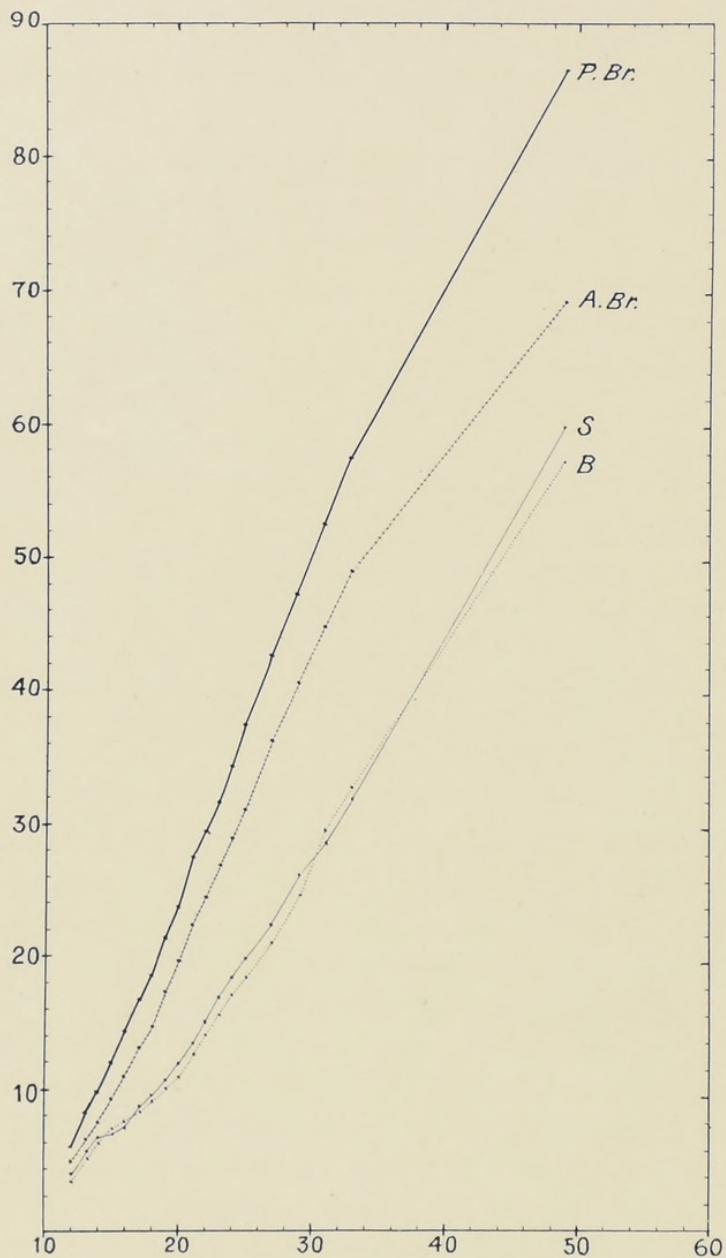


Fig. 38. Rate of growth of feathers in length in the male Brown Leghorn. The four curves represent the average daily increase in length of twenty feathers in each of four regions from the twelfth to the forty-ninth days of regeneration. P. Br. is for posterior breast region; A. Br., anterior breast; S., saddle; B., back; abscissae, in days; ordinates, in millimeters. From Juhn, Faulkner and Gustavson, 1931.

hen-feathering in the saddle with a low concentration of female hormone in the blood, that did not affect the breast feathers at all; and thus confirmed the conclusion. They also noted that breast feathers grow at a much more rapid rate than saddle feathers and suggested a causal relationship between rate of growth and threshold of reaction.

Juhn, Faulkner, and Gustavson (1931) then made an extended study of this subject. They studied average daily rates of growth in the posterior part of the breast, the anterior part of the breast, in the back, and in the saddle. The results are shown in the accompanying graph (Fig. 38). By a long series of experiments they then determined that there is a direct relationship between the growth rates of the male feathers and the concentration of female hormone in the blood required to change the type of the regenerating feather from male to female. The relationship is, in fact, roughly proportional to the linear growth rates recorded, concentrations of about the proportions of 3:4:6 being required for female modification in the saddle, anterior breast, and posterior breast, respectively. These differences are sufficient, in view of the "all-or-none" character of the reactions, to bring about areal gynandromorphism of plumage. They also found an antero-posterior gradient of growth in the plumage of the breast, and medio-dorsal transverse gradients in other feather tracts, as well as in the breast, that were reflected in the results of various experiments.

These results were applied by the writer to the explanation of bilateral gynandromorphism, which has been described in ten distinct cases reported in the literature (Lillie, 1931). He found in four of the cases that a decided hypertrophy of the side bearing the male plumage had been figured or described by the authors; in two of the cases this happened to be the right side and in two it was the left side. In the other cases the conditions of symmetry of the bird's body had not been considered. In all cases, in which the internal anatomy was described, there was evidence of ovarian deficiency, and thus presumably of an abnormally low supply of female hormone. In the more numerous cases of lateral hemihypertrophy known in human subjects there is often, at least, an excessive growth rate of epidermal structures on the hypertrophied side. If we assume that this is the case also for feathers, the principle of relationship between growth rate and threshold of reaction would necessarily determine, in cases of ovarian deficiency of a certain degree, that the more rapidly growing side would produce male feathers and the more slowly growing side female feathers. It is at least certain that the condition can be

explained in principle on the basis of the relationships experimentally determined between growth rates and hormone threshold.

III. THE PATTERN OF THE INDIVIDUAL FEATHER

Although feather patterns are almost infinitely diversified, there are undoubtedly certain fundamental physiological principles that underlie all. The physiological analysis to be presented is based upon experiments with one breed of fowl; nevertheless the fundamental factors are present here as they would be in any other case; and it would probably be possible to reach a common agreement as to what they are. Assuming this, it will be seen that the analysis is probably significant for the interpretation of feather pattern in general. In each case there are certain genetic and mosaic factors pertaining to species, race, and feather tract that are special; for the purpose of physiological analysis these are taken for granted.

Like the entire organism the feather is a bilateral structure with a more or less pronounced tendency to asymmetry both in form and pattern. All of its variations and modifications are to be referred to its axis (the rhachis), to its apical and basal ends, to its free margin, and to its outer and inner surfaces. The modifications to be considered are restricted to the vane proper. The structural elements concerned are the rhachis, the barbs and barbules, and the pigment.

We shall deal first with experimental modifications of pattern; and afterwards with the development of the feather as a means of interpretation.

1. Experimental modifications.

a. By injections of thyroxin.

The feathers in which the effects of thyroxin are most clearly marked belong to the saddle, back, and neck-hackle tracts of the male or capon. These feathers agree in being long, acuminate, and lacy, i. e., with barbules confined to the basal region of the barbs, to an extent which increases regularly from near the apex to the base of the vane (Fig. 39).

In preparation for the experiment feathers are plucked previously, so that regenerating feathers of known age are present. Accurately measured subcutaneous injections of Squibb's crystalline thyroxin are then administered. Figures 42-46 record the effects of single injections of increasing amounts of thyroxin in saddle feathers of five different birds; the figures are photographs of regenerating feathers plucked several weeks after the injection. The weakest injection (0.5 mg.) is recorded as a narrow spindle-shaped pigmented area

centered on the rhachis; the next (1 mg.) produces a similar but broader mark with its widest point above the center; in the succeeding cases (1.5, 5.0, and 10 mg.) the mark becomes progressively wider until it reaches the margin. The form of the mark records the absorption and excretion of the thyroxin; its modifications through the series are due, so far as width is concerned, to increasing lateral extension with increase in dose, and, so far as its form is concerned, to more rapid absorption than excretion with rising doses. The mark is caused by the extension of barbule formation farther from the rhachis than normal, and by the formation of large active melanophores wherever barbules appear. It will be noticed also that the feather becomes shorter and broader as a whole with increasing dosage, though even the highest dosage employed is not sufficient to induce premature molting, as excessive doses will do.

The important thing to notice, however, is that there is a decreasing susceptibility to thyroxin in each barb from its base to apex. In other words, the threshold of reaction to thyroxin forms an ascending gradient along each barb. The study of the development of the feather shows conclusively that all levels of forming barbs are present simultaneously at each stage of regeneration, so that the failure of more apical levels to show thyroxin effects with the lower doses can be due to nothing else but a difference in susceptibility.

Interesting patterns can be produced by injections of thyroxin at suitably spaced intervals. Two examples are shown in Figures 40 and 41 in the case of neck hackle feathers. Fig. 39 is a normal control; the pattern in Fig. 40 was produced by injection of 1 mg. thyroxin every seventh day during regeneration, and in Fig. 41 by injection of 1.5 mg. every sixth day. Variations of amount and interval produce yet other variations on the theme.

b. By injections of female hormone.

The female hormone, prepared from sources previously mentioned, affects all kinds of feathers that are sexually dimorphic, causing an abrupt change from male to female type during the period that it is effective. Its action thus differs from the action of thyroxin not only in the number of kinds of feathers affected, but also radically in type of reaction. The changes produced by thyroxin are never of a sexual nature; those produced by the female hormone are always of this nature. However, as only a few factors are concerned (general form of the feather, presence or absence of barbules, presence or absence of chromatophores, and the color and arrangement of the pigment produced) superficial resemblances between the effects of thyroxin and of female hormone do appear, especially in the lacy feathers.

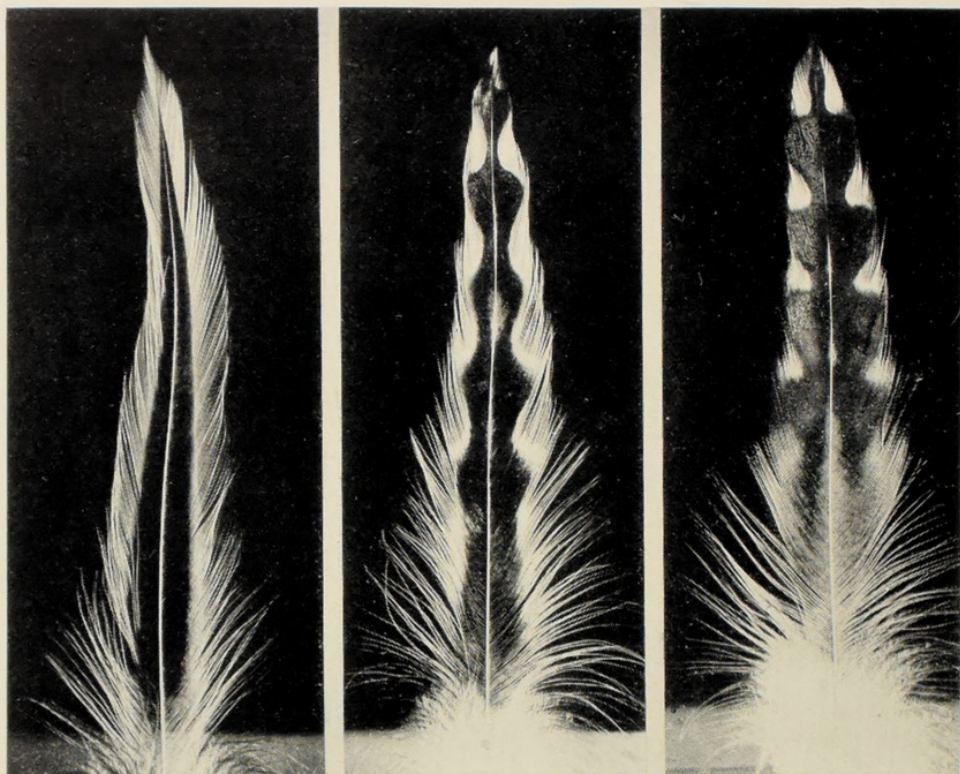
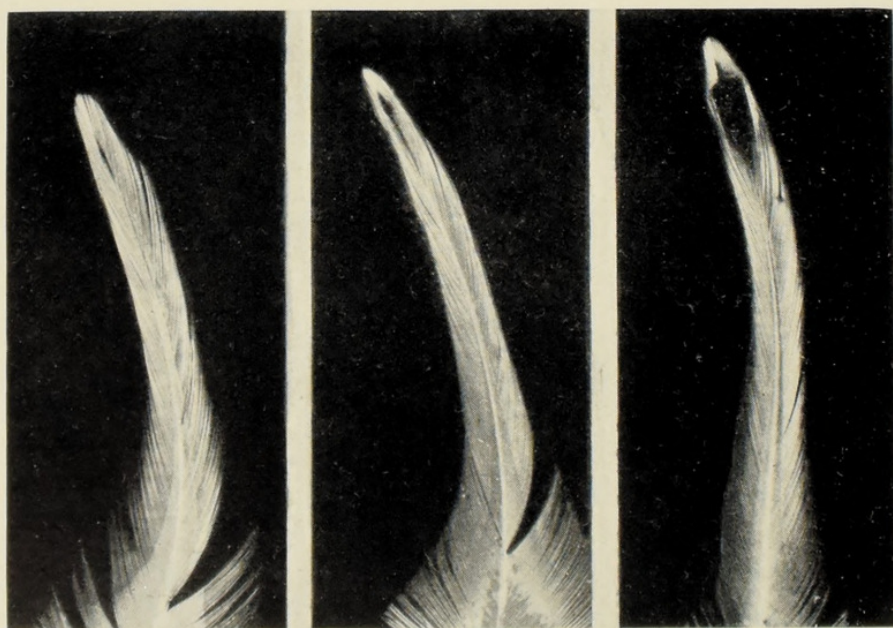


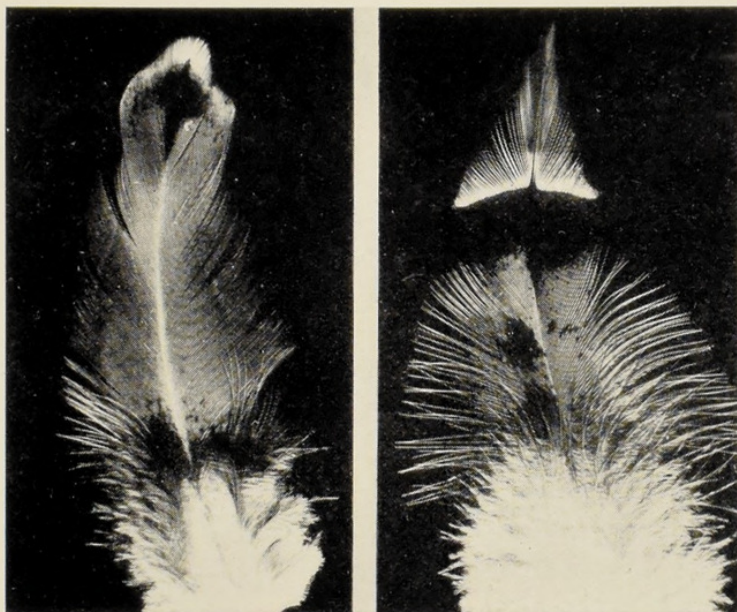
Fig. 39. (Left). Neck hackle feather of male Brown Leghorn; normal control. From Lillie and Juhn, 1932.

Fig. 40. (Center). A neck hackle feather from a male Brown Leghorn that had received 1 mg. of thyroxin by subcutaneous injection every seventh day during the growth of this feather. From Lillie and Juhn, 1932.

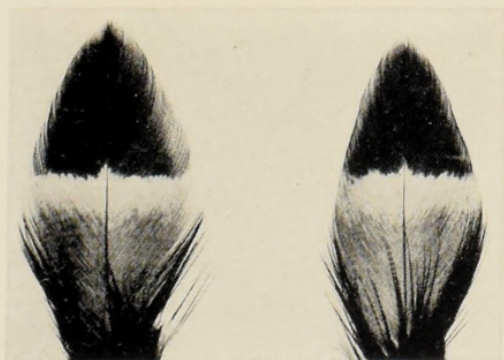
Fig. 41. (Right). Same type of feather as in Fig. 40 from a bird receiving 1.5 mg. of thyroxin every sixth day during the growth of this feather. From Lillie and Juhn, 1932.



Figs. 42-43-44. Tips of saddle feathers from Brown Leghorn males recording increasing single doses of thyroxin. Fig. 42 (left), 0.5 mg. Fig. 43 (center), 1 mg. Fig. 44 (left), 1.5 mg. (See also Figs. 45 and 46). From Lillie and Juhn, 1932.



Figs. 45-46. Tips of saddle feathers from Brown Leghorn males recording increasing single doses of thyroxin (continuation of figures 42-44). Fig. 45 (left), 5 mg. Fig. 46 (right), 10 mg. From Lillie and Juhn, 1932.



Figs. 47-48. Left group. The formation of female bars on a male background by injection of female hormone on three successive days during growth (500 rat units injected each day). Fig. 47 (left) from right anterior breast. Fig. 48 from left anterior breast. From Lillie and Juhn, 1932.

Figs. 49-50. Right group. The formation of male bars on a female background by omitting every seventh day of an otherwise daily injection of female hormone during the entire growth of the vane (60 rat units daily for twenty-seven days). From Juhn and Gustavson, 1930.

In the case of the feathers of the saddle, back, and neck, the patterns produced by single or repeated doses of female hormone bring out the same principle of a gradient of thresholds along the axis of each barb in a manner similar to thyroxin (see figures in Juhn, Faulkner, and Gustavson, 1931). There is no need, therefore, to give any details of these experiments.

The special properties of the breast feathers bring out certain consequences more clearly. Only one change is concerned, viz., in the color, from the black of the male to the salmon-colored, or orange, of the female. Breast feathers in general have the highest threshold for female hormone of all contour feathers; and in the breast itself the posterior feathers have a higher threshold than the anterior feathers. The bases of the barbs in any given feather have a relatively low threshold, and the threshold of reaction rises towards the apex. Increasing concentrations of hormone record marks extending from the rachis towards the margin of the vane.

However, another factor enters into the realization of the female marking produced. This is the *principle of reaction rate*. The margin of the vane (apical sections of barbs) has a much more rapid reaction rate than the axial part. This operates in two ways: first by reducing the period of time (latent period) after attainment of threshold-concentration in the blood before onset of reaction, and second by increasing quantity of reaction occurring in a given time. Thus, female reaction may occur within 24 hours after a sufficient dose, in the margin, whereas from 48 to 72 hours are required in intermediate and axial portions of the vane with any dosage above threshold requirements. The consequence of difference of latent period is that a single dose may record a mark at the margin of the vane alone if it is heavy enough, and if it can be excreted before 48 to 72 hours after injection, a time which covers the latent periods of the remainder of the vane.

The principle of reaction rate is of equal importance with the principle of gradient of threshold in determining the form of a physiologically induced pattern.

By virtue of the two principles of threshold and rate of reaction, transverse bars of female color may be produced in breast feathers by suitable injections of female hormone for two or three days, because the margin of the feather, although having a more rapid rate, records the effect for a shorter period of time owing to its higher threshold than the axial part. Differences in rate and threshold may thus balance one another, producing equal effects all the way across the vane (Figures 47 and 48).

Female bars may thus be produced on a male background by injections for short periods of time; or male bars may be produced on a female background by running a continuous series of injections during the entire growth of the feather, except for stated interruptions, during which the hormone is excreted to below the threshold of the female reaction (Figures 49 and 50).

The patterns that we have hitherto considered are transverse to the axis of the feather in their general arrangement. But it is obvious, according to the same principles, that if one side of the vane of any feathers should have a higher threshold than the other, a correspondingly intermediate dosage of female hormone would affect only the side with the lower threshold, and thus a longitudinally gynandromorph feather would be formed such as have been described by Pézard, Sand, and Caridroit (1926), by Bond (1913), and which has been realized in our own experiments (Lillie and Juhn (1932).

2. Gradients of growth-rate in the development of the feather.

If the same principle of relationship between levels of threshold and rate of growth that we found to obtain between feather tracts should also apply to the individual feather, then we could transpose our experimentally determined gradients of threshold into gradients of growth rate. This was the consideration that induced us to study anew the development of the individual feather (Lillie and Juhn, 1932). For all the details I must refer to the original paper; the conclusions alone can be stated here.

The feather forms form a complete ring of cells established as a thickening of the epidermal layer of the feather papilla at its base, immediately bounding the umbilicus. The original embryonic form of the feather is thus a ring. The rhachis arises by concrescence of the two ring halves, accompanied by continuous growth of the ring, or *collar* as we shall call it; the point of concrescence establishes the dorsal side of the ring, the point opposite being the mid-ventral line. The rhachis is thus composed of two lateral halves fused together. It continues to grow in length so long as the collar maintains its activity. The halves of the collar are continually flowing from the mid-ventral line in opposite directions into the rhachis, the energy for the motion being furnished by very active cell-division and growth. The development of the rhachis is thus from apex to base, as has long been known.

The barbs arise as outgrowths of this ring parallel to one another, perpendicular to the ring, and closely applied to the surface of the pulp. Each arises next to the mid-ventral line, and its attachment to

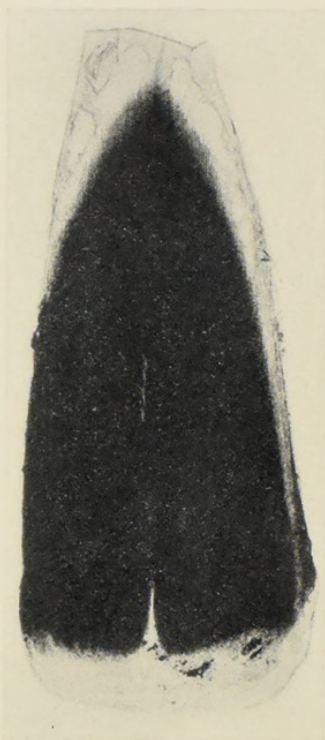


Fig. 51. Split preparation of a feather germ twelve days after beginning regeneration from the breast of a Brown Leghorn capon. The wall of the conical feather germ was split along the ventral side and spread out flat on a microscope slide after removing the pulp. The rhachis is in the center of the photograph. The youngest barbs are at the margins. The unpigmented base is the collar, bounded by the umbilicus below. From Lillie and Juhn, 1932.

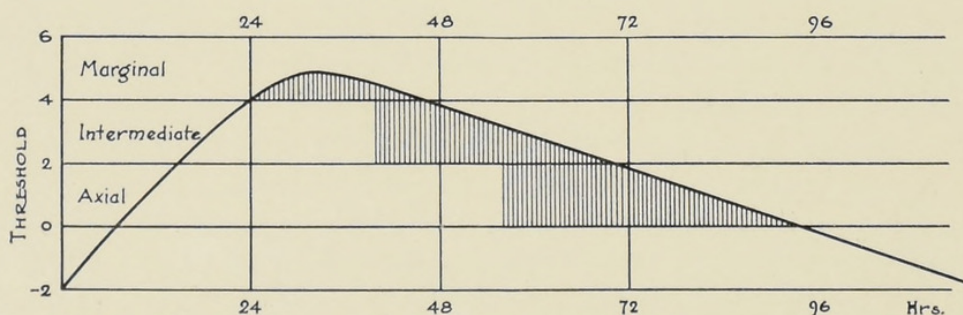


Fig. 52. Half vane; intermittent hormone action. *Curve of intensity.* Effect of female hormone on the breast feather of the Brown Leghorn capon according to a particular dosage. Such a curve of intensity will result in the formation of an even bar from center to margin of the vane (*cf.* Figs. 47-48). Other dosages will produce yet other curves of intensity, resulting in different patterns. The ruled areas indicate duration of reaction—in the present case deposition of pigment of the female type—in the parts of the vane concerned. The ordinates represent the thresholds of reaction of the parts of the vane from axis to margin, and the abscissae represent time in hours. See discussion in text, page 208.

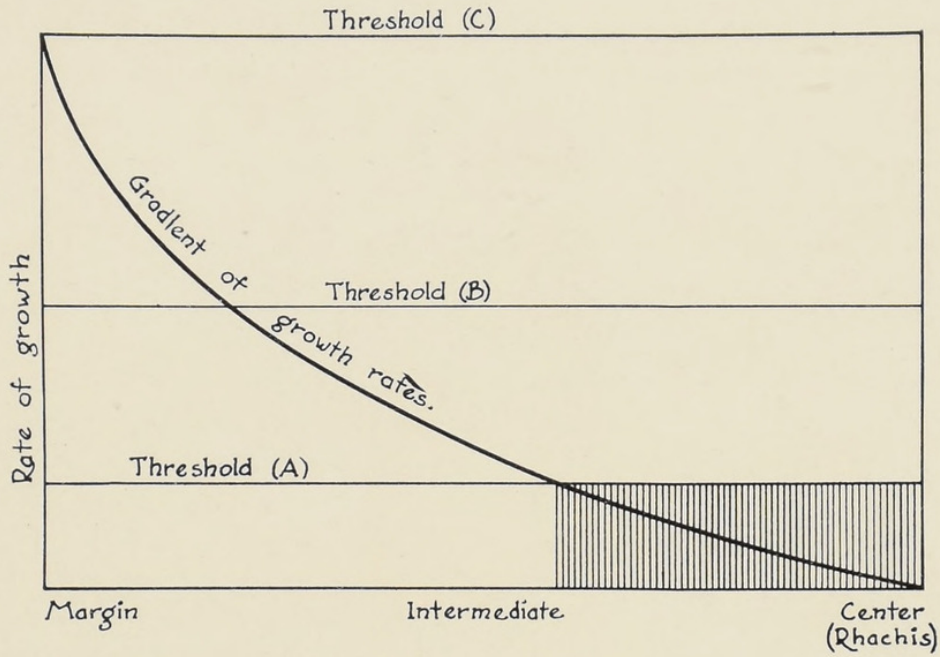


Fig. 53. Half vane; constant hormone action. The hormone action is supposed to maintain a constant level of intensity corresponding to Threshold *A* or Threshold *B*, or Threshold *C*. The reaction is represented for Threshold *A* only, by the ruled area. Rate of growth is plotted as ordinates against position in the vane from margin to center. The intersection of threshold, which is directly proportional to rate of growth, with the curve of gradient of growth rates gives the position in the vane to which the reaction extends from the center (=rhachis).

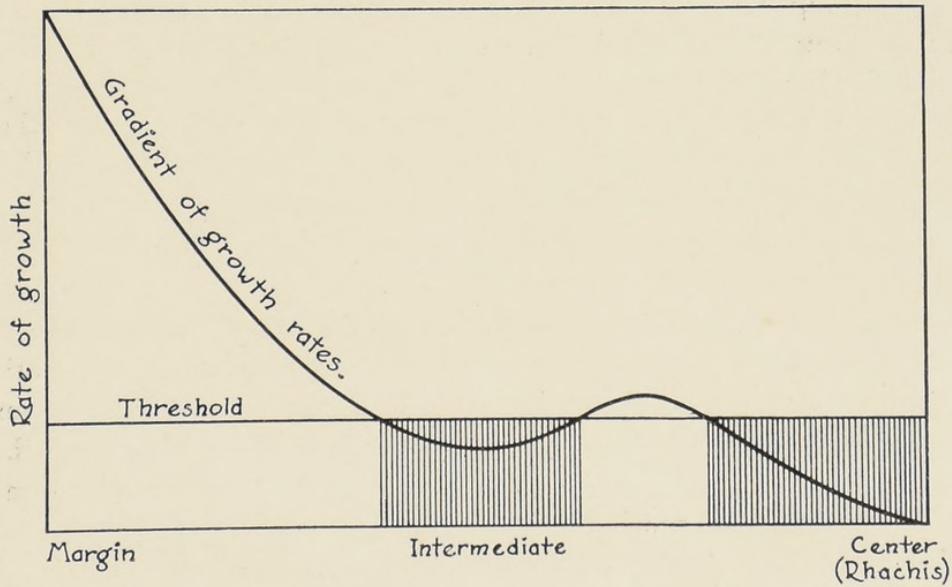


Fig. 54. Half vane; constant hormone action. The curve of growth rates represented here is entirely theoretical, and is postulated to explain longitudinal stripes of intermediate position in the vane. See text, page 210. "Center"=rhachis.

the collar is fixed. As it grows in length it is carried along one side or the other of the two halves of the collar by the flowing movements concerned in the formation of the rhachis until it reaches the point of concrescence on one or the other side of the definitive rhachis, when its growth is fully completed. The time required for transfer from mid-ventral to mid-dorsal line and completion of growth is about ten days in the case of barbs from the middle of the vane of the breast feather. The apical region of the barb is formed first and adjacent regions, to base, in succession; the growth is apico-basal.

There are thus two time-gradients in the feather; from apex to base along the rhachis, and from margin to center along the barbs.

The characters of each barb are finally determined for all the elements that enter into its composition within a very narrow zone adjacent to the collar, *the zone of determination*. It is within this zone that all hormone effects are registered: above it development cannot be altered; below it the cells are still purely embryonic. It will be seen, on reflection (*cf.* Fig. 51), that the zone of determination, from the dorsal to the ventral surface of the feather germ, intersects all barb levels. Thus in any given experiment all levels of barbs are accessible to the hormone.

The growth-rate of the rhachis is approximately uniform, during the formation of the vane at least. This is clearly indicated by the curves in Fig. 38. The slight decrement shown after about thirty days for the feathers of the breast indicates the transition from the vane to the fluffy part of the feather. Certain slight pattern changes along the axis of saddle feathers have suggested, however, that there may be a slight decrement of growth-rate from apex to base not detected by the somewhat rough measurements. The outstanding fact, however, is the approximate uniformity of growth-rate along the axis of the feather.

The rate of growth of the barbs, on the other hand, decreases very greatly from apex to base along a well-defined gradient of growth (*cf.* Fig. 53). The determination of this principle was based upon the possibility of establishing a base line just above the collar throughout its entire extent by suitable hormone injections (Lillie and Juhn, 1932), which make a colored band. In the course of the subsequent growth this base line is moved unequally upward along the axis of feather germ. The inequality of movement registers the unequal rates of growth of successive levels of the barbs, which can be represented in a curve of rate of growth, as in Fig. 53.

The form of the curve has been estimated as accurately as possible from the data at our disposal for the breast feather. It is not, however, to be regarded as mathematically exact. The indication conveyed by the curve that the lateral half of the vane may be divided roughly into three longitudinal zones—an axial zone with slowest growth rate, an intermediate with slightly higher growth rate, and a marginal with greatly increased growth-rate—is of significance. In the case of the saddle feather of the capon there are indications that the form of the curve differs in some details, though the great difference in rate between the margin and the remainder of the vane obtains here also. The indications are that curves of growth-rate of the barbs differ typically between rounded and acuminate contour feathers.

The experiments definitely prove that there is a close agreement between threshold of reaction and growth-rate along the axis of barbs. The various patterns formed by injections of hormones are fully explained as to their form by the gradients of growth-rate. The finer composition of the patterns, however, depends upon other inherited capacities and potencies of the particular feather concerned.

IV. GENERAL DISCUSSION

It is reasonable to suppose that the principle of a gradient of growth rates along the axes of the barbs during the development is a general one. It goes far towards explaining the more general features of feather pattern, if we are further allowed to assume that genes operate in the developing feather in manners similar to hormones. A single determining factor, such as a hormone or gene, may produce great variety of results (patterns) depending on curve of intensity and periodic activity.

No pattern is exactly symmetrical; for feathers, like other structures exhibiting bilateral symmetry, always possess an underlying asymmetry, more or less pronounced. There exists every grade of departure from bilateral symmetry in the feathers of fowl down to quite extreme asymmetry. The grade of asymmetry bears certain definite relations to the main axes of the entire body, or the wings, as will be more precisely defined in a paper to be published later. Symmetrical patterns therefore grade into asymmetrical patterns by imperceptible degrees.

It should also be noted that, as the two sides of the vane develop independently of one another, any pattern of the entire vane depends for its symmetry on simultaneous and equal processes in the two halves of the collar. Any disturbance of the processes that affects the two

sides unequally will result in a certain amount of asymmetry. Thus it is probably very seldom that the two halves of a transverse bar fit one another exactly on the rhachis. That such fitting is, however, usually so close is a revelation of precision in the developmental process.

As a symmetrical pattern is thus composed of two equal halves, it is sufficient to consider one side of the vane.

For descriptive purposes patterns may be divided into transverse, longitudinal, and concentric.

1. Transverse patterns.

These are due to *intermittent factors* operating during the development of the feather.

The most complete form of the transverse pattern is the bar. We have already seen how, with intermittent action of hormone, the factors of threshold and rate of reaction may be so equalized as to produce a bar of even width across the vane. This depends, as we have already seen, on a rise and fall of hormone concentration of such a kind that its highest point is above the threshold requirements of all transverse levels, and its beginning and end below all thresholds.

The matter can be presented in diagrammatic form as follows (Fig. 52): The ordinates represent threshold of reaction, and the abscissae time in hours. The rise and fall of hormone action is plotted as a curve derived from the general results of numerous experiments and according to dosage of female hormone described in a previous paper (Lillie and Juhn, 1932). This curve intersects all threshold levels twice—in its ascending and in its descending limb. Reaction begins in the margin, owing to its rapid rate, at about 24 hours; it ceases at about 46 hours, owing to excretion of hormone shown in the descending curve. Reaction does not begin in the intermediate portion of the vane until about 40 hours, owing to its slower rate of growth; it lasts until about 70 hours, when the curve falls below its threshold. In the axial portion of the vane reaction does not begin until about 56 hours owing to a yet slower rate, and it lasts until 90 hours, or more, when the curve falls below its threshold also. Thus, an even bar of reaction is recorded all across the vane, because the decreasing time of action from axis to margin is compensated by increment of growth-rate. The threshold levels are, of course, not sharply divided in three as the exigencies of the diagram demand, but flow into one another as indicated in the curve (Fig. 53).

If the curve of hormone action does not rise to the threshold of the marginal portion of the vane, axial patterns form, of a width dependent on the height of the hormone curve, as in the case of thyroxin patterns, in the saddle and neck feathers (Figs. 40-46). The form varies with the relations between the ascending (absorption) and descending (excretion) limbs of the curve. If the descending limb of a curve exceeding the threshold level of the margin should be very steep, and fall below the axial threshold without intersecting the reaction period of the axial portion of the vane a marginal mark would be made stopping short of the axis. In the case of hormone action this means very rapid excretion. Theoretically, the descending limb might intersect the reaction zone of both marginal and axial portions, missing the intermediate reaction zone entirely. This has been realized in our experiments (Lillie and Juhn, 1932). Theoretically, also, the descending limb might intersect only the beginnings of the marginal, intermediate, and axial zones, leaving three spots in a transverse line across each side of the vane. In all of these cases the patterns are modifications of the bar.

A special form of transverse pattern is confined to the tip of the feather, as in so-called spangled breeds of fowl. Dr. Juhn and the writer have pointed out that the developmental history of the tip of the feather differs slightly from the remainder and have suggested that this may be a basis for tip patterns (Lillie and Juhn, 1932, pp. 135-136, 138-139).

We have dealt with hormones as intermittent factors determining transverse patterns by their operation upon the form of development characteristic of the feather germ. Their operation is restricted by the processes of absorption and excretion, and the time factors involved. In the barred breeds of fowl we have a genetic determining factor. One of my students, Dr. G. Montalenti of the University of Rome, has studied this pattern and found that its development follows the same course as that of bars determined by hormones. The only difference is the greater precision and more rapid control. It is obvious from his study that the gene in question exhibits rhythmic activity according to a curve of intensity, with ascending and descending limbs, and that the even width of the bar is due to a gradient of threshold of reaction combined with reaction rates precisely similar to those determined by us for the Brown Leghorn. This paper will be published shortly.

Inherited patterns of the individual feather may thus depend on the same principles of growth and development as physiologically induced patterns.

2. Longitudinal patterns, unlike transverse patterns, which are due to factors operating intermittently, are dependent on factors acting constantly throughout the development of the feather. If a physiological factor, such as a hormone, be of constant low intensity, it will record a longitudinal stripe next to the rhachis (Fig. 53, Threshold *A*); if it be of slightly greater intensity, but still below the threshold of the margin, it will record a wider stripe leaving an unmodified margin (Fig. 53, Threshold *B*); if its intensity throughout be above the threshold of the margin also, the entire vane will be affected (Fig. 53, Threshold *C*).

Constant factors can thus record a positive (axial) and a negative (marginal) stripe side by side, but cannot record two or more positive stripes, so long as the gradient of growth-rates is a descending curve from margin to rhachis. If, however, the gradient should descend for a short distance, then ascend again, before making its final descent to the margin, a constantly acting factor of proper intensity would record two positive stripes separated by a negative stripe and followed by a marginal negative stripe (Fig. 54). Such a gradient of growth rates is purely imaginary, though it is conceivable that it may be found to exist in feathers of certain patterns. Its interest is in helping to show the range of control of pattern theoretically possible on the principle of relationship between rate of growth and threshold of reaction. In this connection it may further be noticed that with such a gradient of growth rate and a factor acting intermittently, such as the barring factor, at a certain grade of intensity, spots would be produced, arranged in both transverse and longitudinal rows, as in the guinea fowl.

3. Concentric patterns may also be derived theoretically from the principles already laid down. In the case of the thyroxin mark, for instance, the pattern is not simple, but is composed of three effects: the first to appear in point of time is a more or less pronounced blanching of pigment freshly deposited; shortly after, the formation of barbules is stimulated; then the deposition of melanin pigment occurs. Thus, there are three serial effects. When the mark fails to reach the margin, the three zones thus created are concentric. They

occur, as a matter of fact, in Figures 43 to 45; but, as they are not sharply contrasted, it requires careful examination of the actual specimen to see them (*cf.* Lillie and Juhn, 1932). The concentric pattern thus depends for its origin on differences of threshold of the elements composing the mark under conditions of a suitable intensity curve.

The principles that we have stated reveal only a small part of the mechanism that nature uses in the production of certain qualities that we have termed pattern in the constitution of the individual feather; they enable us to understand certain abnormalities such as gynandromorphism whether in the individual feather or in the entire plumage; they may be useful in experimental modification or control of some plumage characteristics; they also have broader biological applications. The experiments show, I think, that the plumage of birds is a wonderful material for experimental analysis, and I hope they may enlist the interest of ornithologists to extend them to other forms. Certainly we have here a very little explored and, in all probability, a very fertile field for experimental research.

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