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Field functions in plumage: the cape[1]).

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(With 2 figures in text.)

A group of papers from the Whitman Laboratory has stressed the importance of the plumage as a means of studying relations between embryonic orders of origin and adult field patterns. The study of these gradient properties, which in the plumage may be evaluated quantitatively, is proving of special interest. It is therefore a privilege to contribute a study which forms one of the series to this number of the Vierteljahrsschrift of the Naturforschende Gesellschaft, Zürich.

This volume honours Professor KARL HESCHELER on the occasion of his seventieth birthday and it is more than pleasure for one of his former students to have this opportunity of recalling the continued interest in biological problems which he so ably and for so many years maintained at the Zoological Institute of the University of Zurich.

The present paper deals with the relation of the order of origin of the embryonic papillae of the cape to the feather patterns developed here by the adult, these patterns being interpreted as reflecting the persistent physiological properties determined as gradient sequences in the single papillae by embryonic field forces.

The description is restricted to the adult male of the Brown Leg-
horn, a breed where normal female plumage is determined by the
female hormone and normal male plumage occurs in the absence of
either sex hormone. The plumage response to the female hormone
sets the action of this secretion entirely apart from that of other
organs, thyroid, hypophysis, etc. It is of course clear that the pre-
sence of all these latter internal secretions is essential to the deve-
lopment of pigment or certain structural features of the feather as
such, in comparable measure as their presence is essential to the
economy of the entire organism. But the definite distinction rests in
the fact that diminution or elimination of any of these secretions
results in either sex in an abnormal development of plumage just as
it introduces certain abnormalities of the organism while the plu-
mage which develops either in the presence of the female hormone
or in its absence is entirely normal for the standards to which the
breed in question was developed. Accordingly the action of these
glands, hypophysis, thyroid, etc., is taken for granted and the male
plumage is considered "autonomous" in the sense that its patterns
develop, not because of the presence of a specific hormone acting
within physiological levels but as direct resultants of a given genetic
constitution and physiological differentials. While the subject proper
of this paper thus deals with an example of the development of
"autonomous patterns", it will be necessary to introduce it with a
brief review and discussion of some preceeding studies from the
Whitman Laboratory which deal with feather patterns induced by
means of female hormone, because these have led to the formula-
tion of certain concepts which have in turn directly suggested the
investigation of gradient and symmetry properties of plumage and
of their embryonic origins.

We may be permitted here to abstain from literature references
to plumage modifications by surgical procedures; these valuable
experiments scarcely serve in quantitative interpretations and are
furthermore very fully cited in recent text-books.

When female feathering was first obtained in the male by
means of injection of the chemically prepared female hormone dur-
ing the regeneration of previously plucked feathers, it was found
that certain plumage areas would respond to definitely lower con-
centrations of the hormone than would others and that the feather
areas with lower threshold also were characterised by slower growth
as measured by the linear increase of the entire feather (JUHN and

GUSTAVSON, 1930). This correlation of threshold of reaction with rate of growth of plumage made it clear that the female hormone could serve as an indicator of the growth characteristics of single feathers or of feather components, for it may reasonably be as- sumed that subthreshold doses act within the system, thus outlining its capacities at given times or levels of growth, though maximal doses may, and in the cases examined to the time of writing do, com- pletely alter the absolute velocities of the reacting system.

The determination of the growth characteristics of single fea- thers forming cross-sections of given plumage tracts and of compo- nents of individual feathers are of particular interest since step- wise increases in dosage of female hormone show that these charac- teristics are the basis for the development of pattern. Furthermore, it is implicit that the relations established in the induced patterns shall apply with equal validity to patterns developing "autono- mously".

Successive investigations of plumage patterns have been pri- marily guided by this point of view and the procedures adopted have in general been to establish the reaction possibilities as such of the growing system by means of increasing, graded hormone dosages which give the point of lowest threshold first, and then, in order of increase, the gradient from that point. The determination of the growth curves of best fit to these pattern gradients presents greater difficulties since the location of the differential is not, apparently, identical for all feather tracts. For instance, in the breast and saddle, the regions first studied, the correlation of linear growth rate and hormone threshold is valid and it is equally true of comparisons between certain tracts, such as saddle and tail. However, within tracts composed of highly asymetrical feathers such as the wings and the tail, the growth partition between the two vane-halves of single feathers is apparently of greater significance in the determi- nation of pattern than is the linear growth rate of entire feathers (FRAPS, in press).

Further investigation will therefore be needed to complete the "physiological map" which the plumage, so to speak, represents but it is definite in its major outlines. Of first importance is that the plumage clearly represents a system of gradients and moreover, it is a system in which the single points (individual feathers) may be evaluated in terms expressive of their growth intensities and other physiological differentials, a prime prerequisite in the quanti-

tative definition of a field or gradient (see FRAPS and JUHN, 1936, Discussion).

The observations of JUHN and GUSTAVSON (1930) already indi-cated the presence of an antero-posterior gradient in rates of growth and in reaction to the female hormone in the breast and saddle of the male Brown Leghorn but these records were obtained from averages of a number of feathers measured in separate areas loca-ted in anterior and posterior regions of the respective plumage tracts. The significant differentials evident from these results sug-gested more detailed investigation with measurements of single regenerating feathers comprising antero-posterior and transverse rows in the plumage of male and female Brown Leghorns, and these, carried out by JUHN, FAULKNER and GUSTAVSON (1931), filled in the gaps of the earlier study and demonstrated a distinct, conti-nuous antero-posterior gradient in rate of growth and hormone threshold in breast and dorsal tracts. Evidence for a transverse gra-dient in the male breast and saddle were also obtained but later measurements suggest that in the breast, the high point is located excentrically within the tract (FRAPS and JUHN, 1936).

Transverse gradients may be demonstrated as transverse sequen-ces of induced patterns and they are also manifest in the "autono-mous" patterns of certain plumages. In either case, for this measure of the transverse gradient, comparisons are made of the relative extent to which specific pigmentation or structural features are res-tricted in opposed vane-halves of single feathers. That is to say, this measure of transverse gradients in the feathering represents ac-tually a measure of the degree of asymmetry of the various feathers comprising such a sequence.

Pattern asymmetries in fully formed feathers find their expla-nation in the recognition of the feather as a bilateral structure from its origin (LILLIE and JUHN, 1932). During the organization of the main part of the feather, barbs destined to form one vane-half are each derived from opposite faces of the ventral triangle which is usually located somewhat asymmetrically opposed to the rhachis primordium. Barb elements which represent successive apico-basal levels and which extend along the collar from the point of origin to the point of attachment to the rhachis describe a gradient which may be shown in their respective thresholds of reaction to the female hormone, the high point being (in breast and saddle) at the ventral locus.

The ventral triangle (in asymmetric feathers, as are the great majority), is clearly organized as an asymmetric field, elements deriving from one face having a higher threshold than elements deriving from the other. This physiological partition of the ventral field carries over in most interesting manner in the formation of the afterfeather, a structure, which in the fowl, occurs only in certain feather tracts. LILLIE and JUHN (1937) describe the main steps in the development of the afterfeather in a preliminary note. At a certain point in the growth of the main feather, the ventral triangle divides to form two daughter triangles, each of which thus corresponds to one half of the undivided field. Subsequent to this partition, one half of the vane of the main feather and one half of the vane of the afterfeather, are each derived from one of these daughter triangles. In saddle feathers of Barred Rock-Brown Leghorn hybrids, there often is a very distinct separation of black and white in the fluffy region. The transition occurs frequently along transverse levels but occasionnally asymmetric markings are encountered. In these last, homologous portions of main- and afterfeathers vane-halves are identical in colour. That is, elements deriving from one daughter triangle and growing through similar periods, are similarly pigmented. The controlling mechanism here is undoubtedly strictly comparable to the one effective during formation of the vane of the main feather, in the phase of the undivided ventral field, and through which induced patterns may be restricted to one vane-half.

This analysis into component physiological attributes of the feather germ lead to the recognition of the significance of certain patterns induced in transverse feather rows in either of the paired breast tracts of the Brown Leghorn male. These have not been specifically described but are mentioned in a series of papers (JUHN and FRAPS, 1934, HOLMES, 1935; FRAPS and JUHN, 1936). In these experiments, use was made of the differences in threshold of opposite vane-halves of single feathers to the female hormone and very low dosages were employed for the reasons outlined earlier in this paper. The injections were always given on alternate sides of the bird's body and at a distance from the feather tracts. This point requires emphasis since GREENWOOD and BLYTH (1935) describe asymmetrical patterns in the breast tracts of the Brown Leghorn male which they attribute to direct modification by diffusion of the hormone from the point of injection, located within the tract; and which, while of undoubted interest and importance, can scarcely be interpreted as relative to the problem of asymmetry as such.

In the experiments of JUHN, a system of numbering was adopted so that each modified feather could be located with reference to position in the breast tract and compared directly with predecessor and successor generations. The transverse rows selected were the ones into which the plumage readily separates. Each such row forms an angle with excentric peak. The feathers are numbered according to position: no. 1, is medial, no. 6, at the peak, and no. 9, at the lateral margin. Sequences of transverse rows were distinguished as a, b, c, etc. in antero-posterior order. Relatively symmetrical female salmon marks were found in the number 6 position, but feathers from positions no. 1, and no. 9, showed asymmetrical female marks, that is, marks restricted entirely or predominantly to one vane-half, and these asymmetric marks were mirror-images of each other, clearly indicating a center of symmetry w i t h i n each breast tract.

This observation pointed toward some connection between the order of origin of the embryonic papillae and the order of asymmetry shown by the patterns of the feathers which these papillae later proliferate.

The embryological investigation, carried out by ANNE HOLMES (1935) showed as a fact, that the feather papillae first to form were in positions corresponding to the number 6 of the adult, and that papillae to the right and left of this first, corresponding to positions 5 and 7, arose simultaneously but somewhat later, and so on. The analysis of the extension of the papillae along their position lines in anterior and in posterior direction is of very definite interest but not of immediate relevance to the problem under discussion. Here it is of significance to note only the correspondence between the order described by the forming papillae with reference to the first to arise, the center, and the order of symmetry, with reference to this same center, shown by the patterns of the feathers from these papillae and described in the preceeding lines.

HOLMES' study was not restricted to the embryology of the breast tracts alone but included the majority of the plumage regions so that we now possess a most valuable source to which analysis of adult patterns or of juvenile pattern sequences may be returned. In the greater number of feather regions, HOLMES found the papillae first to arise to form an unpaired line, more frequently excentrically located as in the breast, but sometimes coincident with the mid-line of the body of the bird, as in the saddle.

Of considerable interest are those plumage regions which differ from the ones described in having two lines of papillae forming simultaneously with papillae later arising to each side and between them. Examples of this order of origin are found when the dorsal tracts are followed in anterior direction. In the saddle, the first line of papillae is unpaired, in the back, the line forks and continues paired but separated by a space which increases in anterior direction, in the cape one follicle fills into this space, and more anteriorly yet, the space between the two first lines of papillae increases and a greater number of follicles come to occupy it.
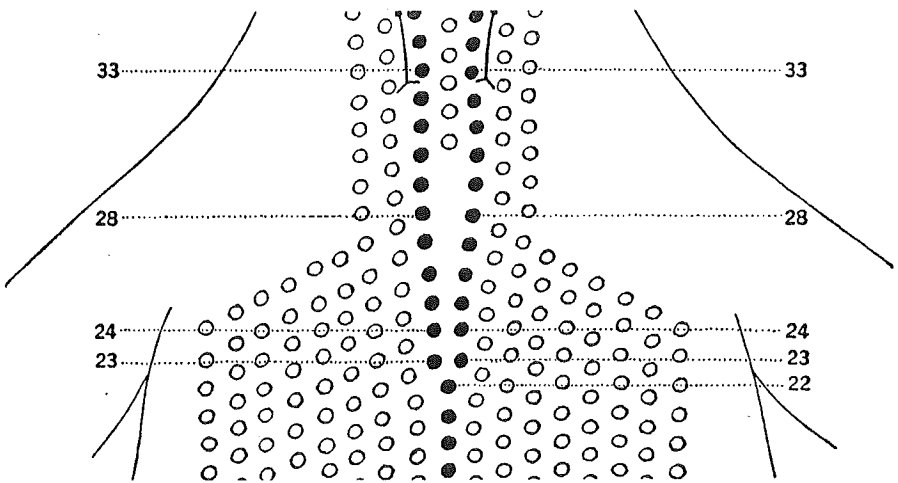

Fig. 1.

From HOLMES, figure 5, diagram of the dorsal tracts. Included here are the anterior region of the saddle, to no. 22; the back, to no. 28; the cape, to no. 32. The solid disks represent the papillae arising simultaneously, the circles the papillae subsequently forming. See text.

Figure 1 is a segment, taken from HOLMES' figure 5, a diagram of the dorsal tracts, and it is representative of the situation under discussion. The solid disks indicate the papillae of the lines of origin of the tract: to number 22, they represent the saddle, to number 28, the back, to number 33, the cape and from there on they continue into the hackle and the head. It is to be noted that these regions grade into each other so that the numbers indicating their extension in the long axis are approximate.

The feather area analysed here is the cape, where, according to HOLMES' (page 526) "The first papillae in this region arise as an anterior extension of the lines of origin of the back and are indicated in the diagram by papillae 29—32 (solid disks) on each side of the backbone. Laterally, successive rows of papillae of the second and third order arise, toward the outer margins of the tract, and a central line of papillae arises between the two lines of origin . . ."

In the adult Brown Leghorn male, the more posterior feathers of this area are reddish orange, barbule-free at the barb tips in the apical segment, and greenish black, fully barbulated, in the basal vane segment. The apico-basal extent of the black portion differs in opposite vane-halves of certain of the feathers composing single transverse rows and it is this difference in extent of black which is used here as a measure of the asymmetry of the individual feather.
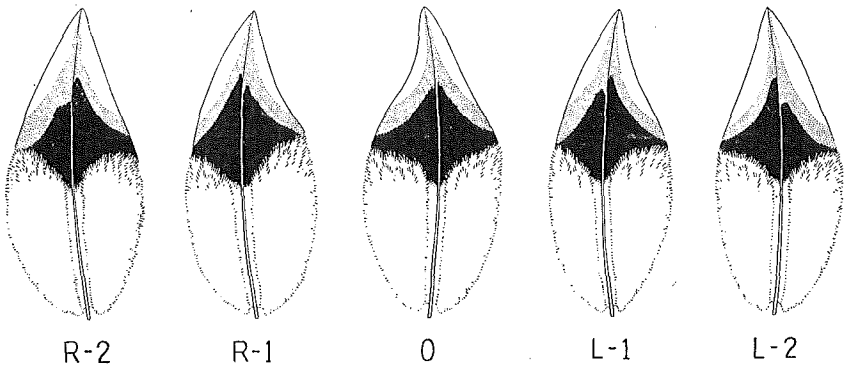

R-2   R-1   0   L-1   L-2

Fig. 2.

Drawings of the five central feathers of the cape from Brown Leghorn ♂ 8414. Feathers nos. R–1 and L–1 are grown from the papillae of simultaneous formation, feathers nos. 0, R-2 and L-2, from the papillae arising subsequently. See text.

Figure 2 represents feathers grown from the papillae of the positions given by HOLMES: Nos. R—1 and L—1 are from the papillae first and simultaneously to form, the solid disks of figure 1. No. 0 is from the papilla which arises between these two lines of origin, and nos. R—2 and L—2 are from the papillae which arise laterally. Feathers from further lateral positions are not drawn; their asymmetry accords with that of nos. R—2 and L—2 respectively

but increases in degree with increasing distance from the line of origin.

The feathers illustrated are from Brown Leghorn ♂8414 and were drawn to scale by Mr. Kenji Toda, staf artist of the department of Zoology.

When the feathers formed from simultaneously originating embryonic papillae are compared for pattern distribution in opposite vane-halves, it is seen that the feathers no. R—1 and L—1, grown from the paired papillae first to arise, are slightly asymmetrical in pattern and that they are mirror-images. In each of their lateral neighbors, feathers nos. R—2 and L—2, the asymmetry reverses and becomes opposite; R—2 and L—2, accordingly, also are mirror-images but with more pronounced asymmetry than in the first pair. Feather no. 0, proliferated from the papilla which arises in the embryo between the two lines of origin, is obviously relatively symmetrical.

The order of pattern asymmetries in the cape coincides in certain significant points with the situation as it is found in the breast tracts but differs in certain others; such differences as occur probably find their explanation in the presence of two centers in the cape as compared to the single center of each breast area.

We may distinguish for convenience in comparison, center feathers, and feathers of medial and lateral series. In the breast, the center feathers are symmetrical, with pattern asymmetries reversing to either side. In the cape, the center feathers each show a slight asymmetry and pattern reversal occurs only in the lateral feathers and with immediate reference to these centers. When the lateral series of the cape are compared with lateral and medial series of the breast, it is seen that all three coincide in having increasing degrees of asymmetry associated with increasing distance of position from the center (Juhn and Fraps ,1934; Fraps and Juhn, 1936).

The differences in the two tracts, consist in a: the slight asymmetry of the center feathers of the cape as opposed to the symmetrical center feather of each of the breast tracts, and b: the occurence of the symmetrical feather, no. 0, of the cape to which no direct opposite exists in the breast. It seems entirely possible however, to advance an interpretation harmonizing these apparent incongruities. We have seen that in the breast feathers of progressive

distance position from the center show increasing degrees of asymmetry of pattern. We may consider these evidence for the action of embryonic field forces. These forces originate in the position of the tract which the papilla first to form will occupy later. From this point there is a distribution of forces which may be interpreted as either increasing, if we believe that asymmetry is impressed upon originally symmetrical follicle primordia, or as decreasing, if we believe that the asymmetry is primary and that relative decreases are imposed upon the primordia. Whichever alternative may be adopted, the actual observations clearly show a quantitative gradient, extending in the breast, from the center, in medial and in lateral direction.

To these gradients in the breast, the lateral gradient in the cape is precisely similar. There accordingly is no reason for questioning, in the cape, the presence of gradients, extending from each center in medial direction. The patterns of the two center feathers and of the no. 0 feather appear, in fact, to demonstrate their presence clearly. The paired papillae first to arise (see figure 1, solid disks), form in relative proximity and in each the slight asymmetry (see feather patterns, figure 2, nos. R—1 and L—1), may well be ascribed to the action of a medially directed force from the opposite center. Following this reasoning, we should expect to find the feather of the papilla which arises between the centers, at points of section of these medial gradients, to be symmetrical, and this is again the case (see figure 2, no. 0).

Pattern development in the cape is thus seen as but another example of the action of the sequence of determinative processes which have been postulated for the plumage in general and which are supported by studies of the embryology of feather tracts, the dynamics of feather growth in the normal juvenile and adult, as well as by conclusions from experimental modifications. The adduced evidence must be consulted in the pertinent articles, some of which are cited here, but the general hypotheses may be briefly reviewed in conclusion.

The separate plumage areas are believed to arise as segregates in the sense of LILLIE (1929). These segregates are assumed here to differ quantitatively only (JUHN, 1938). Within each of the segregates, embryonic gradient forces are thought to act for very limited periods but as imposing persistent, quantitative, "residual" fields (FRAPS and JUHN, 1936).

These quantitative residuals, established as differentials between tracts, between feathers of single tracts and between components of single feathers, are considered the pattern determinants since given pigmentation or structural features are clearly limited to given dynamic levels. It has been emphasised consistently that these differentials determine the d i s t r i b u t i o n of characters only and nowise participate in their origins. Significant interpretations of early development may be expected from further studies from WILLIER's laboratory since it is already reported (WILLIER, RAWLES and HADORN, 1937), that headskin from black embryos grafted to wing positions of white hosts forms black wing tissue, showing apparently that at the time of grafting the feather gradients develop according to host position but that pigmentation is independent.

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