J. exp. Biol. (1978), 74, 187–195
With 6 figures
Printed in Great Britain

THE OPTOKINETIC BASIS OF HEAD-BOBBING IN THE PIGEON

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(*Received* 19 *September* 1977)

SUMMARY

1. Head-bobbing of pigeons during walking and landing was studied using high-speed motion photography.

2. The analysis of film records indicated that head-bobbing whilst walking consists of two phases: one where the head is 'locked' in space but moves backward relative to its forward moving body; and another where it is thrust rapidly forward to a new position.

3. The fact that head-bobbing is abolished when pigeons walk on a treadmill suggests it is primarily a visual response rather than an equilibratory response.

4. Data are presented which show that stabilization during the 'lock' phase allows a small degree of slippage which is the probable source of error signals for compensatory head movements.

5. The head-bobbing that appears to occur during landing is shown to be illusory.

INTRODUCTION

Perhaps one of the most striking features of avian locomotion is the apparent forward and backward movement of the head during walking. This behaviour occurs in at least 8 of the 27 orders of birds including relatively common species such as pigeons, doves, hens, starlings, pheasants, coots, rails, sand-pipers, phallaropes, parrots, magpies and quail. Although head-bobbing is described by some authors (Fremlin, 1972; Kare, 1965; Walls, 1967) as a 'forward and backward movement of the head' it in fact consists of a phase where the head is 'locked' in space (but moves backward relative to the forward moving body), followed by another phase where it is rapidly thrust forward to a new position. The fact that the head is so well stabilized during the stationary phase of head-bobbing suggests that it is equivalent to the pursuit phase of optokinetic head movements where head velocity almost perfectly matches stimulus velocity. Dunlap & Mowrer (1930), and more recently Friedman (1975), have shown that these head movements appear to be under visual control and that they are neither initiated by the vestibular system nor synergistic with leg movements.

The experiments to be reported here were designed to investigate head-bobbing with a view to relating this behaviour to the adaptational properties and asymmetries of directional specificity of broad-band motion specific units in the pigeon optic tectum (Frost & DiFranco, 1976). The first series of observations were aimed at characterizing the head-bobbing itself, while a second series of experimental observations of birds walking on a treadmill were designed to see if head-bobbing was a visual or equilibratory response. Finally the apparent head-bobbing which seems to occur just before landing was also studied.

MATERIAL AND METHODS

Head-bobbing records were made by motion photography with a Bolex H116 reflex 16 mm camera using Kodak Tri-X film typically shot at 64 frames/s. Head, breast, wingtip and foot positions were measured by projecting single frames of the movie, at exactly twice life size, onto a tracing paper screen with a LW Photo-Optical Data Analyzer Model 224-A projector equipped with a frame counter and single frame advance mechanism. To characterize the head-bobbing behaviour under relatively natural settings, observations were made on feral pigeons whilst they were walking on relatively flat terrain at various sites on the university campus. An analysis of these films indicated that head-bobbing consisted of two phases, one in which the head appeared to be 'locked' in space, while the body moved forward, and another phase where the head was thrust rapidly forward to a new position. Two alternative hypotheses concerning the functional significance of head-bobbing were considered: one which supposed the head movements were primarily to maintain the equilibrium of the bird during walking; and alternatively that it was primarily a visual response involving periods of stabilization of the bird's visual world.

To differentiate between these two explanations experimental observations were made on the head movements of male white Carneaux pigeons (Palmetto Pigeon Plant, Sumter, S.C.) whilst they were walking on a treadmill. The treadmill consisted of a tightly stretched 13·6 cm wide canvas belt placed around 5 cm diameter rollers, one of which was driven by a Bodine Fractional Horsepower Gearmotor and speed control unit. A steel plate located just under the top surface of the canvas belt provided a solid 39·0 × 13·0 cm walking surface for the bird. To stop the bird from dismounting at will (or taking off when flying speed was reached) a clear plexiglass box measuring 47·7 × 17·0 × 32·6 cm was placed over the treadmill. This box also permitted the bird a relatively unobscured view of its surroundings. It was found that the pigeons quickly adapted to the treadmill apparatus and could be readily induced to walk when the motor speed was set to an average walking speed.

RESULTS

The analysis of movie film of feral pigeons walking is presented in Fig. 1 where the spatial position of the head (eye), body (breast) and feet is presented as a function of time. This record is typical of many analysed and reveals the following salient points: (1) during walking the pigeon's head movement consists of two phases, one where the head is 'locked' in space (but moves backward relative to the forward moving body), and another phase where it is thrust rapidly forward to a new position; (2) the body moves forward at a relatively constant velocity; (3) the head-bobbing movements are not necessarily related to leg and foot movements of the bird. A pictorial representation of the movements of various parts of the body of white

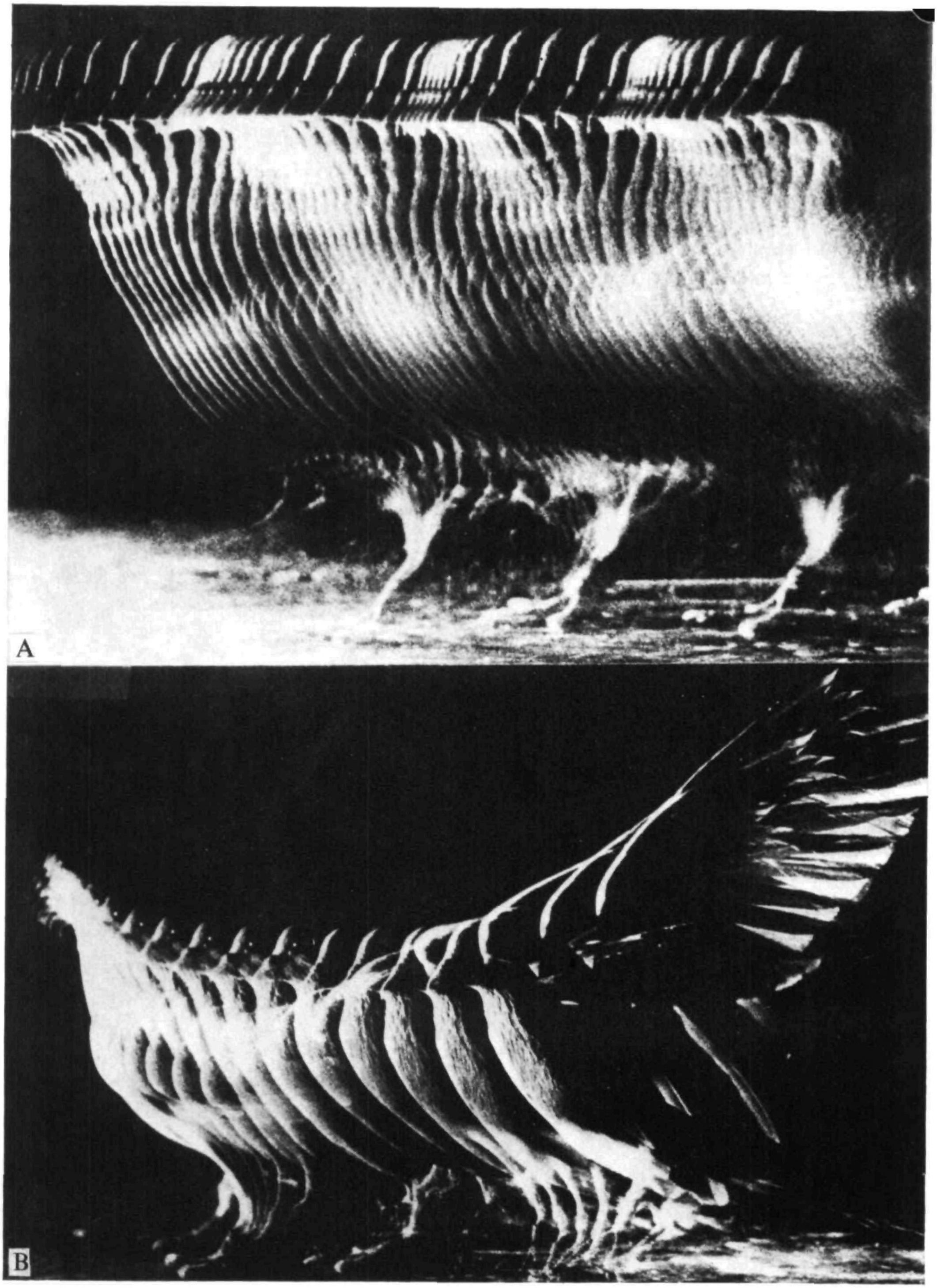

Fig. 2. A: Stroboscopic photograph of pigeon walking showing the typical 'hold and thrust' action of head-bobbing. B: Stroboscopic photograph of pigeon landing showing smooth trajectory of head although head-bobbing is often reported during this manoeuvre.

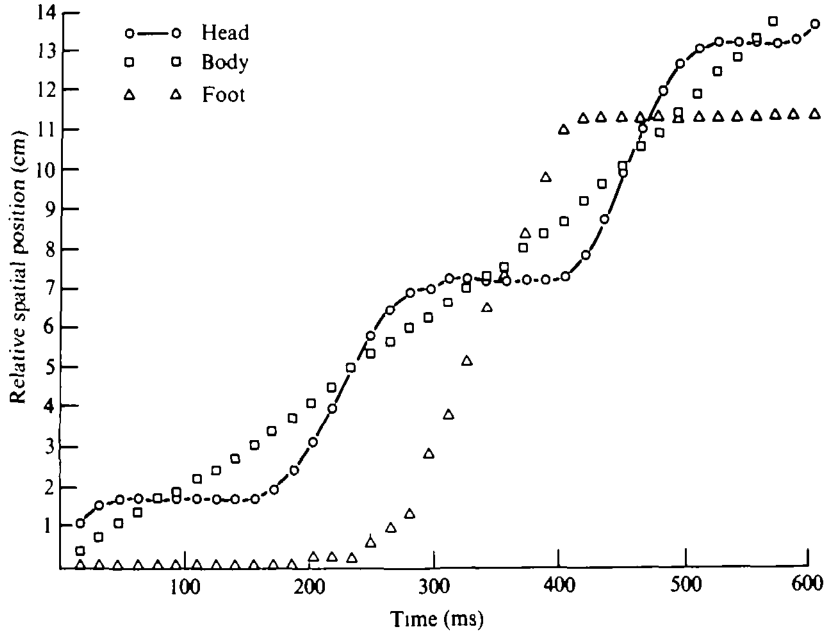

Fig. 1. Pigeon head, breast and foot position as a function of time, during normal walking. Data points were obtained from a frame by frame analysis of movie film shot at 64 frames/s. Note the characteristic 'hold and thrust' pattern of head movements, where the head is apparently locked in space for a period of time, and then rapidly moved forward to a new 'hold' position.

Carneaux pigeons during walking, and just prior to landing, is presented in the stroboscopic photographs in Fig. 2.

From sections of record similar to that presented in Fig. 1 the velocity of forward head thrusts has been calculated to be approximately 0·61 m/s, and the percentage of time the head is stationary during walking is approximately 63 %.

When pigeons were placed on the treadmill, and walking induced, the normal hold and thrust type of head-bobbing described above was abolished. If the bird's walking velocity matched the belt velocity then no head-bobbing movements were produced. Normally, however, there were minor momentary discrepancies between walking speed and belt speed, resulting in small forward and backward oscillations of the body which in turn occasionally precipitated a slight adjustment in head position. Fig. 3 shows measurements of the spatial position of head (eye), body (breast) and foot taken from a section of film where the bird was walking on the treadmill at the relatively fast speed of 60 cm/s. This pattern of responses was quite typical of all treadmill data and shows that the head was held still for considerable periods of time and only slight positional changes were produced. During normal walking, however, several hold and thrust movements would have occurred in an equivalent period of time or over an equivalent distance.

While filming head movements of birds on the treadmill a serendipitious observation was made on one pigeon which helps converge on an explanation of head-bobbing. After completing the filming of a particular bird, the treadmill was inadvertently turned to a very slow setting instead of completely off as intended. After

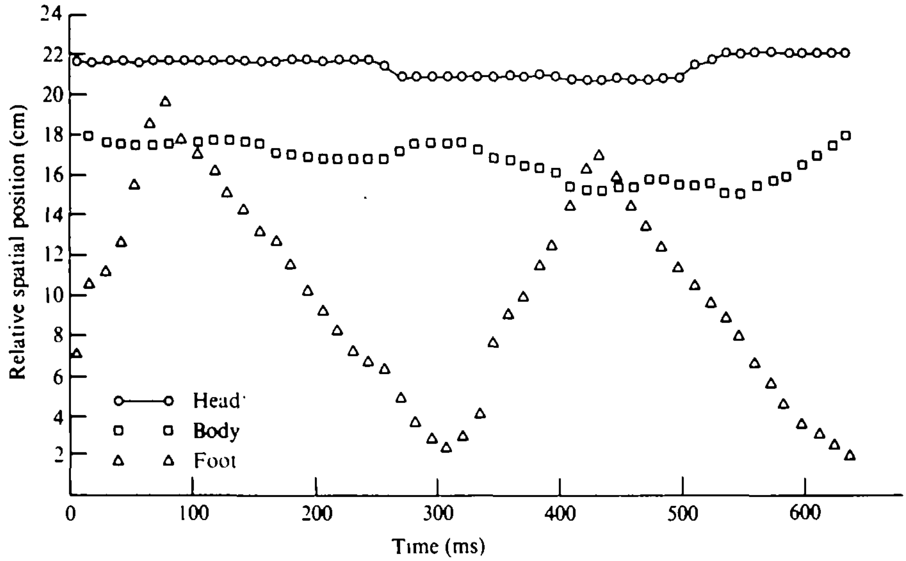

Fig. 3. Head, breast and foot position as a function of time for a pigeon walking on a treadmill moving at 60 cm/s Film shot at 64 frames/s. The 'hold and thrust' head movements typical of normal walking have been abolished.

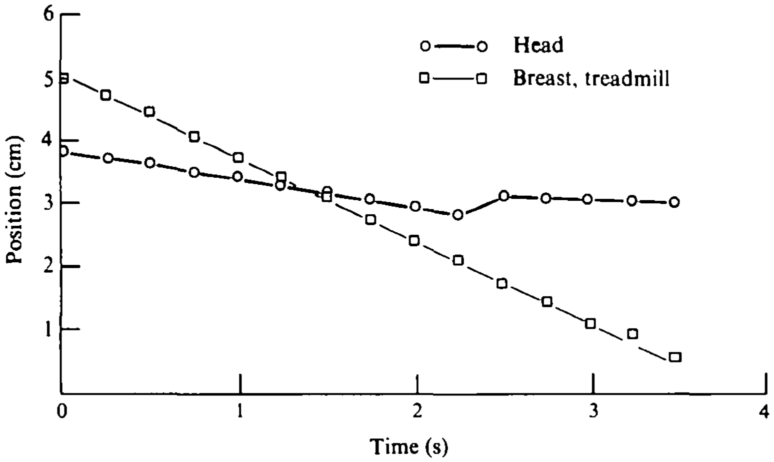

Fig. 4. Head and breast position as a function of time for a pigeon moved very slowly backward on a treadmill so that no walking was induced. Belt speed of treadmill 1·2 cm/s. Film shot at 16 frames/s. and positions in every fourth frame plotted. The bird exhibits attempted head stabilization but a slow slippage is apparent.

a short time we noticed that the bird's head was slowly and progressively pushed forward until it eventually toppled over. Further observations indicated that toppling, or extreme changes in posture, could also be produced by very slow forward (opposite direction to that eliciting normal walking) treadmill movements. It appeared that the extremely slow (imperceptible to us) speed of the treadmill was not sufficient to induce walking in the bird, but was sufficient to stabilize its head even though this sometimes resulted in loss of equilibrium.

Some time later we attempted to film this behaviour but with limited success, possibly because the treadmill no longer operated reliably and smoothly at very

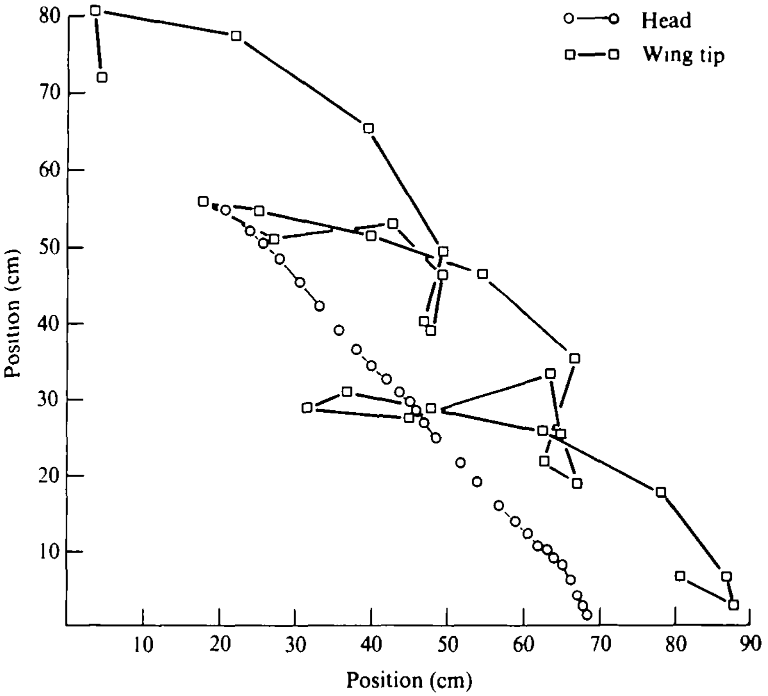

Fig. 5. Changing head and wing positions during landing. Film speed 64 frames/s. Positions on successive frames are plotted and these points joined. Note that the trajectory of the head is smooth thus suggesting that the apparent head-bobbing observed under naturalistic conditions, and when the movie is projected, is illusory and due to wingbeat patterns.

slow speeds. Nevertheless, data similar to that presented in Fig. 4 were obtained, where it can be seen that at relatively slow speeds where no walking is induced, head stabilization occurs but is less than perfect. Slippage of approximately 3·6 mm/s occurs and results in small forward head thrusts. However, a gradual change in head position relative to body position, similar to that reported above, can be seen in this figure.

Naturalistic observations of pigeons landing provides a clear impression that they begin to 'head-bob' upon reaching relatively slow forward speeds just prior to touchdown. However, sensitive to the fact that the apparent and widely accepted 'backward and forward' movements during walking are illusory, the landing of feral pigeons was filmed to confirm this impression. Even when these sequences were viewed in slow motion it still appeared that head-bobbing was occurring but, as Figs. 5 and 6 show, this impression was also illusory. The trajectory of the head proceeds smoothly through space and probably appears to 'bob' because of the forward and backward 'figure of eight' movement of the wingtips. Fig. 6 illustrates the pattern of head movements during the transition from flying to walking where it can be seen that the head is held steady in the horizontal plane during the final few centimetres of descent, and is stabilized while the wings are being folded.

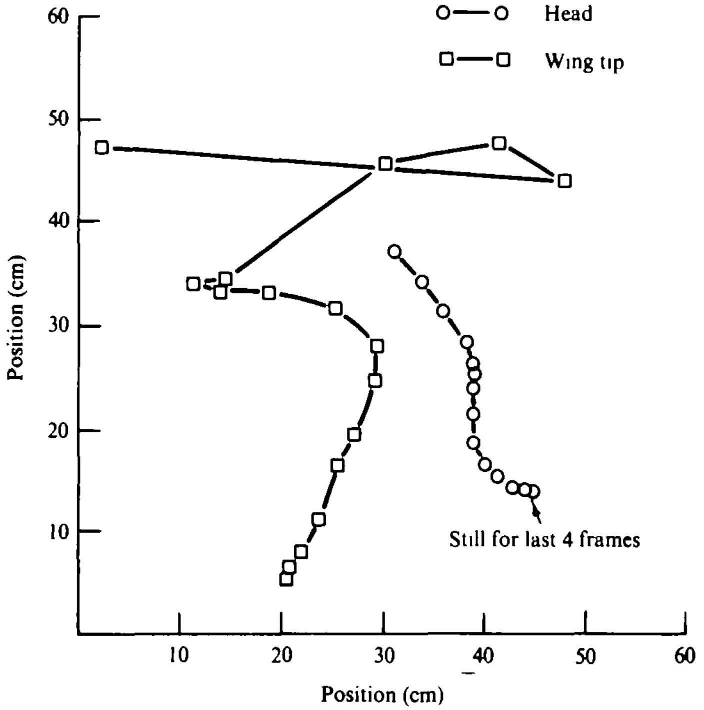

Fig. 6. Changing head and wingtip positions during the transition from flying to walking. Film speed 64 frames/s and data plotted as for Fig. 5. While wings are being folded head moves down only but not forward, and then is thrust forward and held steady for the last four frames.

DISCUSSION

The results of these experimental observations confirm the data of Dunlap & Mowrer (1930) who were the first to show that 'head-bobbing' in birds consists of two phases, one where the head is locked in space and another where it is rapidly thrust forward to a new position. The high speed motion photography used here indicated that the head is very well stabilized during the stationary or hold phase, and that during the forward thrust the velocity approaches that of the saccadic like return flicks of optokinetic head movements (Frost & Thomson, 1972). In a recent paper, which appeared while this study was in progress, Friedman (1975) demonstrated that head-bobbing in the Ring Dove (*Streptopelia risoria*) was under visual rather than vestibular or rhythmic control. Our treadmill induced walking observations also converge on this conclusion, and the toppling and extreme postural changes induced by very slow treadmill velocities likewise show the untenability of the equilibrium hypothesis. Head-bobbing does, however, produce a powerful visual illusion that the head is moving forwards and backwards as the bird walks. This is quite consistent with empirical studies on induced visual movement perception (Duncker, 1929; Wallach, 1959), where the immediate frame of reference or context has been shown to exert dramatic control over the phenomenal appearance of motion. In this case the frame of reference is the bird's body, relative to which the head *is* moving backward but at the same rate as the body is moving forward, thus achieving stabilization in space.

An equally compelling illusion involving apparent head-bobbing just prior to landing was also investigated. It was first thought that head-bobbing might occur at relatively slow forward velocities, independently of whether they were achieved through flight or walking. However, analysis of film records revealed that the head followed a very smooth trajectory practically right until touchdown. Once again the wing beat and body oscillations forming the immediate frame of reference produced an illusory appearance of motion, but in this case apparent head-bobbing, where in fact none was occurring.

Dunlap & Mowrer (1930), after concluding that head-bobbing was controlled almost exclusively by visual stimuli, raised a very interesting question: 'How can visual stimulation produce 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?' (p. 105). Observations by Friedman (1975), and those reported in the present study, confirm that head-bobbing is exclusively under visual control. The slow slippage of head position evident during extremely slow treadmill speeds could possibly, however, provide sufficient visual error signal to generate these compensatory head movements. If the slippage rates in the range of 2·5–3·6 mm/s, consistently found under these conditions, are equivalent to those required to produce the 'hold' in normal head-bobbing (which often has a duration around 120 ms), then slippage of the order of 0·37 mm/hold is to be expected. Clearly changes in spatial position of this order of magnitude would be very difficult to detect in normal head-bobbing records.

Recently Frost & DiFranco (1976) reported that many broadly tuned directionally specific pigeon tectal units preferred posterior to anterior motion in the visual field, and had an even more clearly defined backward null direction. The habituation and adaptation characteristics of these 'backward notch' units are such that they exhibit the notch only in the adapted state, achieving this through a more rapid differential adaptation to backward (anterior to posterior in visual field) moving stimuli (Frost & DiFranco, 1976; Woods & Frost, 1977).

A functionalistic interpretation of these 'backward notch' units proposed by Frost & Thomson (1972) suggested that these units might be specialized to respond to object motion by specifically vetoing the self-induced backward flow of motion produced while a bird was in flight (Gibson, 1950, 1966). The rapid differential adaptation to backward motion (Frost & DiFranco, 1976) was consistent with this idea, for when a pigeon is still, these units would recover and thus respond to motion in any direction through their receptive fields. But upon becoming airborne again, the rapid differential adaptation to the backward movement in this specific subclass of units would ensure that the backward flow of self-induced motion was not confused with object motion.

One of several potential problems with this interpretation was that this type of unit might also be maladaptively desensitized to backward motion while the bird was walking. Considerations of this sort provided the initial impetus for the observations reported here. The 'hold and thrust' ratcheting of the bird's head through his visual world while walking could possibly be interpreted as a response mechanism which would keep 'backward notch' units in a recovered or semi-recovered state and thus better able to detect object motion in the backward direction through the visual field. However, another interpretation of head-bobbing (which is not mutually exclusive to that outlined above) suggests that both the stationary, or hold phase, and the thrust phase have important visual functions (Welty, 1963). This view suggests that during the stationary phase object motion will be most readily perceived, while during the rapid forward thrust of the head depth information through motion parallax will be extracted. Experiments are currently in progress to test this notion.

Detection of motion and depth have obvious survival value to predator or prey alike. In the case of motion perception the role of head/eye fixation and pursuit movements are reasonably well documented, and the 'hold' phase of head-bobbing in birds may well be linked with this function. Although depth perception may be influenced by many variables, stereopsis and motion parallax are generally regarded as the most powerful determinants of this function. Stereopsis may be considered most appropriate for specifying location of objects in praxic space nearer the body (Hughes, 1977) and obviously requires binocular overlap. Experiments by Walk & Gibson (1961) on a variety of species, and by Wallace (1959) on the desert locust, also attest to the utility and ubiquity of motion parallax as a cue to depth. The lateral position of the eyes of many birds, and the consequently reduced area of binocular overlap, suggests that motion parallax could well play an important role in their perception of depth. If the joint constraints of relative stabilization for motion detection (bearing in mind the rather small eye movements exhibited by most birds), and head movement for motion parallactic depth information are considered, then head-bobbing might well be an expected consequence.

One further observation on the locomotion patterns of head-bobbing of birds seems warranted. If motion parallax is operating in these species then relative velocity specific neurones, similar to those postulated by Nakayama & Loomis (1974), and found by Mandl (1974, 1976), would probably be involved. Since the bird's walking velocity is clearly slower than its flying velocity the rapid forward thrust of the head could serve to place it in the range of velocities produced during flight, thus permitting analysis by the same neural structures. The data presented above indicate this is at least plausible.

I wish to thank Mrs Diane DiFranco and Dr Roger Ward for help with some of the initial observations, Mr Stefan Michalski for his technical assistance and photography, Miss Patricia Brooks for typing the manuscript and Mr Gaetan Tremblay for preparing the figures. This research was supported by a National Research Council of Canada grant no. A0353.

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