SACCADIC EYE MOVEMENTS ARE COORDINATED WITH HEAD MOVEMENTS IN WALKING CHICKENS

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SUMMARY

1. Saccadic eye movements during walking were studied in chickens using cinematography.
2. Saccades were made during about 80% of the thrust phases of head bobbing, and not made in the hold phases.
3. The coordination of saccades with head movements maintains clear vision for the largest possible proportion of the time.
4. The absence of saccades in hold phases and in some thrusts is probably not the result of insufficient time to organize a saccade.

INTRODUCTION

The work reported here grew out of the fact that there are no published data about eye movements in walking birds, despite the assumption that the characteristic head bobbing gait of many birds has particular relevance for their vision.

The head bobbing of chickens and other birds is divided into thrust and hold phases. During the thrust phase the head moves abruptly forward. In the hold phase the head is stabilized with respect to the visual world as the body advances beneath it. Films of birds on a treadmill show that the head actually moves forward very slowly during the hold phase (Frost, 1978). The patterning of this behaviour is dictated by visual stimuli, and is independent of stepping motions (Dunlap & Mowrer, 1931; Friedman, 1975; Dagg, 1977).

The form of avian head bobbing and its dependence on visual input are well characterized. However, theories regarding its function remain highly speculative. Neither of the two major hypotheses takes into account eye movements made during head bobbing.

One theory is based on the idea that movement in the environment is more easily detected if the eye is still (i.e. in hold phases) and that movement parallax (Gibson, 1950) generated when the eye is moving contributes a monocular depth perception (Welty, 1963). Thus head bobbing is considered to alternately optimize these two modes of visual exploration. This and the following theory emphasize monocular vision because many birds' eyes are laterally placed and thus they have only a monocular view of much of their visual field.
Frost (1978) proposes that the thrust may provide retinal image motion in a preferred velocity range. The idea is that there are units in the visual system optimally responsive to stimuli in the velocity range provided by thrusts, and further, that the absence of backwards movement of the head keeps these units in an unadapted state.

The above theories are, of course, not mutually exclusive and the actual explanation may well involve a combination of them. However, the theories involve, explicitly or implicitly, the assumption that eye movements are negligible during head bobbing. There is no evidence that this is so. Since the direction of gaze, and the velocity of retinal image movement are affected by eye movements as well as head movements, it seems important to examine them.

As an animal looks around the world, the direction of gaze is shifted by rapid, volitional eye movements called saccades. In the chicken and other birds saccades are accompanied by an oscillation of the eyes (Nye, 1969; Wallman & Turkel, 1977). The relation of saccadic eye movements to the thrust and hold pattern of head bobbing was examined in walking chickens. It was found that saccades are not made in the hold phase but accompany most of the thrusts.

MATERIALS AND METHODS

Head movements and saccades made by 4-week-old white leghorn chickens (Gallus domesticus) crossing a 15×15 cm arena were photographed from above using a ceiling-mounted Bolex H-16 ciné camera loaded with Kodak 4-X film and running at 16 frames/s. Films were analysed in slow and stop motion in a Craig Senior editor. Head movements were correlated with saccade occurrence. Saccades in the chicken are made with both eyes simultaneously, and include an approximately 25 Hz oscillation (Wallman & Turkel, 1977). This oscillation makes it easy to detect a saccade if the chicken’s head is stationary. When the chicken thrusts its head forward its image on the film is blurred. To detect saccades even when the chicken’s head was moving, a red-filtered photocell was attached to the chicken’s head with collodion. The photocell was illuminated by a red-filtered spotlight. A lightweight transparent ‘parasol’ was mounted above the photocell so that the shadows from India ink stripes on the parasol fall on the photocell. The parasol is mounted in the following way. The bird is anaesthetized with Halothane and the upper surface of the eyeball is exposed. To prevent discomfort to the animal the incision is infiltrated with Xylocaine, and Ophthaine 5% is instilled into the eye. A small post on a piece of Lexan plastic is glued to the eyeball with Histoacryl, a surgical adhesive. Then the parasol is mounted on the post.

When the parasol moves, its shadow causes the output of the photocell to vary. This output is used to trigger the lighting of an LED (light-emitting diode) in the field of the camera. To ensure that the LED only lights during saccades, the signal from the photocell is filtered to pass only a narrow band of frequencies around 24 Hz. The filtered signal is amplified and used to trigger the LED. Thus the LED only lights when the shadow falling on the head-mounted photocell moves with the 24 Hz frequency characteristic of saccades in the chicken.
To verify that the LED was responding to every saccade and was not responding to non-saccadic events, it was checked in two ways. First, the lighting of the LED was compared in one bird to the output of a magnetic search coil apparatus (Robinson, 1963). A coil was mounted on top of the parasol, and the LED was observed to see if it lit with every saccade. Several runs of 2–3 minutes each were made, during each of which the bird would make about 150 saccades. The LED would light during all but one or two of the saccades in each run. Even saccades with a net change in the horizontal position of the eye of less than 1° were detected by the photocell. Additionally, during photography, six General Radio model 1540 strobe lights synchronized to run at slightly more than twice the film speed (35 Hz) were used to get a clear image of the parasol during the rapid movement of the head. The flashes were frequent enough so two flashes could occur during one frame of film. When this happened, the two successive images of the parasol could be compared to see if a saccade was occurring. This method also verified that the LED was lighting when a saccade was occurring, and not lighting when a saccade was not.

As the films were analysed the occurrences of saccades made while the chickens were walking and standing were noted, and the intervals between them recorded to the nearest frame (62.5 ms). Only sequences in which there was steady progress across the arena were used for analysis of walking.

**RESULTS**

Films of alert, walking chickens were examined to determine the relationship of saccades to the thrust and hold phases of head bobbing. These films confirm earlier reports that avian head bobbing consists of only forward movement, rapidly in the thrusts, and very slow in the hold phases (Dunlap & Mowrer, 1931; Friedman, 1975; Frost, 1978). Table 1 shows the incidence of saccades during the hold phases. Saccades are absent during the hold phases of walking, in contrast to standing chickens. Chickens standing still make some saccades with head movements and some while the head is stationary. To ensure that this apparent difference between standing and walking behaviour was not merely the result of sampling error, the hypothesis that saccades did occur during hold phases, but, by chance, were not recorded was tested. The cumulative probability of a saccade’s occurring with increasing time since the last saccade was calculated on the basis of data from standing birds. Subtracting the value for any particular time interval from unity yields the probability of a saccade’s not having been made in that length of time. This probability declines with increasing time since the last saccade. The cumulative probabilities of saccades not occurring in the observed hold phases of two birds are included in Table 1. The data on Table 1 show that the absence of saccades in hold phases is not a chance occurrence. Saccades are not made during the hold phases of walking.

If saccades are not made during hold phases, they must be made during thrust phases, or else be absent entirely during walking. The absence of saccades would not mean that chickens could not change the direction of gaze while walking. Chickens often make abrupt turns of the head as it is thrust forward. The angular velocities of these turns are in the range of 80°/s to 500°/s. This is in the range of saccadic velocities...
Table 1. A tabulation of the number of saccades observed during hold phases of head bobbing

(None of the hold phases observed contained a saccade. The cumulative probabilities of saccades not occurring in hold phases are included for two birds. Saccades are excluded from the hold phases.)

<table>
<thead>
<tr>
<th>Bird</th>
<th>Number of hold phases examined</th>
<th>Number of saccades in hold phases</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>N3609</td>
<td>13</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>N4056</td>
<td>49</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>N4171</td>
<td>73</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>N3838</td>
<td>48</td>
<td>0</td>
<td>0.003</td>
</tr>
<tr>
<td>N3807</td>
<td>56</td>
<td>0</td>
<td>0.016</td>
</tr>
</tbody>
</table>

reported for monkeys and humans (Fuchs, 1967). Despite the high-velocity head turns which could potentially substitute for saccades, it still seemed important to search for saccades during walking. There were both theoretical and empirical reasons for believing that saccades would be made by walking chickens. Considerations of processing efficiency predict that during visual search the least costly means of acquiring a new fixation target will be used (Russo, 1978, p. 90). Since the eyes are less massive than the head, eye movements should be a more efficient means of changing the direction of gaze. Additionally, preliminary films of birds made before the parasol and photocell were used seemed to show at least occasional eye movements during the thrusts.

Films of four birds showed that of 134 thrusts, 109 (81%) were accompanied by a saccade. Saccades are not eliminated during walking, but are restricted to the thrust phases. An explanation of the absence of saccades in some of the thrusts was sought. The simplest reason seemed to be that there might be too little time prior to the saccadeless thrusts to organize a saccade. Saccadic eye movements have a relatively long latency (e. 200–300 ms) (Rashbass, 1961; Becker & Fuchs, 1969). This leads to a minimum intersaccadic interval of about 200 ms even during the repetitive movements of optokinetic or vestibular nystagmus (Cheng & Outerbridge, 1974a, b). This minimal interval seems to be the result of the complexity of programming the saccadic movement.

When a chicken is standing in one spot, the interval between successive saccades varies between 160 and 2250 ms. Most of the intervals are 250–750 ms long (see Fig. 1). In a walking chicken the interval between saccades is from 300 to 940 ms, with most falling in the range of 250–500 ms (Fig. 2). Since the major change from standing to walking is not a shortening of the minimum interval but an elimination of the longer intervals, it seems that there is a similar minimum latency for a saccade in the chicken of 150 to 200 ms.

The intervals preceding thrusts without saccades were examined more closely. This was done to explore the possibility that the reason for the absence of saccades was that there had been too little time to organize one. The times from the initiation of the previous saccades to the times of the thrusts without saccades were compared to the intersaccadic intervals for the thrusts with saccades using the Mann–Whitney U test.
Saccadic eye movements in chickens

Fig. 1. Histograms comparing the distribution of intervals between the initiations of successive saccades for bird N3807 while standing and walking. There is no change in the modal interval between saccades, but a large reduction in the number of long intervals when the bird is walking.

Fig. 2. Histograms for two birds, showing the intervals between the initiation of a saccade and the succeeding thrust. Two conditions are compared: intervals preceding thrusts with saccades and intervals preceding thrusts without saccades. For each bird the two distributions were compared using the Mann-Whitney U test (Conover, 1971) to see if the thrusts without saccades were preceded by less time than the thrusts with saccades. In each case the results were non-significant. There is evidently equal time available for programming saccades prior to both types of thrusts.
The distribution of saccades has important effects on visual input. Abrupt movement of the image on the retina tends to reduce the retina's response to visual stimuli (Brookes & Holden, 1973). Saccades obviously cause appreciable image movement in the whole visual field. Knowing that saccades accompany most thrusts, one can then infer the amount of time available for clear vision while the chicken is walking. Hold phases, which will permit the clearest vision, account for an average of 56% (range 50-61%) of the time spent walking. This is in good agreement with a published value for the pigeon of 63% (Frost, 1978).

**DISCUSSION**

It is easy to interpret some aspects of the coordination of eye and head movements. It is more difficult to see the usefulness of some of the other findings, but they may be relevant to existing theories of avian vision. The results show that during walking clear vision is maximized by synchronization of saccades and head thrusts. Although saccades occur only during thrusts, they are not an obligatory feature since some thrusts are made without saccades. In the hold phases, however, saccades must be in some way suppressed because none of the hold phases contained a saccade. It is probably accurate, therefore, to consider the hold phases fixations.

During thrusts with saccades there is probably no visual input. The sensitivity of the visual system is reduced by saccadic suppression (Volkman, 1962; Brooks & Holden, 1973). These thrusts therefore probably have no particular visual function, other than to move the eye to a new viewpoint.

Thrusts without saccades probably do have some special function. Since these thrusts are preceded by sufficient time to organize a saccade, it is likely that saccades are suppressed during them. It is possible that the function of thrusts without saccades is to provide the visual system with input not available during the hold phases or thrusts with saccades.

Motion parallax will be one type of visual input which can occur during thrusts without saccades. Motion parallax is the apparent relative movement of objects at different distances during a translation of the eye (Gibson, 1950). Motion parallax provides unambiguous cues to relative depth of stationary objects, but not of moving objects. Motion parallax will be most pronounced in the monocular fields on either side of the head. Welty (1963) proposes that thrusts may function in just such a manner.

On the other hand it is possible that thrusts without saccades are not made to generate visual input, but to sensitize the visual system to ensure optimal receptiveness in the subsequent hold phase. The entire visual field will move backwards during a thrust, near parts at higher velocities than more distant parts. Thus a wide range of retinal slip velocities occurs during a thrust. This would be exactly suited to de-adapting directionally sensitive units with a backwards null direction. Such units have been reported in the optic tectum of the pigeon (Frost & DiFranco, 1976). Frost (1977) advances the notion that thrusts function to de-adapt these units.
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There are two kinds of thrusts, those with and without saccades. It is difficult to sustain a theory involving visual input during thrusts with saccades. However, both Welty's and Frost's theories about the possible function of head bobbing may be correct for the thrusts without saccades.

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REFERENCES


