HEAD MOVEMENTS AND EYE FUNCTIONS OF BIRDS

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The forward and apparent backward movements of the head which pigeons, chickens, and certain other fowls display while walking have been commented on by various persons orally, but seldom in print. In general, it seems to be assumed that these movements result, more or less incidentally, from the act of walking itself, being somewhat comparable to the swinging of the arms of a human being or the flopping of the ears of a mule. But this, we shall see, is an erroneous supposition. To the casual observer it also appears that as a chicken or pigeon walks along the head is moved forward, allowed to go backward somewhat, and then thrust forward again; even after some rather careful observations, the senior author still retained the impression that the pigeon's head moved back slightly. Martin A. Mikesh[1] contended that the backward movement is illusory, that the fowl's head goes forward only, and that during the apparent backward movement the head is really at rest. But so far as we know, no crucial photographic study, which would permit a definite analysis of this point, has ever been previously attempted. In view of its bearing upon the general problems of vision, equilibrium, and vestibular functions, in addition to its intrinsic interest, the problem seemed to be of sufficient importance to warrant making a series of motion pictures of certain birds during pedestrial locomotion and of their reactions to certain passive bodily movements. Thus far, the study has been restricted to pigeons, chickens, starlings, and ducks; but sufficient data have been obtained to prove that the apparent backward movements of the

[1] Quoted by E. E. Slosson: Catching up with the world. Collier's, January 15, 1927. Dodge has expressed in conversation the same opinion regarding the pigeon. Mickesh's opinion that other domestic fowls show the same phenomenon does not hold for ducks and geese.

head are illusory and to suggest a host of problems of more than passing interest.

In order to obtain a performance of the birds which could be satisfactorily photographed, a special walk was constructed, 12 feet long, 21 inches high, and 15 inches wide, and elevated about 4 feet above the floor of the room in which the experimental work was done. The back and floor of the walk are of oiled redwood, which gives a photographically dark background; the top is of poultry wire, while the front is constructed so that it may be either left open or covered with wire. Only when working with starlings was it necessary to cover this side of the walk. To facilitate analysis, three-eighth inch strips of white celluloid were fastened vertically on the back of the walk about 3 inches apart with every fourth strip slightly taller than the others, for purposes of identification.

The birds were placed at one end of the walk with food at the opposite end. After a few feedings, sometimes after one feeding (apparently fowls have "insight"!) they would go to the other end of the walk immediately upon being released.

The pictures were taken indoors with a Bell and Howell 16 mm. camera, having two speeds—16 and 32 frames per second. Two mercury-vapor arcs were used for illumination, in addition to ordinary daylight. In preliminary work, the bird was followed by the camera along the entire length of the walk. However, for final work the camera was fixed in position, focused on a section of the walk, and the fowl allowed to walk by it repeatedly. The 24 pictures in Plate I are reproduced from successive frames comprising the major part of a strip of film resulting from one walk by the camera running at 32 frames per second.

It will be seen by reference to the plate that there is no real backward movement of the head at any time during the pigeon's excursion along the walk. Invariably the head is thrust forward and then stopped momentarily, although the body continues to advance and is sometimes well up under the head, bringing the neck into a position of acute flexion, before the next forward thrust is made. Behavior of this type may easily give one the impression that the head is in alternate forward and backward motion, but reference to the background of the picture shows definitely that the head moves backward only in relation to the rest of the body but never as far as its position in absolute space is concerned.

Chickens and starlings in walking make head movements of the same general type as those made by the pigeon, but the forward thrust of the head is somewhat more irregular, there being sometimes one, sometimes two or more such movements distinguishable during a single step. Careful examination of our films, however, reveals that there is never any real backward translation of the head.

In the case of the duck, the relative movements of the head and body in walking are quite different from those of land fowls: the head moves forward at the same rate as the body, with no significant flexion of the neck in the plane of progression. Like most water-fowl, the duck has a sort of drunken-sailor gait, the body rolling from side to side considerably as it walks; however, there is a nice compensation for this, the neck flexing so that the head moves forward in practically a straight line. That these as well as other differences in the behavior of ducks and land-dwelling fowls are due to variations in native habitat and characteristic mode of locomotion seems to be a highly plausible hypothesis, but one which must await further investigation before it can be fully verified.

Birds which ordinarily hop instead of walk have not as yet been included in our photographic study for the reason that they do not display conspicuous head adjustments during locomotion. However, for purposes of comparison, if for no other reason, an investigation of their peculiar mode of progression and the problems of vision involved therein would doubtless be worth while, and we hope to be able to carry it out eventually.

The fact that the progression head movements of land fowls seem, in general, to synchronize rather closely with phases of the leg-movement cycle would naturally suggest that kinesthesis arising from the legs may be an essential part of the stimulation pattern of the head thrusts. But this possibility is eliminated by the fact that when the fowl is carried either forward or backward by the experimenter, the same type of head movements are manifested as normally occur in walking. However, if the speed at which the fowl is carried is so rapid that adequate head compensation is physically impossible, virtually all head movements are abandoned, and the head is thrust forward and held in much the same position as that displayed by a rapidly running chicken or a flying bird. Miles[2] has studied the pursuit movements of the eyes of human beings during linear progression and has found that these movements are adequate only when the subject moves past the visual field rather slowly. As the rate of progression increases, pursuit movements become increasingly inadequate until finally they disappear almost completely, giving the subject the impression that the visual field is rushing past him and that he is more or less stationary.

It occasionally happens, especially in a novel environment, that a fowl, when carried, does not make the simple walking type of head adjustments described above, but resorts to "peering" movements, which consist either of moving the head into various planes by means of flexing the neck and then thrusting the head away from the body in a different direction, or of simply changing the angular position of the head with reference to the neck and the rest of the body. This type of behavior is apparently due to the rather restricted field of vision of the bird at any given instant and the resulting necessity, despite the presence of two or more retinal foveas in some species, of moving the head into a great number of different planes in order to permit a complete survey of the total surroundings. These peering movements should not be confused with head movements of progression, and should be carefully differentiated from the latter, both in respect to their general character and cause. (Plate II.)

In addition to these two types of head movements in fowls, there is still another type which deserves mention. It has often been noted that when adult chickens are held in the hands and moved about carefully, they will frequently move the head with reference to the body so as to keep the head in a fixed position

[2] Miles, W. R.: Visual illusions of motion during train travel. Journal of General Psychology, 1929, ii, 141–143.

in space, no matter how the body is moved, providing, of course, that the limits of stretch and flexibility of the neck are not exceeded. If these limits are exceeded, the peering or progression type of head movements result; but, unless the speed of movement is excessive or the fowl greatly disturbed emotionally, the head never moves uniformly with the body. The senior author began a study of this phenomenon with motion pictures in 1926, and we have carried the work further this year. Pigeons and starlings have been found to show much the same type of behavior in this connection as do chickens, although the compensation never seems to be quite so perfect. (Plate III.)

Ducks, on the other hand, show a distinctly different type of behavior in this respect. When the body is moved in the vertical plane, the head compensates in much the same fashion, though not so adequately, as in the chicken; but for short to and fro longitudinal and transverse movements, the head travels with the body, sometimes even exceeding the distance which the body travels. When the duck is oscillated moderately about the vertical axis, the neck remains rigid and the head swings with the body, but when oscillated about either the transverse or longitudinal axis, excellent head compensation is obtained. Adding a slight up and down movement to oscillation about the transverse axis produces the most striking head compensation of any type of motion. It has also been found that the duck will continue to gobble food from an assistant's hand when the body is moved or oscillated vertically, but as soon as any kind of horizontal motion is introduced, feeding is seriously interfered with, the head tending to move with the body or sometimes further than the body in the same direction.

These differences between the duck and the land fowls are at first surprising, but appear reasonable enough when we consider that much of the duck's existence is normally spent bobbing up and down on waves with comparatively little motion in the horizontal plane, whereas birds which spend a considerable portion of their time walking about on land move far more in the horizontal than in the vertical plane and might naturally be expected to display superior adaptation to horizontal motion, whether it be of the active or passive type.

Except for oscillation about the longitudinal, or anteroposterior, body axis (which seems to involve peculiar kinesthetic and vestibular factors), these compensatory head adjustments, both in land and water fowls, disappear as soon as the eyes are blindfolded. The same is true of peering movements as well as the movements which ordinarily occur when the bird is carried by the experimenter. A blindfolded fowl rarely walks spontaneously, but may be made to walk in a fairly normal manner by being guided by the experimenter's hand. But even in this case there are no conspicuous head movements, thus demonstrating rather convincingly that compensatory head adjustments, at least those varieties considered above, are prompted almost exclusively by visual stimulation. There are, of course, the peculiar nystagmic movements which result from protracted rotation; they have been found to involve a curious mixture of visual and vestibular stimulation, but this type of behavior, along with the head movements involved in pecking, defense reactions, and adjustments produced by auditory stimuli, lie beyond the scope of the present paper.

The types of movement which are of primary concern to us here may be listed as follows:

I. Head movements which occur when the fowl walks normally or is carried by the experimenter.
II. Head movements which are involved in the act of "peering."
III. Head movements which occur when the fowl is moderately oscillated or moved to and fro through short distances.

These movements in turn may be reduced to a still more fundamental classification:

A. Head movements which represent an attempt to retain the existing visual field, and which are analogous in function to the pursuit, or "drift," phase of human eye movement.
B. Head movements which result in a shift of the visual field, and which may be functionally compared to the quick, or "saccadic," movements of the human eye.

It will be seen that compensatory head movements resulting from both linear and angular oscillation of the body, along with the apparent backward phase of walking head movements, fall into A of the above classifications; they are produced by an attempt on the part of the bird to hold the region of visual fixation as long as possible. Peering movements and the forward thrust of walking head movements, on the other hand, fall into the other class, their purpose being that of shifting the visual field.

At this juncture a rather complicated question arises: If compensatory head movements (with the exception of those produced by oscillation about the longitudinal body axis or by protracted rotation, noted above) are prompted exclusively by visual stimulation, how is it that a constant visual field, such as exists when the head and body are both at rest, may not produce any specific head movements, yet when the body is in motion, if the head is really at rest, what is it that causes the head to compensate and thus remain at rest, at least as long as the physical construction of the neck permits? In other words: How can visual stimulation produce head compensation to bodily motion unless that motion is apparent, and how can this motion be apparent unless the head moves sufficiently to produce a perceptible change in the position of the head with reference to the visual field? Or, in other terms: How can a stimulus produce a protracted response (the slow compensatory adjustment of the head) which, theoretically, eliminates the stimulus (the motion of the environment with reference to the head)? Leg and body kinesthesis have already been eliminated as essential causative factors in the production of compensatory head movements, first, by the fact that head movements occur even when the legs are held in a fixed position and the body carried by the experimenter, and second, by the fact that, once the bird is blindfolded, the stimulation arising from the act of walking does not produce head movements to any appreciable extent. A somewhat dubious alternate explanation is, that the head is not actually at rest, as the pictures in Plate I would seem to indicate, but is moving forward very slightly, just enough to produce sufficient change in the bird's visual field to prompt the compensatory effort. At present, however, even this explanation is only conjecture, for we have no experimental data relevant to this point; in fact, it is difficult to see just how an experimental technique suitable for investigating this problem could be worked out, except, possibly, by an elaboration and refinement of the photographic method, and even then, in the advent of negative results, there would be no assurance that the method had been adequate.

It seems evident, whatever the immediate causal mechanism may be, that the purpose of the head adjustments above discussed is primarily that of providing the fowl with a series of sharp visual images during both active and passive bodily movement. In the human being this end is accomplished by some mechanism, as yet obscure, which renders the eye anesthetic during the greater part of the saccadic movement[3] and permits visual impressions to be recorded only while the eye is at rest or moving very slowly in the socket. In fowls it is not yet certain whether or not the eye is blind during quick eye movement, as in humans; but our photographs show quite clearly that vision is prevented during quick head movements by the act of nictitation, or pseudo-blinking. During virtually all rapid head adjustments, including both those which occur during natural locomotion as well as those resulting from passive movement, the thin, translucent membrane, sometimes referred to as the third eyelid, flicks across the eye, thereby temporarily blinding the bird and excluding the troublesome blur which might otherwise occur.[4]

It has been found that nictitation in the chicken is sufficiently slow to be readily observable and can usually be photographed with the camera running at the rate of 16 frames per second. But in the pigeon the act is difficult to note and can be adequately photographed only at 32 frames per second. Nictitation occurs not only during spontaneous head movements but also during forced head movements, either linear or angular, providing that these movements do not occur in too rapid succession and are of

[3] Holt, E. B. Eye-movement and central anesthesia. 1903, Harvard Psychological Studies, Vol. I. (Psychological Review Monograph Supplements, No. 17), p. 1–45.

[4] This statement holds for adult and nearly mature birds of the varieties employed. For some varieties of pigeon, and for certain other birds, the statement apparently needs modification.

sufficient magnitude and vigor to be comparable to spontaneous head movements. This suggests that nictitation may, at least in these cases, be of vestibular or perhaps kinesthetic origin, but since the elimination of visual stimulation also eliminates the possibility of observing nictitation itself, this point is as yet unsettled.

There is also a periodic nictitation which seems to be fairly independent of any kind of head movement; its purpose, apparently, is to insure a constant and uniform supply of lacrimal fluid to all parts of the cornea. At least this supposition is supported by the fact that nictitation persists, though less frequently, even when the real eyelids are closed. Nictitation may, in addition, have the function of protecting the eye from threatening objects or from very intense light. It also seems likely that it is in some way connected with visceral disturbances; but more definite information of this point, as well as on several other questions raised in this paper, will have to be postponed to later parts of our work.

PLATE I. ENLARGEMENTS OF SUCCESSIVE FRAMES IN A MOVIE FILM OF A PIGEON WALKING, TAKEN AT 32 FRAMES PER SECOND

The order of succession is downwards in the columns, commencing at the left. The camera was fixed in position, the pictures therefore showing the same sixteen vertical stripes in each.

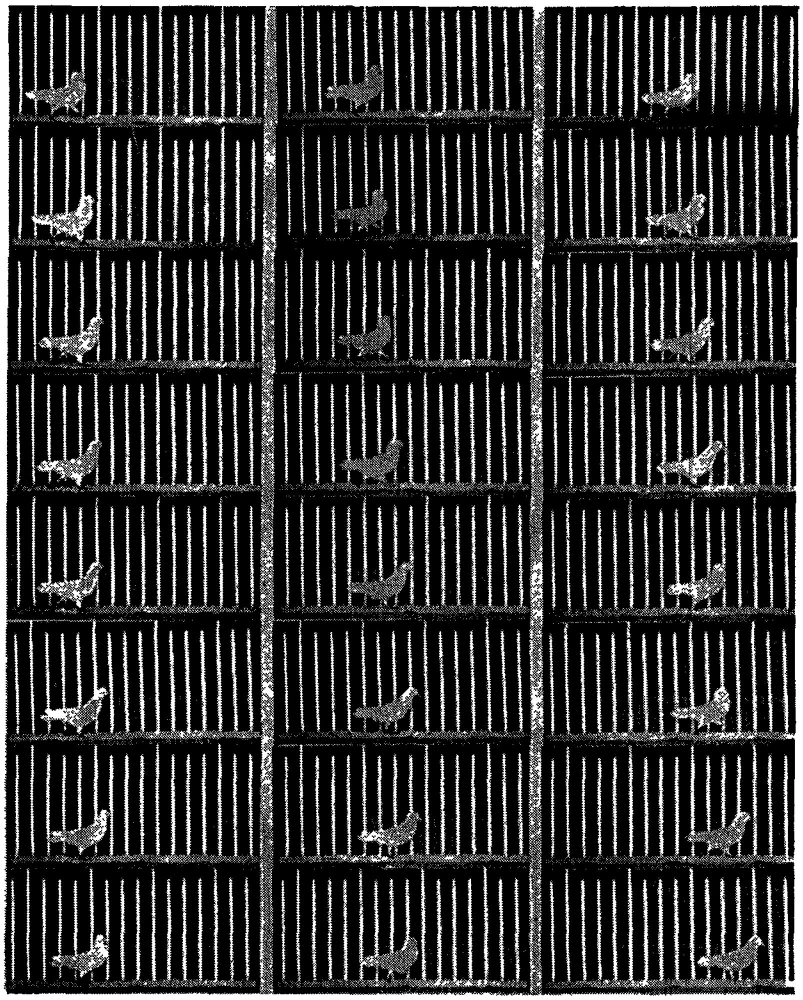

PLATE II. PEERING MOVEMENTS OF A PIGEON WITH STATIONARY BODY

In order downward from the upper left, the frames are selected at intervals of from $\frac{1}{8}$ sec. to $\frac{1}{2}$ sec. from a film taken at 16 frames per second, to show successive head positions in typical "peering."

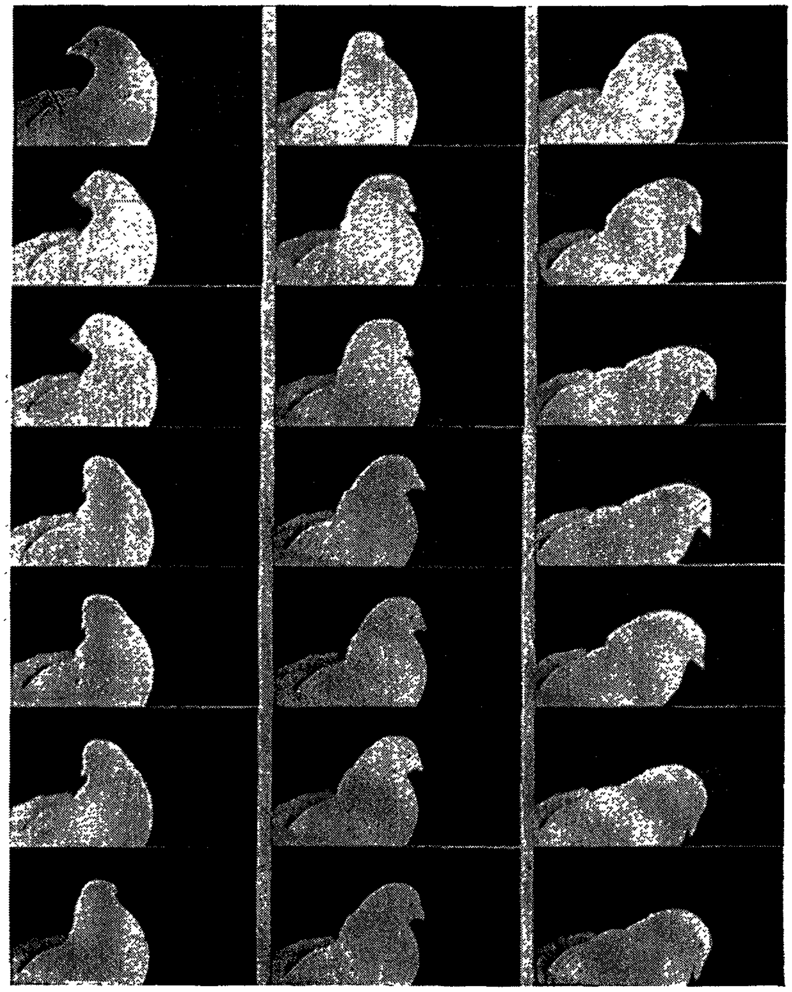

PLATE III. FIXATION ADJUSTMENTS OF FOWL WITH BODY IN LINEAR MOTION

In order from the upper left downward, the pictures present 21 frames from a total series of 50 taken at 16 per second, the fowl's body being moved backward and then forward approximately 7 inches in each direction during the series. These are alternate frames, except in the middle of the series where the direction of motion of the body was reversed. The camera was fixed, and the left edges of the pictures are the vertical reference lines.