# SPATIAL DISORIENTATION IN BIRDS

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The aircraft was on final approach through the rain and fog. At approximately 500 feet it went into a spiral dive to starboard, striking the right wing against the approach lights. The aircraft was destroyed.

Blackburnian Warblers were migrating on a night of a low ceiling and the visibility restricted in moderate rain. On reaching a floodlighted area, some fifty birds crashed into a hangar and were killed.

Initially there does not seem to be much in common, except the weather, in these two unfortunate occurrences. Yet, under analysis, there may be a great deal of similarity. In both cases the fliers were attempting to fly through deteriorating weather conditions, picking their way through a maze of light and shadow, of reflected and refracted light shining through rain, an opaque obstructing medium. It is suggested that the cause of both the crashes was exactly the same. The fliers became confused by the abruptness of intense lighting, and, using the primary sense of orientation (sight) in conjunction with erroneous sensory stimuli, suffered a complete loss of spatial orientation. Birds, particularly the nocturnal migrants when flying at low level are susceptible to, and suffer from vertigo and spatial disorientation the same as man.

For the purpose of this discourse it is assumed that: (a) the aerodynamic forces acting on the wings of a bird are the same as those acting on the wings of an aircraft; (b) only nocturnal migrants are under consideration; (c) the sense organs are used for the same basic purposes in both birds and man; and (d) while the senses of the bird may be more acute, the psycho-physiological reactions to the stimuli are similar in birds and man.

Although the aerial environment is applicable to both birds and man, each has its own peculiar environment in which it flies and this is not readily examinable by direct observation. This environment is made up of stimuli appreciated by sensory organs and perceived by the brain. The reactions to the stimuli are based upon knowledge, and each reaction must be correct in the proper place at the proper time. Because the human pilot is sensitive to similar stimuli, man can visualize the aerial world of other fliers. It is only through a comparison of the bird with man's knowledge of flying that we can deduce how a bird flies.

As spatial disorientation is extremely common (90 per cent incidence) amongst all-weather pilots, the most expedient way of determining the happenings and causes of spatial disorientation in birds is to consider first the human pilot.

### THE HUMAN PILOT

Before discussing the orientation senses in relation to flying, let us review the actions of the senses of orientation governing the locomotory organs. These organs have the sole purpose of propelling the body or appendages in a given direction for a given distance. Under certain circumstances these organs can become useless, as when the governing apparatus, the orientation senses, is impaired in its function. Consider the children's game of Blind-Man's-Buff or Pin-The-Tail. The child is subjected to a mild case of vertigo, or spatial disorientation, and is asked to achieve a specific goal. Although the locomotory organs are functioning perfectly, the orientation senses are impaired causing an erratic approach toward the target. Although the child is subject to gravity, it has difficulty in maintaining a vertical orientation. It is therefore reasonable to conclude that controlled locomotory action is dependent upon spatial orientation.

For the human on the ground, spatial orientation is necessary only within a two dimensional field. The aviator must have a true spatial orientation. He must be capable of determining a three-dimensional move; of assessing his position relative to a fixed object (the runway) and a moving object (another aircraft); and of determining his position relative to the horizon.

Flying on a cloudless day, the pilot is at the center of a vertical hemisphere. When he is straight and level the ground occupies the bottom half of his visual field and the sky the upper half. The pilot can fly a straight line across the ground because he can see where he is going. During a level banked turn, the horizon rotates at the middle of the visual sphere, going up on one side and down on the other. It is interesting to note that the pilot's immediate reaction is to reorient himself by moving his head and body to maintain a proper horizontal and vertical alignment with the horizon. If the pilot increases the bank but maintains a straight course, his orientation senses will inform him of a side-slip. However, if the bank is made in a turn, the acceleration forces may indicate the turn, or something entirely different, depending on the severity and smoothness of the turn and the forces involved. If the pilot exerts a heavy back pressure or forward pressure on the control column, the orientation senses will inform him of accelerations in these directions even to the extent of overriding the forces of straight and level flight. However, the orientation senses are not as acute as vision in their perception of changes in speed and direction.

The discrepancies between the senses (sight and balance) in flight lead to certain orientation problems peculiar to flying. Prior to the development of specialized instrumentation, the pilot had to remain in sight of the ground because there was no means of establishing a horizontal or vertical datum from which to orientate himself. Even today, with modern instrumentation, pilots are still subject to attacks of vertigo and spatial disorientation, even to the extent of crashing. Studies have shown that disorientation is, almost without exception, the result of normal psychophysiological processes associated with certain characteristics of flight and of the pilot aloft (Clark and Graybiel, 1955). Therefore, disorientation could be considered to be normal in the sense that it is a perceptual process correlated with the sense organs functioning normally in an abnormal environment.

There are certain characteristics peculiar to flight which make orientation in the air more difficult than on the ground: (a) In flight the pilot loses contact with the ground. He lifts himself above the normal visual aids used to maintain a vertical orientation, i.e. trees, buildings, etc., and is forced to use the horizon to maintain the attitude he desires. (b) The pilot must maintain a three-dimensional orientation, direction, distance, and altitude. The pilot must be aware of his spatial position with respect to the horizon, to fixed objects and to moving objects. (c) The pilot must appreciate the unusual physical forces to which he will be subjected. In the air, while still subject to gravity, he is also subject to accelerative forces which may be continuously changing both in magnitude and direction, even to the extent of negating gravity. (d) The speed and altitude of the aircraft impose further stresses on the senses of the pilot. A more acute sense of spatial orientation is required for flight near the ground than at high altitudes. The increase in availability of visual cues closer to the ground may not necessarily increase the ease of orientation; the abundance of cues may, in fact, lead to confusion. Similarly, spatial disorientation at high altitudes may occur because of the greater sparsity of visual cues.

The above is very basically the pilot's problem in maintaining spatial orientation and he must learn to appreciate these problems before he can fly. However, there are additional problems which may impose further stresses: (a) Visual cues may be reduced or be missing entirely. In the air, gravity is a minor cue, and the horizon may be completely obscured. Thus the pilot is forced to use his instruments to obtain a reference to the horizontal. In this situation he has an indication of his attitude, but his relative position to external objects is completely unknown. (b) False cues may be presented to the pilot by natural phenomena outside the aircraft. Cloud formation, precipitation, lights, reflections and refractions of lights, Aurora Borealis, etc., all may cause spatial disorientation. Accelerations may override gravity and be substituted for gravity, particularly if the accelerations are maintained for a prolonged period. (c) The discrepancies which exist between the senses themselves and between the senses and the instruments may be exaggerated when the "G" forces of a tight turn override gravity and indicate the vertical is in the direction of the force while the instruments indicate the vertical in another direction. There is also the phenomenon of recovering from a turn and still having the impression of being in a turn, although the visual cues belie the sensation.

There are other factors which must be considered. A seemingly minor point, but actually a very important one, is that the vertical axis is usually obtainable only when a horizontal reference is provided while flying. The vertical axis is the predominant one to a person on the ground; yet when flying, it cannot be accurately determined by itself. Therefore, the horizontal axis becomes the predominant axis. The establishment of the horizontal datum is vital to spatial orientation, as all flying is based upon the aircraft's attitude relative to the horizon, not to the vertical.

Graybiel (1951) states, "Visual perception may become inadequate for partial spatial perception due to inadequate perceptual data. There are many causes for this centering around (1) celestial factors such as darkness, brightness of sun etc., (2) atmospheric conditions such as rain, fog, etc., (3) inadequate visual framework and (4) factors relating to the plane such as small size of windows, glare, etc." Another cause can be ground lighting such as street lights, approach lights, floodlighting. While no statistics are available, it is suggested that the majority of the cases of spatial disorientation occur at night. The optimum conditions for spatial disorientation seem to be a night with low cloud and moderate to heavy precipitation, and the aircraft near, (within 2000 feet) or in the base of the cloud. If the aircraft is near any illuminated area, flying becomes a difficult task, because the pilot is subject to sporadic visual cues which are readily misinterpreted. The refracted and reflected surface lighting is coming from angles which are not usually experienced. There is a pronounced diffusion of surface lighting in precipitation similar to the haloes around the sun or moon when seen through cirrus or thin alto-stratus cloud. The horizon is no longer easily identifiable. It is under these circumstances, particularly if the pilot is trying to fly partly with reference to outside visual cues and partly on instruments, that spatial disorientation is most likely to occur.

Armstrong (1952:281) states, "It has been established beyond all doubt that vision is absolutely necessary for aerial equilibrium. If vision is eliminated during flight, all of the other organs of equilibrium have been found inadequate and the pilot becomes hopelessly confused." Davis (1953) states "It is apparent that the normal vestibular apparatus is not sensitive enough for aerial equilibrium and due to the illusion of reversal of motion it may be, under certain circumstances, a distinct hazard to flight." In the light of these two quotations it would appear that the visual sense is the predominant sense of spatial orientation while the vestibular apparatus has a questionable role. Guyton (1961:678–79) states, "In summary, then, the semicircular canals detect the rate of change of rotation, which is called angular acceleration. The function of the semicircular canals, therefore, could not possibly be to maintain static equilibrium during linear acceleration, or when a person is exposed to steady centrifugal forces." The tactile, visceral, and proprioceptive senses each contribute to the general perception of orientation but are incapable, either individually or in concert, of correctly and exactly orienting the pilot in the air, or interpreting the direction of the forces acting upon him.

A final point to be considered is the background knowledge of the pilot. Graybiel (1951) states, "Spatial orientation may be looked upon as a phenomenon of perception which represents the individual's interpretation of stimuli originating in various organs of special sense." Interpretation of stimuli is the correlation of the visual cues with the other sensory cues. The interpretation must be based on knowledge which is derived either from previous experience or some other source. However, the knowledge used may be very basic or minimal, or it may be based on assumptions of the normal. In attempting to rationalize the situation, the pilot may accept false cues, both visual (physical) and sensory, as true cues and react accordingly. Therefore, under flying conditions which tend to promote spatial disorientation, there must be a conscious reasoning and knowledge of the problems of orientation or complete vertigo and spatial disorientation is the usual result. Restoration of spatial orientation can be achieved only through a correct interpretation of the accepted visual cues.

To summarize, the following two major groups of factors must be accepted:

*Physiological Factors.*—(1) Sight is the most important sense associated with spatial orientation. (2) The vestibular, tactile, visceral, and proprioceptive senses each contribute a small part of the necessary intelligence to maintain orientation, but these senses are not generally effective, either in concert or individually, and may at times contribute to disorientation. (3) Knowledge and ability to assess both visual (physical) and other sensory cues is essential to maintaining or regaining spatial orientation. Knowledge of the phenomenon itself is vitally important.

*Physical Factors.*—(1) The loss of visual cues by darkness, precipitation or fog, or any combination thereof; (2) inexperience in flying in such conditions that visual cues are lost; (3) conflict between the cues to orientation. This may be a conflict between visual and other cues, particularly when centrifugal force replaces normal gravity; (4) prolonged turns at a constant speed with rapid recovery to straight and level flight; (5) unusual maneuvers at night; (6) gradually entering any unusual position without being aware of it; (7) sudden accelerations and decelerations at night; and (8) failure of the pilot to constantly recognize his position in the three-dimensional world of flight.

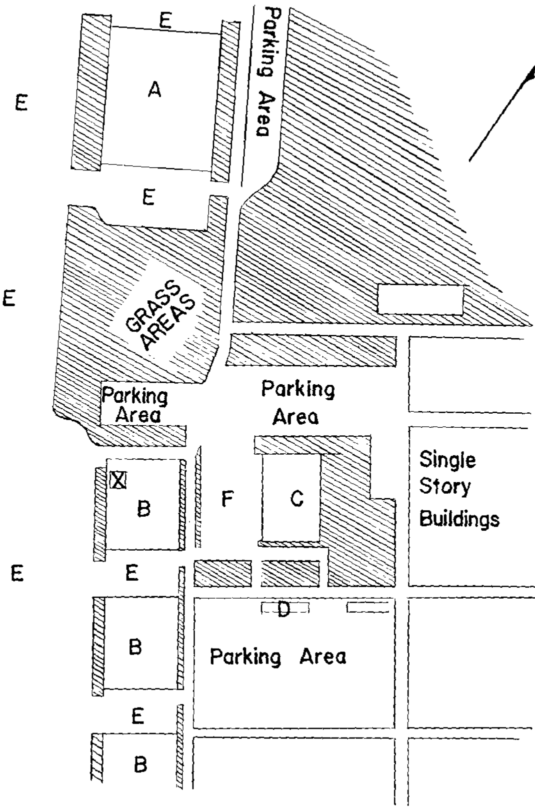


FIG. 1.

## THE BIRD

Before proceeding with any analysis of a bird's orientation faculties, let us review a few instances of avian crashes.

In September, 1961, Blackburnian Warblers were migrating through the area of a Royal Canadian Air Force Base. The weather situation was one of low ceilings and restricted visibility in rain. The geographic plan of the station is as shown in Figure 1. The fronts of the hangars (B) were floodlit facing the tarmac (E). The revolving light beacon (X) on the control tower was in operation. Three hundred yards east the floodlights of the Motor Vehicle section (C) were shining on the parking area (F). The floodlight on both the hangars and the Motor Vehicle section are forty feet above ground on the fronts of the buildings, while the revolving beacon on the tower is 80 feet above ground. The lights from inside the vehicle section were shining through the opaque glass in the doors.

As far as can be ascertained, the birds were flying in a south south-easterly direction as they had been during the previous five nights. Of the five birds which came to grief against hangar (A), two were on the north end and three on the south end. No birds were found around the control tower (X), and only three along the rest of the hangar line (B). However, 30 birds were found dead in front of the Motor Vehicle section (C) and 23 more were found against a secondary garage (D) 100 yards south of (C). Restricted space could not be a contributing factor as there is unlimited room for the birds to avoid these obstacles. The hangars, (B) are no higher than two-storied structures. Why, then, did these birds fly into the buildings?

Hochbaum (1955) reports a Mr. Don Knox, "We had a week of very foggy weather November 12 to 18 and the trees and fields of stubble were coated with hoar-frost. The sun was hidden for days and at times it was difficult to see more than ten feet ahead in daytime. On the evening of the 15th, Mr. Knox decided that it would be a good time to burn an old straw stack, so set it afire about 7:30 p.m. Next morning as he was driving along the road he noticed a few dead ducks scattered here and there but thought little about them as ducks often strike the telephone lines and kill themselves. A little later he noticed something unusual going on in the stubble field and went to investigate. Mr. Knox was amazed to find hundreds of dead and dying ducks, some with smashed bodies, some with broken legs and wings, and others less seriously injured but apparently dazed and unable to navigate properly."

Baldwin, (1963) states: "In the fall of 1962 at the Long Point Lighthouse, on a night when migrants were swarming around the revolving light, the writer was disturbing warblers, thrushes and sparrows from the long grass at the base of the floodlight tower (a recent innovation) where they had fallen or were resting. Time and again birds would flutter up from the long grass to a height of five or six feet and then fly directly at the white concrete structure."

A report of bird kills around TV towers is contained in a study by Tordoff and Mengel (1956). In their description of the tower they state, "The tower is lighted by a series of red lights, some flashing and others steady." These lights undoubtedly are obstruction warning lights for aircraft. In a further paragraph they note "all major kills at Topeka occurred when the migrating birds encountered either a cold front or a stationary front lying over eastern Kansas. Typically, this frontal weather included rain, fog, and cloud ceilings down as low as 800 to 1000 feet. Weather of this type presumably forces the migrating birds to fly below the cloud ceiling and thus brings them within the altitudinal range of television towers."

Stoddard (1962) cites innumerable examples of birds striking TV towers under similar weather conditions. All these towers must conform to a certain standard of illumination as provided by various aeronautical governing agencies. Why do birds fly into these illuminated obstacles?

Howell (1955) cites examples of birds being killed by ceilometers around airports. He states "that it occurs only when certain factors coincide; these are an overcast of 5000 feet or less, a wind with a velocity of at least five miles an hour from the north, and a large volume of migration. It might be added that these weather conditions are usually associated with a cold front." Amelia Laskey (1956) notes that "On the night of September 24–25, 1955 more than 1400 birds of 51 species were killed or injured at Sewart Air Force Base, Smyrna and a few at Berry Field, Nashville. After a week of warm weather with temperatures reading 90 to 97 degrees, there was a sudden change on September 24. Rain and northerly winds prevailed with temperatures for that day ranging from 73 to 68 degrees. When the rainfall ceased in the afternoon, the cloud ceiling was only 500 feet."

Laskey (1956) reports that "at 9:45 p.m. there were hundreds fluttering rather high in the beam." It is interesting to note Howell (1955) when he states "We concluded that the probable cause of death was aerial collision between migrants followed by flying or falling against the ground. While we could not report an actual eyewitness account of aerial collision between migrants such collisions have since been witnessed by Capt. R. L. Edwards, at Maxwell Air Force Base, on the night of October 7–8, 1954."

Prior to discussing the physiological make-up of a bird, it is necessary to discuss briefly its mental capacity. Herrick (1924) states, "It is everywhere recognized that birds possess highly complex instinctive endowments and that their intelligence is very limited." Van Tyne and Berger (1959) corroborate this statement of Herrick. A limited knowledge and reasoning ability affects everything the bird does. When a strange situation is forced upon it, the bird cannot rationalize the situation, but employs the trial and error method. If given enough practice the bird will eventually learn to solve the task. However, once the task is learned and time interval between practices increased, the memory or knowledge of the situation fades and the bird again resorts to trial and error.

When the bird is confronted with natural phenomena, it has an adequate mental capability and can adapt itself to meet the changing situation. However, in dealing with unnatural phenomena (i.e. outside electrical lighting, buildings, TV towers, etc.,) the bird does not have the necessary knowledge or the ability to reason. Also these phenomena erupt at a very alarming rate which tend to preclude adaptions. Therefore, the bird with a knowledge of unnatural phenomena or the ability to recognize them, must have a greater facility for reasoning that the present class of Aves, or be hatched in an area where such phenomena are a part of its natural environment (urban dwellers.)

Perhaps the bird is compensated for a lack of mental ability by a highly attuned reflex action and acute visual capability. Mann and Pirie state, "Small birds, hunting for minute seeds and insects also require good eyesight, and it is obvious, both from their way of life and from the structure of their eyes and brains that birds rely on sight more than any other sense except the proprioceptive one." It would seem that the eye of the bird is its basic source of knowledge and the basic sensory organ for its actions. Van Tyne and Berger (1959) classify the eyes as the most important sensing organ of the bird.

The bird is more capable of acute night vision than humans. The author has seen innumerable birds fly out of the beams of headlights and flashlights into the dark. None have ever been seen to crash into any obstruction. It cannot be suggested that the birds are blinded in one eye. If this were the case, the birds would normally maintain a circular flight path but they definitely do not. Therefore, it can be accepted that natural darkness is a phenomenon that the bird is familiar with.

Other sensory organs of bird may be used for spatial orientation. The visceral senses of a bird may be used in flying. A glimpse at a bird, while it is flying, will reveal the silhouette of a high-wing monoplane. The high mounted wing gives a stabilizing advantage through pendulum effect, with the viscera positioned at the bottom of the pendulum. An appreciation of a roll around the bird's fore and aft axis could be realized through its visceral senses. Suppose the bird were flying on a straight course at a constant 45 degrees to the horizontal. The heavier parts of the viscera would tend to realign themselves with gravity. While the movement of the viscera would be slight, it be would appreciated the same as the dispersement of the human viscera on laying down. The realignment of the viscera would be sufficient for the bird to realize that its body is not aligned with gravity. Also, if the bird in level flight suddenly tried a loop or a bunt, the viscera through its slight movement would give an indication of positive or negative "G" loading. Therefore the viscera of a bird can appreciate both accelerations and gravity.

A second means of appreciating a bank would be through the "tactile" senses of the feathers. The weight of a bird while in a bank is still acting through gravity but the lift, generated by the wings, is acting at right angles to the bird's lateral axis. Because the lift no longer balances the weight, the bird will tend to side-slip. The side-slip induces an increased airflow over the lower wing as the airflow is now coming from ahead and below, instead of a straight ahead. The change in direction of airflow causes an increased air pressure against the downward side of the bird's body. The body, because of its inclination, produces a blanking effect against the inclined airflow over the upper wing. The blanking effect produces a decreased lift on the upper wing, and a decreased air pressure against the feathers on the upper side of the body. Thus the bird, by "tactile" sensory perception, can evaluate a comparison of airflow pressures and appreciate the fact that it is flying on an inclined plane.

Did Hochbaum (1955) recognize the "tactile" and visceral senses in his statement: "Not only is the blindfolded bird able to balance its head when held in the hand, but when it is cast into the air, body and head quickly assume the posture of flight. Like a cat falling with its feet to the ground, the blindfolded bird quickly adjusts to its belly-down flight attitude when cast aloft." In the air the bird senses only differential air pressure on its various surfaces and the "G" forces on its viscera. Therefore, the bird, conscious of not sensing its weight on its lower body surfaces against land or water, can only assume that it is in the air. Consequently, it will quickly assume the position of flight, whether right side up or not is of no great importance. The pendulum effect of the body, particularly with a reversed center of gravity, will quickly return the bird to its normal flight attitude.

Also the visceral senses will indicate an abnormal flight attitude. The "tactile" senses of the feathers will also inform the bird of an abnormal attitude. Thus the bird has many stimuli, other then the vestibular apparatus, to re-orient itself. However, the bird was not flying under these circumstances and did not attempt to fly until it was properly oriented.

It is suggested that the bird did not balance its head by use of the vestibular apparatus when cast into the air. When cast into the air, the bird was aware of being in the air. Once this knowledge was realized the bird assumed a flying posture. Through the use of its proprioceptive senses, it realized that it had not assumed the proper posture for flight. The relationship of the head, neck and body in a flight posture is a natural or learned posture, thus the bird readily assumes the posture.

Mann and Pirie (1950) state that "the proprioceptive sense is the sense of passive position and the movement of the body in space." Here again is a relative sensory perception. It is suggested that the proprioceptive perception of visceral movement can indicate a bank and be discerned by the bird. However, the proprioceptive sense is much more important. The proprioceptive sense is generally accepted as a sense of musculature position. A bird can be conscious of flapping, dragging its feet, bending its neck etc., but the knowledge will in no way affect its spatial orientation at the moment. If we reword Mann and Pirie's statement to read "the proprioceptive sense is the sense of movement of the body relative to its passive parts," then the proprioceptive senses may indicate a future spatial orientation. The proprioceptive sense is used to control the bird's posture and govern its airspeed.

The vestibular apparatus is conceded to be the main internally-cued organ of orientation. Thus the position of the vestibular apparatus is of great importance. By analogy, the vestibular apparatus is comparable to the gyro-horizon system of an aircraft. This system must be mounted on a fixed platform although the gyro is allowed its own rigidity in space. The aircraft is then allowed to turn around the gyro. Similarly, the vestibular apparatus is mounted in the head. Hochbaum (1955) makes a point of stating that "this steadiness of the head must be of tremendous importance to a bird's safe arrival from flight, especially in landings made under turbulent conditions or in wooded places. While this stability of the head, regardless of body posture, no doubt serves the visual process during flight, it does not result from the function of the eyes, that is to say, visual orientation alone is not responsible for this balance." Of course Hochbaum is right; the rigidity of the head is maintained by the vestibular apparatus. The only way the bird can maintain a datum for spatial orientation is to maintain a rigidity of the head since it acts as a mounting for the acceleration sensors of the vestibular apparatus. However, the vestibular apparatus has to be confirmed by some means. The only means of doing this is with the eyes and the horizon.

The vestibular apparatus is sensitive to accelerations, but not to a constant acceleration or a fixed position. Hochbaum (1955) states: "The circle was not invariably the pattern in all hooded tests. Some birds adopted flights that varied widely from the circle but these variations, though individually distinct, always followed a pattern of curves that carried the bird downwind from the starting place." It would appear that the vestibular apparatus is not sufficiently acute to sense minor discrepancies which can be introduced until the bird has no directional control. Therefore, the eyes of the bird have to establish its initial horizontal orientation and then the vestibular apparatus accepts this position as the normal. Any large deviation from this established position is sensed as an acceleration and a deviation from the normal. The bird must constantly recheck its horizontal orientation by visual cues to maintain its spatial orientation. This way the bird maintains its spatial orientation, sensing disturbances to its equilibrium, as far as the head is concerned through its vestibular apparatus; and to its body through the "tactile" sense of its feathers and its visceral senses. It changes its body posture relative to its passive head through its proprioceptive senses to correct sensed accelerations. Thus the bird uses all of its orientative senses to maintain its spatial orientation; but the basic sensory organs are its eyes—from which it received its initial orientation.

## FLIGHT CHARACTERISTICS OF THE BIRD

*Good weather.*—Locomotion towards any definite goal is dependent on the stimulus applied by the goal and the spatial orientation of the subject. Therefore, before a bird will fly, it must have a motivating factor, and "know which way is up." Spatial orientation is necessary even before the bird leaves the ground. No matter how strong the motivating factor is, locomotion in a desired direction is impossible if the bird is not spatially orientated. We have only to watch the pheasant handlers at a dog trial. The handlers get the birds dizzy, or subject to spatial disorientation, and the birds sit where they are put. When the pheasant tries to move, its locomotory organs are not impaired, but its guiding senses cannot effectively control the locomotory organs. The visual senses can determine which way to go and the sight of the keeper and the dog impel action; but, because the pheasant is spatially disorientated, the desired action cannot be achieved. Therefore, it would seem that spatial orientation is a prerequisite to any desired locomotion.

When the bird is on the ground or water, there is an over-abundance of cues for the bird to remain spatially orientated. The weight of the bird itself on its legs gives it an indication of gravitational forces. A glance at the

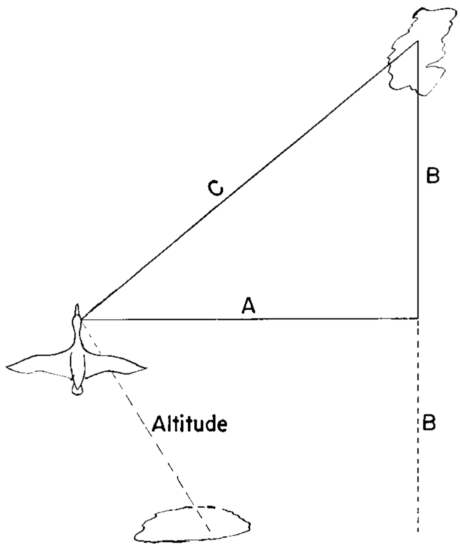


FIG. 2.

surrounding vegetation will determine the vertical. Even when far removed from land, the bird sitting in the water can determine the vertical by its weight on the water surface and the visible horizon. The viscera of the bird is in its normal alignment with gravity. The vestibular apparatus has remained undisturbed by any excessive acceleration. Thus the bird remains well orientated on its land/water environment.

As the bird leaves its land/water environment, it is properly orientated to the vertical and horizontal axes by its gravitational, visceral, vestibular, and visual senses. The first three provide enough stability for the bird to maintain a co-ordinated climb until the transition is made to a horizontal orientation from the vertical orientation.

In the air, the bird must have true spatial orientation. It must be able to determine a three-dimensional move (Fig. 2). The bird must be aware of its altitude, the lateral displacement of its objective (A), the forward or rearward displacement of its objective (B), and the desired route to achieve the objective (C). The bird must also be capable of assessing its position in space relative to fixed objects, to moving objects in space as well as on the ground, and to the horizon. These are the very same problems which confront the human pilot.

On a clear day with good visibility orientation is no particular problem. The bird is flying at the center of its sphere of vision. As Hochbaum (1955) states, the horizon is always at eye level. Therefore, the upper half of the bird's visual sphere will be sky and the lower half ground. During straight and level flight, these hemispheres of ground and sky will be maintained. When the bird banks to turn, it inclines its head and body to the horizon. This action is not to be confused with the body oscillations of an approach to landing. In our case, the downward eye will have an increased amount of ground visible when the upper eye will have less. Thus the bird has a visual comparison to evaluate its spatial position. The accelerations produced by the turn could be sensed by the vestibular apparatus. However, unless the roll or bank was exceedingly abrupt, it is doubtful if the bird would appreciate the vestibular accelerations. As Queeny (1947) demonstrates, ducks use the eyes as the primary organs of orientation even during such maneuvers as a stall-turn. A glance at the horizon confirms the roll or bank. When the bird wishes to resume straight and level flight, it uses its eyes to re-orient its head to the horizon. The proprioceptive senses then realign the body with reference to the head and level flight is resumed. Finally, the vestibular apparatus realigns itself to the primary axes.

It is submitted that the vestibular apparatus is not as important as has been previously suggested nor is it exact in its perceptions of accelerations. Ducks can be observed turning their heads through many planes while flying, even to the extent of looking backwards, yet no deviations of their flight paths are noticed. The bird is still able to maintain its flight path by the use of its senses and its latent flying ability. Therefore, it is suggested, the accelerations which affect the vestibular apparatus must be strong enough to affect the other orientation senses, excluding the visual sense. However, any sensual perception of acceleration, whether tactile, visceral or vestibular, is immediately confirmed by the eyes.

When the bird encounters turbulence, its whole body and head become subjected to various accelerations. The predominant sense is very difficult to suggest. A straight vertical displacement of the bird would probably be appreciated more by the visceral and tactile senses rather than the vestibular. A horizontal displacement would be appreciated by the visceral and vestibular senses. However, it is unlikely that a straight line displacement would occur because of the bird's inertia. Therefore, a varying percentage of each sense would be appreciated. However, the bird can still see the horizon, evaluate what is happening and reorient itself accordingly.

During its descent for a landing, the bird must reverse the previous transition of orientation cues. Initially the bird selects a general landing area while using a horizontal orientation datum. The bird must continuously assess its groundspeed and track to the landing points; its flight course and the wind velocity; the rate of descent and airspeed; the approach angle to the landing area and any obstructions; and the changing distance to the landing point. The bird must also maintain an awareness of its spatial orientation (relative to the horizon) and its postural position.

As has been previously explained the postural position is determined through the proprioceptive senses. The postural position of the bird is the basic determinant of the bird's airspeed. Therefore, it must have positive knowledge of its body position. However, its airspeed is sensed by the tactile acuteness of the feathers and the alula. Van Tyne and Berger (1959) state, "The presence of wing slots increases lift which is needed especially at the take-off. The alula functions as a wing slot when it is drawn forward away from the rest of the hand." By inference a bird needs a high lift capacity when flying at low airspeeds. Therefore, the bird's airspeed is determined by its proprioceptive senses and the tactile senses of the feathers.

The vestibular apparatus is needed to maintain a proper vertical and horizontal orientation of the head. Only by maintaining a constantly level head can the changing angles and vectors of a descent and landing be assessed. The bird is also making a visual transition of horizontally orientated relatively high level flight to a vertically orientated low level flight. However, the transition is being done in much less time and with a greater need for accuracy. The bird subconsciously appreciates a general vertical orientation from the overhead light, but this is not accurate enough for landing. The bird's eyes can give the vestibular apparatus a datum, but not continuous information. Therefore, to maintain its spatial orientation, the bird must maintain its head in a fixed position relative to the horizon which the vestibular apparatus is trying to do.

The eyes are busily engaged in assessing the vectors of a descent and landing, since these factors can only be determined through the bird's eyes. It has no other way of gaining the required information for a successful landing.

In summary, flying during good weather is relatively easy for the bird. The bird is flying at the center of its visual sphere. By using its eyes the bird can visually assess its attitude relative to the horizon. However, the bird can assess only the position of its head. The postural position and wing position must be done through its proprioceptive senses. Accelerations from outside the body are sensed through the viscera, vestibular apparatus, and the tactile senses of the feathers. The airspeed of the bird is sensed by the tactile sense and the alula, but it is governed by the posture of the bird. The steadiness of the head is imperative on landing. Only if the head is maintained in a fixed plane can the eyes give a proper recording of the changing vectors. The vestibular apparatus must be able to maintain a rigidity in space of the head comparable to a gyro. However, the regulatory organs for

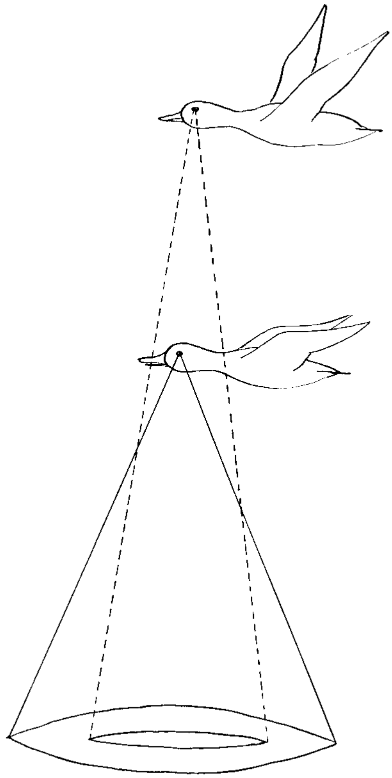

FIG. 3.

the vestibular apparatus are the eyes, as only the eyes can give instant recognition of the vertical and horizontal axes.

*Poor weather.*—The weather situations which bring about restricted visibilities are low ceilings with precipitation, and/or fog. Flight through restricted visibilities from any cause is exactly the same, except that fog may arrest any but purely local movement.

The bird is forced to reduce its flight altitude to that which will afford a safe passage. As many a marsh hunter has experienced, ducks will and do move in the fog, but at very low altitudes. The visible horizon is the restrictive factor forcing the bird to fly low. Whereas in good visibility the bird was flying at the center of its visual sphere, in poor visibility it is flying at the apex of its visual cone. The periphery of the cone's base is the radial horizontal visibility, or less. The altitude of the bird, or the apex of the cone is determined by the radial visibility, the bird's speed and its reaction time, not by the vertical visibility. As altitude is increased, the horizonal visibility decreases until the bird can only see straight down.

As the bird requires initiating cues for the vestibular apparatus it must fly at an altitude where it can see a horizon. Therefore an acute cone must be changed to a cone with the largest base. Consequently the bird will fly at a much lower altitude in order to extend its visible horizon (Fig. 3). Also by flying at a low altitude the bird has extended its required reaction time for its airspeed by increasing the visibility distance. It must be remembered that the bird may be theoretically still flying within its sphere of vision limited by the obscuring medium; but this is of no consequence unless something is visible within the sphere.

The method of spatial orientation used by a bird flying through adverse weather is exactly the same as when flying in good weather. The visual sense must provide the datum for spatial orientation. The vestibular apparatus accepts these axes as the datum and senses any deviation. However, the bird sets weather minima below which it will not fly because it cannot maintain its spatial orientation, and its reaction time at its airspeed is too great for a particular visibility.

Nocturnal flight is conducted in exactly the same manner as diurnal flight. The weather will have exactly the same effect on the bird's flight during nocturnal periods as diurnal periods. The bird is faced with exactly the same problems, but they may be of greater intensity because of darkness. However, as Hochbaum quotes Lincoln (1950) "the nights are rarely so dark that all terrestrial objects are totally obscured, and such features as coastlines and rivers are just those that are most likely to be seen in the faintest light, particularly by the acute vision of the bird and its aerial point of observation." Thus darkness is not an inhibiting factor to nocturnal travel but may be a restrictive factor as far as altitude is concerned.

## ANALYSIS OF CASES

Let us now apply our knowledge of how a bird flies to the cases previously described when the birds were flying under conditions of poor visibilities and low ceilings and unnatural phenomena. Until reaching the lighted areas, the birds had been flying over the open countryside at an altitude high enough to maintain adequate visual cues for spatial orientation, yet below their normal cruising altitudes in clear weather. Suddenly they were surrounded by lights of various and varying intensities with shadows at a variety of angles. The birds used their knowledge in an attempt to orient themselves and escape from the area. However, their knowledge was of natural, rather than unnatural, phenomena. Such reorientation, based on natural phenomena applied to unnatural phenomena is the initial step toward spatial disorientation.

Consider the first situation—the Blackburnian Warblers flying into the light and shadow. The shadow line from the flood lights extends out from the building at an angle of thirty degrees below the horizontal. Prior to entering the area the bird had been using the natural shadows, the land shadow against the horizon, for spatial orientation. As it approaches the area, the lights are above or level with it and to one side of it. There is also reflected light from the adjacent buildings. The closer the bird approaches the lights, the more defined the shadows become and the natural horizon becomes more diffuse until it fades completely. Having lost its natural datum for orientation, the bird seeks new visual cues in the lights and shadows of the artificial situation. What the bird sees it accepts as true because of its lack of knowledge. Accepting erroneous visual cues, the bird re-orients itself to the false horizon. Having rolled to a plane inclined from the true horizontal but parallel to the false horizon, the bird attempts to fly straight and level. The vestibular apparatus appreciated and accepted the roll to the new position. However, the roll was appreciated as an acceleration to a new position rather than a return to equilibrium. The visceral senses also show a displacement from the true horizontal or vertical. Now the bird has discrepant cues (visual and sensory) to the horizontal. As the bird maintains the bank it will start a descending turn. The "tactile" senses of the feathers and the pendulum effect of the bird's body inform it of an incipient spiral dive. As the bird's brain notes the incipient dive, it starts to take normal corrective reactions; but these reactions do not achieve the anticipated results because the corrective action is to a false horizon. These correct results, according to the inclined plane, promote further accelerations which confuse the bird. The bird is attempting to correlate compounding sensual information with visual information. As will be noted, it is the bird's inability to analyse the visual and sensory cues that is the basic cause of spatial disorientation. Unfortunately spatial disorientation, when flying, is a phenomenon which occurs with lightning rapidity.

In the case of Baldwin's observations of the bird flying directly into the lights, the situation is slightly different. The situation is a case of straight loss of visual cues. This situation is analogous to the poacher with his strong light after pheasant. The pheasant remains perched in the light without moving, not because of hypnosis, but because it has lost its visual cues to spatial orientation. The proprioceptive, vestibular, and visceral senses maintain the pheasant's balance on the tree, but it is afraid to fly because it cannot resolve the problem of spatial orientation without visual cues. The light has obliterated any background and consequently all the pheasant can see is the light. This is exactly what happens when the bird flies into the lights. It loses its visual cues to the horizontal. The vestibular apparatus can measure only accelerations and when they stop, but not when the bird returns to the normal position. Consequently, the bird is comparing sensory information with visual information and is unable to resolve the problem because there is no visual information. In this particular case it is quite conceivable that spatial disorientation does not occur until such times as the bird takes evasive or corrective action. At that time the vestibular apparatus would be subjected to accelerations. Once the accelerations are reduced to zero the bird has no indication of the true horizontal except tactile and visceral senses, and these senses are not accurate enough for flying. Therefore, with an absence of visual cues, the bird has no means of orienting itself and is forced to accept any cues it can find. If the lights or the shadows are used as a datum, spatial disorientation is the inevitable result.

The refracted and reflected electric light in precipitation produces the same result. With the sun or moon shining on a reflected surface, the bird can maintain a constant bearing or azimuth and angular altitude to the reflected image. (Celestial light is, for practical purposes, made up of parallel rays). However, when the bird attempts this normal reaction with the unnatural light, it immediately begins to fly a curve, because the unnatural light is disseminated radially from its source. Thus the visual senses appreciate a fixed horizon, but the sensory apparatuses appreciate the accelerations of the arc of the flight path. There is a tendency for the rate of turn to increase thereby compounding the accelerations. As the rate of turn increases, there is a change in the angular altitude of the light. To offset the change the bird would have to change its degree of roll thereby producing further accelerations. Now the bird has a visual cue to the horizontal and discrepant sensory cues. Since it cannot resolve the information, it becomes spatially disorientated.

The refracted and reflected light in precipitation produce the same results through exactly the same causes. Because it has a very localized source this light is not directly overhead, but at any angle between the bird and the source of light. This angle is dependent on the proximity of the bird to the source of light. Whether the bird is misled into reasoning that the light is the Aurora or halation from high clouds, is unknown. The bird, however, accepts the light as the true horizon and reorients itself accordingly. The sensory apparatus detects the accelerations. As soon as a comparison of visual and sensory cues is effected, spatial disorientation is imminent. An analysis of the weather conditions in Stoddard's report (1962) will show that on all of the twenty-four occasions, parts of the TV tower were obscured on thirteen nights, the tower was clear on nine nights but there was precipitation on five of these nights. There is no comment on the tower for two occasions. A further observation from this report is that an halation ring did develop in low cloud and Scotch mist. In these cases the birds have no horizon as a visual cue to the horizontal whether proceeding to or from the tower and are consequently subjected to spatial disorientation through the same causes as previously illustrated.

In the case of airport ceilometers it is evident that the birds are suffering from spatial disorientation, if not complete vertigo, as Laskey (1956) reports "hundreds fluttering high in the beam." In this situation, the intense lighting is from underneath with darkness on top. The lighting situations is the exact reverse of normal natural light. The ceilometer has obliterated any horizon which the birds had prior to entering the light beam. Therefore the only cues it has are its sensory mechanisms plus its sight. As it attempts to reorient itself by sight, the senses appreciate the deviation from the horizontal and the birds become disoriented. Howell's (1955) conclusions as to the probable causes of death being an impact with the ground would substantiate an inability of the bird to orient itself. It must be noted that very few birds collide in the air and fall to the ground. Birds are capable of regaining flight within a foot vertically of the point of collision. If the bird was not disoriented, no spiral dive and ground impact would occur. As such collisions have been witnessed (Howell, 1955), it must be concluded that the birds were unable to take exasive action, and therefore must have become disorientated.

## SUMMARY

The bird possesses various senses to determine its spatial orientation. The visceral senses give the bird an indication of its body position in space and of the "G" forces acting upon its body during aerial gyrations. The "tactile" senses of the feathers will give the bird an indication of the airflow pressures on either side of its body and wings and allow the bird to sense a bank or a spiral dive. The proprioceptive senses give the bird an indication of its body position relative to its head. The vestibular apparatus can sense the bird's equilibrium. All of these senses, whether singly or in concert, are not sufficient to maintain a proper spatial orientation. The eyes are the predominant organ of spatial orientation, and for gaining cues to maintain spatial orientation. However, where there are discrepancies between the visual and sensory cues, the visual cues will be accepted rather than the sensory cues. The sensory cues still have sufficient effect to cause a metal block or confusion. The bird has not enough knowledge to analyse the situation and is therefore unable to take any true corrective action. The consequences of the situation is that the bird suffers from spatial disorientation and, in some cases, complete vertigo. The only conclusion is that birds are susceptible and suffer from spatial disorientation, and further that the causes of spatial disorientation in birds are exactly the same as those which affect the human pilot, namely; (a) the loss of true visual cues to the horizontal; (b) inexperience in flying under such conditions where visual cues are lost; (c) conflict between the sensory and visual cues to orientation; (d) entering an unusual position without being aware of it; plus (e) the lack of knowledge and reasoning ability when dealing with unnatural phenomena.

LITERATURE CITED

ARMSTRONG, H. G. 1952. Principles and Practice of Aviation Medicine. Third Ed., Williams and Williams Co. Baltimore.

BALDWIN, D. H. 1963. Mass mortality of nocturnal migrants in Ontario. Ontario Field Naturalist, 1:7–15.

CLARK, B. AND A. GRAYBIEL. 1955. Disorientation: A Cause of Pilot Error. Bureau of Medicine and Surgery Research Report No. NM 001 110 100 39, U.S. Naval School of Aviation Medicine.

DAVIS, J. M. 1953. Spatial Disorientation. Proceedings of a Conference on Orientation in Animals, Cornell University, Ithaca, N.Y. 6 and 7 February 1953, Office of Naval Research.

GRAYBIEL, A. 1951. Spatial Disorientation in Flight. The Military Surgeon, 108:287–294.

GUYTON, A. C. 1961. Textbook of Medical Physiology. W. B. Saunders Co., Philadelphia.

HERRICK, C. J. 1924. Neurological Foundation of Animal Behavior. Henry Holt and Co., New York.

HOCHBAUM, H. A. 1955. Travels and Traditions of Waterfowl. Univ. of Minnesota Press, Minneapolis.

HOWELL, J. C. 1955. A comparison of ceilometer mortality at Knoxville and Nashville, Tennessee in 1951 and 1954. Migrant, 26:53–57.

LASKEY, A. R. 1956. Bird casualties at Smyrna and Nashville ceilometers 1955. Migrant, 27:9.

LINCOLN, F. C. 1950. Migration of Birds. U.S. Fish and Wildlife Service Circular No. 16:29.

MANN, I. AND A. PIRIE. 1950. The Science of Seeing, (Revised Edition) Penguin Books, Harmondsworth, Middlesex.

QUEENY, E. M. 1947. Prairie Wings. J. B. Lippincott Co., Philadelphia and New York.

STODDARD, H. L. SR. 1962. Bird Casualties at a Leon County, Florida TV Station, 1955–1961. Bulletin No. 1, Tall Timbers Research Station, Tallahassee, Florida.

TORDOFF, H. B. AND R. M. MENGEL. 1956. Studies of birds killed in nocturnal migration. Univ. of Kansas Publ., Museum of Natural History, 10:4–7.

VAN TYNE J. AND A. J. BERGER. 1959. Fundamentals of Ornithology. John Wiley and Sons, Inc., New York.

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