Inertial Navigation as a Basis for Animal Navigation

JOHN S. BARLOW

*Neurophysiology Laboratory of the Neurology Service,
Massachusetts General Hospital and Department of Neurology,
Harvard Medical School, Boston, Massachusetts, U.S.A.*

The phenomenon of animal navigation has thus far not been completely explained in physiological terms, although it now appears to be well established that several species utilize celestial aids in their navigation. The remarkably successful development in recent years of self-contained *Inertial Navigation Systems* for automatic indication of position and for the control of motion of man-made vehicles (missiles, airplanes, submarines) suggests the necessity of a reconsideration of some aspects of the problem of animal navigation in the light of these developments. The basic principle of inertial navigation is that of determination of direction, and of distance travelled, by means of a double integration with respect to time of acceleration, due regard being made for the fact that the motion is carried out with respect to a spherical, rotating earth. Certain inertial systems of a hybrid type utilize celestial navigation as a supplementary aid; for this purpose automatic star-tracking devices are employed.

From a close examination of published experimental results it cannot be said that an explanation on an inertial basis of animal navigation is in accord with all of the available experimental evidence obtained from animals, but a number of experimental results that have previously appeared to be puzzling are found to be consistent with the possible existence of a physiological inertial system of either a pure or hybrid form.

Accordingly, further investigation of the problems of animal navigation from the standpoint of inertial navigation, a possibility that has in effect long been considered, appears merited. Some additional specific experimental tests, including ones in orbiting earth satellites, are proposed. At least, from the principles of inertial navigation, a full definition and possible explanation in physiological terms of the often-used but ill-defined term, "sense of direction", and of its logical complement, "sense of distance", can be advanced. These two senses, which are complementary and interrelated, may be considered as integrated ones, based on a primary "sense of inertia", for which the specific sensory receptors in vertebrates are the vestibular organs.

Introduction

The problem of animal navigation is one that continues to excite keen interest, and is the basis of a considerable amount of experimental research.

However, despite a great amount of work in the past and the consideration of a number of possible hypotheses, no single theory or combination of theories has been accepted which explains all of the known ways in which animal navigation manifests itself, from the traversing of the laboratory maze by small animals to the homing and migration of some species over thousands of miles.

On the other hand, extremely great progress has been made in the last few years in man-made navigation systems for the establishment of position and direction, and for the automatic control or guidance of vehicles of various types. The latter accomplishment has been made possible by developments in the field of *inertial navigation*. Indeed, it has become possible to control automatically the paths of ballistic missiles, aircraft, ships, and submarines to a prescribed destination with remarkable accuracy by means of inertial guidance. For example, for ballistic missiles an error of as small as a few hundred feet at a target distance of several thousand miles is not uncommon, at the present time.

In view of the as yet unclear basis of animal navigation, it appears appropriate to examine some aspects of this problem in the light of some of the principles by which inertial navigation is accomplished (Barlow, 1961). No attempt will be made to consider all of the theories of animal navigation that have been proposed from time to time (see, for example, Fischer (1928), and Carthy (1956), for a review). The phenomenon of bird navigation has particularly received attention in reviews of recent years (Griffin, 1944, 1952; Matthews, 1955; Kramer, 1960; Precht, 1961; Dorst, 1962; Schmidt-Koenig, 1964). Navigation necessitates knowledge of present position, direction and magnitude of motion with respect to other points of reference (Fernandez & Macomber, 1962). Schmidt-Koenig (1964), who has recently proposed a classification of orientation by animals, has defined navigation by animals as the capacity to maintain or establish reference to a goal other than through recognition of known landmarks. It is this concept that was embodied in Griffin's (1952) Type III homing ability of a bird, as manifested by a choice of approximately the correct direction of its home even when it is carried into unfamiliar territory in a new and unaccustomed direction. A symposium on animal orientation has recently been published (*Ergebnisse der Biologie*, **24**, (1963)).

Inertial Navigation

The term, *inertial navigation* (Klass, 1956; Slater & Duncan, 1956; Draper & Lees, 1957; Anderson, 1958; Draper, 1958; O'Donnell, 1958; Draper, Wrigley & Hovorka, 1960; Fernandez & Macomber, 1962; Pitman, 1962; Pines, 1962) is derived from the fact that it is based upon the *inertia* of bodies,

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i.e. their tendency when at rest to remain at rest, and when in motion to remain in motion, if there is no outside force (e.g. gravitational) acting upon them. Inertial navigation is therefore based fundamentally on Newton's laws of motion. It is important to note that the frame of reference for Newton's laws is, strictly speaking, inertial space, i.e. space that is fixed with respect to the so-called "fixed stars" (cf. Page, 1935, p. 53; Draper, 1958). The general characteristics of inertial guidance systems are shown in Fig. 1.
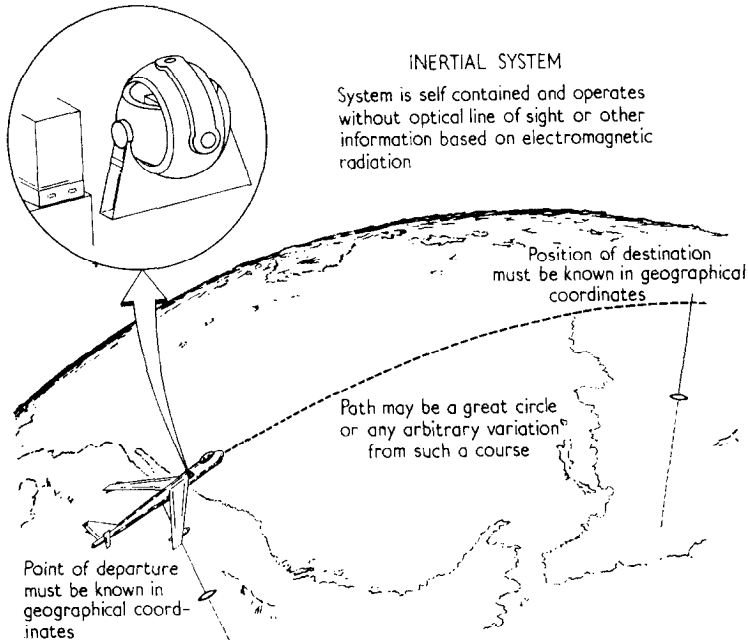
FIG. 1. General characteristics of inertial guidance navigation systems. For automatic control of the flight, the inertial system must be provided with settings of position, speed, and direction, at the time of departure. The position of destination must be set into the system, but the destination may be changed at will during the flight. (Reproduced by permission from Draper & Lees, 1957.)

From the Figure it is apparent that inertial guidance systems for navigation can be completely self-contained, and hence in their basic form they do not require any external information for the purpose of navigation.

In Fig. 2. are illustrated the principles of inertial navigation in a single plane that is either in a gravitational-free field, or is perpendicular to the direction of gravity. The principles are direct measurement of acceleration by means of appropriate sensors, integration with respect to time of acceleration to obtain velocity, and finally a second integration with respect to time to obtain distance. If the geographical coordinates of the starting

point (i.e. the initial conditions) are set in before the trip is begun, the position of the vehicle in terms of geographical coordinates can be indicated continuously during the journey. Once the coordinates of both the initial position and the destination are specified, the outgoing path and the return path can be chosen arbitrarily, as indicated in Fig. 2. The paths can, in fact, be prescribed beforehand, and if it is desirable they can be changed *en route*. If the movement of the vehicle is automatically controlled by the inertial navigation system, then the time course of the journey can also be prescribed or programmed, and it can be changed *en route*.

Outgoing path
(arbitrary)

Destination
(x_1, y_1)

y

x

Return path
(arbitrary)

Starting point (x_0, y_0)

$$\text{Distance}_x = \iint a_x dt^2 \qquad \text{Distance}_y = \iint a_y dt^2$$
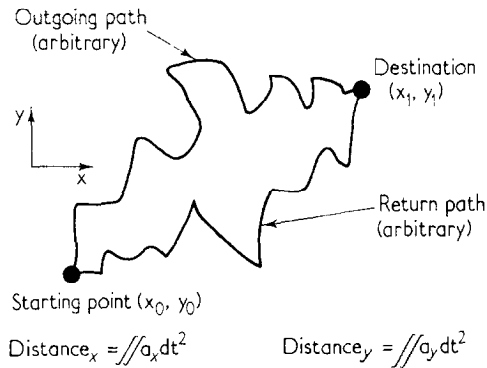
FIG. 2. Schema of inertial navigation. The coordinates of the starting point and destination must be specified, but the outgoing path as well as the return path is arbitrary. The x and y components of the distance at any point in the trip are given by double integration of the corresponding accelerations with respect to time.

It is to be emphasized that inertial systems are entirely self-contained, and require no input of information from the outside; the systems thus operate without a magnetic compass, radio, radar, or optical information concerning local landmarks or the sun or stars. For example, with the aid of a Ships' Inertial Navigation System (SINS), the course of a ship could be specified in advance, i.e. pre-programmed, and an appropriate signal could be derived and fed to the automatic steering mechanisms to steer the vessel along the desired course. Moreover, from information concerning the ship's heading that is required to make good the desired course, and from a determination of the speed of the ship with respect to the water, or of the thrust of the engines necessary to make good the desired speed (with respect to the earth), it would be possible to determine, by means of information obtained entirely within the ship itself, the resultant of the effects on the ship of tidal stream, current, wind and weather (Bailhache, 1960; Draper, Wrigley & Hovorka, 1960). The automatic control of a ship in this manner can truly be considered a remarkable example of cybernetics, representing as it does an ultimate logical

extension of the simple control by man or by machine of a ship's rudder, from which Wiener (1961, p. 11) originally derived the term "cybernetics".

A simplified scheme of the manner in which linear velocity and distance can be obtained from an original measurement of rectilinear acceleration is shown in Fig. 3. The accelerometer consists of a mass (m) whose motion
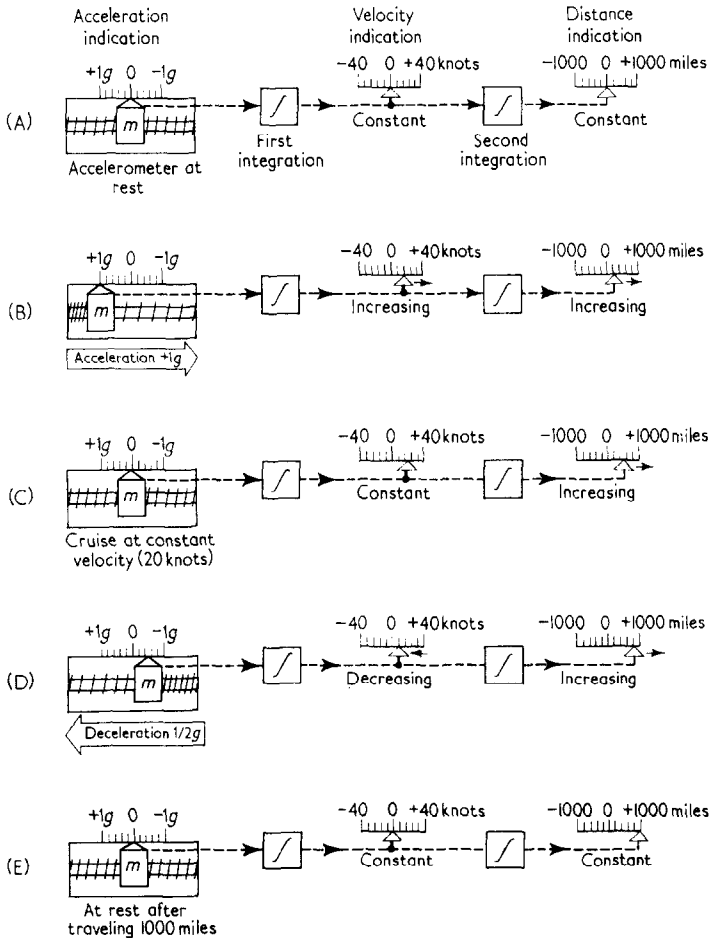

FIG. 3. Illustration of the principle of operation of a rectilinear accelerometer, and integration with respect to time to obtain velocity and distance. The vehicle is initially at rest (A). Then, as it begins to move (B), the mass m of the accelerometer tends to remain at rest, and hence an acceleration of 1 g (32 ft/sec^2) is registered, which continues until a velocity of 20 knots is reached. The vehicle continues at this velocity (C) until just before the end of the journey when, following a deceleration of $\frac{1}{2} g$ (D), it comes to rest, after a distance of 1,000 miles is travelled (E). (Reproduced by permission of the authors and publisher from Curtis & Slater, 1959.)

along the rod (which thus constitutes the "principal axis") is restrained by springs. The accelerometer can be calibrated in terms of the acceleration due to gravity (g) simply by orienting the principal axis vertically with respect to the earth's surface. In its actual operation, however, if the accelerometer is to measure only horizontal acceleration, it is essential that the principal axis of the accelerometer be maintained continuously in the horizontal plane so that there will be no component of the acceleration due to gravity acting upon it; were there a component of the latter present, a spurious acceleration would be registered that would result in errors in the determination of distance, which would increase as the square of time.

In order to make determinations of change of heading, it has frequently been the custom in the construction of inertial navigation systems to employ gyroscopes. According to the particular system, either an absolute reference direction is maintained, as the direction of the spin axis of a gyroscope, or the total angular deviation of the gyroscope axis from some initial direction is determined; accordingly, the terms geometric and analytic-reference coordinate storage are respectively used (Draper, Wrigley & Hovorka, 1960). A system for measuring changes in direction can also be based on the elementary torsional pendulum employed as an angular accelerometer (McClure, 1960, p. 29; Fernandez & Macomber, 1962, p. 147). The manner in which a torsional pendulum can be utilized for this purpose is illustrated in Fig. 4 for the sequence of events that occur in making a 90° turn. It is of interest to note that the absolute direction of the pointer in the Angular Displacement Indication dial on the right in the figure remains constant; the Angular Displacement Indicator therefore is in some respects the equivalent of a compass.

The details of construction of rectilinear accelerometers vary. Instead of being confined to move along a line, as shown in Fig. 3, the inertial element, or mass, may be constrained to move about a pivot; the term, pendulous rectilinear accelerometer is thus used. (In fact, an angular accelerometer of the type described above can be converted to a rectilinear accelerometer simply by the addition of an off-center mass to the former.) In one type of accelerometer, the output signal is in the form of a series of pulses, the interval between which is proportional to the magnitude of the applied acceleration (Curtis & Slater, 1959). This type of accelerometer is of special advantage if the acceleration to be measured is subject to rapid changes over a relatively short time. If two such integrating accelerometers with identical characteristics were operated in push-pull fashion (i.e. so that a positive acceleration results in a decrease in the pulse-interval for the one, and an increase in the pulse-interval for the other), a measure of velocity could be given by the *cumulative difference* between the total number of the pulses

from the two. The same arrangement could be employed with a pair of angular accelerometers based on the principle of the torsional pendulum. The manner in which such a pair of integrating accelerometers could function
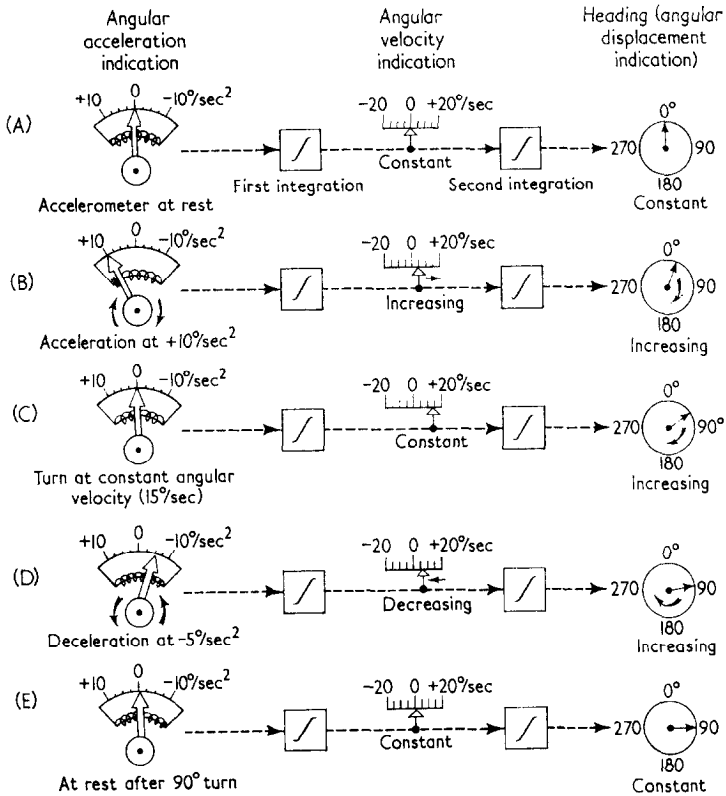

FIG. 4. Illustrations of the principle of operation of angular accelerometer based on the torsional pendulum, and of integration with respect to time to obtain angular velocity and total angular displacement (or heading). In (A) the vehicle is at rest, and its heading is 0°. During the initiation of the turn (B), the torsional pendulum tends to remain at rest with respect to the vehicle, and hence an angular acceleration of $+10°/\text{sec}^2$ is registered, which continues until an angular velocity of 15°/sec is attained. The vehicle then continues to turn (C), at this constant angular velocity, until the turn is nearly complete. Then, following an angular deceleration of $-5°/\text{sec}^2$ (D), the vehicle comes to rest (E), having completed the 90° turn.

is shown in Fig. 5. The five sequences illustrated in this figure, for rectilinear and for angular acceleration, correspond to the five sequences in Figs. 3 and 4 respectively. The velocity (rectilinear or angular) at any instant after the start of the journey is seen to be proportional to the cumulative difference

between the output of a pair of accelerometers (rectilinear or angular respectively). Displacement is then obtained by integration of the velocity.

In actual usage, the output signal of an accelerometer may be amplified and fed back to provide a restoring force to counteract the impressed acceleration, so that the inertial element remains in its equilibrium position with respect
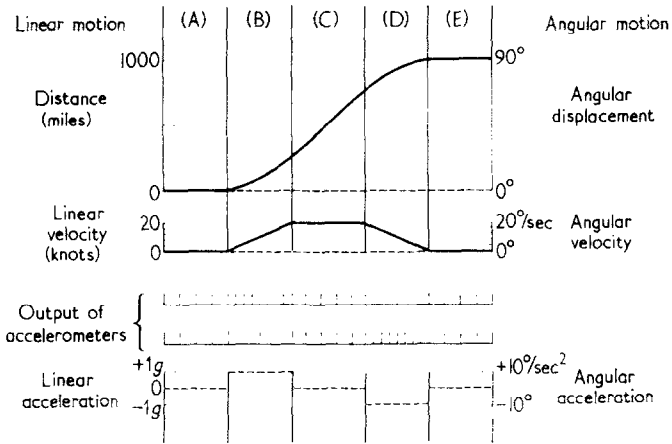

FIG. 5. Schematized operation of a pair of integrating accelerometers for rectilinear or for angular motion. The instantaneous velocity is directly proportional to the cumulative difference between the number of pulses from the two accelerometers. (For the sake of clarity, the spacing between pulses is greatly exaggerated.) Distance, or angular displacement, is obtained by further integration with respect to time of the velocity. The five stages for rectilinear, and for angular motion, correspond to the five stages in Figs. 3 and 4 respectively. When the vehicle is at rest (A), the output of the accelerometers remains the same, and hence the indicated velocity is zero. During the initiation of motion (B), the cumulative difference between the number of pulses for the two accelerometers increases and the indicated velocity increases accordingly. After the initial acceleration ceases, the output of the accelerometers is once again the same, and hence the accumulated difference between their pulse output, i.e. the indicated velocity, remains constant (C). During deceleration (D), the cumulative difference between the number of pulses decreases, and accordingly the indicated velocity decreases, until the termination of the motion (i.e. completion of a distance of a thousand miles, or of a 90° turn), whereupon the cumulative difference is once again zero and remains constant at this level (E), since the output from the two accelerometers is once again identical.

to the accelerometer case. The magnitude of the impressed acceleration is then given by the amplitude of the above-mentioned feedback signal. The range of measurable accelerations can be increased appreciably by the use of this principle.

In the schema depicted in Fig. 2, it is assumed that the accelerometers for the X and Y directions remain fixed in their respective directions, regardless of the angular motions of the vehicle as the latter changes its heading. One

means of maintaining the direction of the principal axes of the accelerometers fixed is that of mounting the accelerometers on a platform that is stabilized by means of gyroscopes. The necessary information for maintaining a stabilized platform in a fixed direction could also be derived from the Angular Displacement Indicator System depicted in Fig. 4, since the latter in effect indicates continuously a fixed direction.

INERTIAL NAVIGATION ON THE SURFACE OF THE EARTH
—THE LOCAL VERTICAL

In the preceding discussion it has been assumed that the motion is either in a gravitational-free field, or that it is perpendicular to the direction of
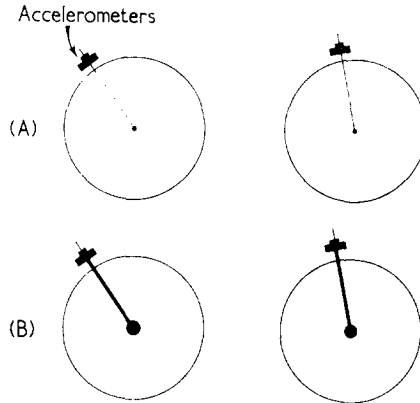

FIG. 6. Idealized methods for maintenance of local vertical (and therefore also the local horizontal) by means of: (A) a rod connected to the center of the earth; (B) a pendulum with its bob at the center of the earth. The latter would constitute a Schuler pendulum with a period of eighty-four minutes. Note that in both instances the accelerometers remain horizontal as they are moved over the earth's surface, and hence they sense no component of gravity, which is directed vertically.

gravity itself. For motion on the surface of the earth, however, the direction of gravity itself changes as the motion proceeds. Since it is essential that the accelerometers, from which distance on the surface of the earth is determined, remain perpendicular to the direction of gravity (as was pointed out above), it is apparent that the inertial system must be capable of continuous determination of the direction of gravity, i.e. of the local vertical.

The problem of the maintenance of an indication of the local vertical can be viewed as depicted on the left in Fig. 6. It is apparent that a platform mounted on an imaginary rod connected to the center of the earth would fulfil the necessary conditions, for the platform would rotate about the center of the earth. A simple pendulum suspended from an airplane, and

having its bob at the earth's center, i.e. having a length equal to the radius of the earth (the Schuler pendulum), as depicted on the right in Fig. 6, would also be capable of maintaining a continuous indication of the local vertical (Schuler, 1923). The bob of such a pendulum, initially at rest at the earth's center, would remain at rest as its support (i.e. the airplane) moved about the earth's surface. (If the supporting surface remained stationary, and the pendulum bob were displaced from its position at rest, it would oscillate with a period of eighty-four minutes.) The schemata depicted in Fig. 6 are, of course, not physically realizable.

The effect of a Schuler pendulum, however, can be realized by means of a feedback arrangement, and one such system for this purpose is illustrated in Fig. 7. The surface on which the north-south (NS) accelerometer is placed is
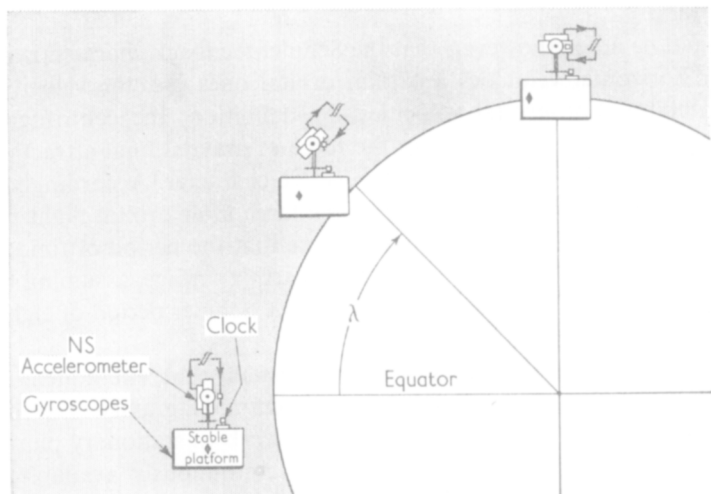

FIG. 7. Principle of a continuous maintenance of an accelerometer in the horizontal plane by means of a feedback loop. The accelerometer base is continuously rotated, as the vehicle travels about the earth, in such a way that the accelerometers are maintained perpendicular to gravity. The feedback loop, by means of which the orientation of the base for the accelerometers is determined from their own output, is indicated by the arrows and includes the double integral sign. The distance travelled is continuously converted to the angle λ by means of division of the former by the distance to the center of the earth.

In order to compensate for the constant rate of rotation of the earth on its axis (15°/hour), the accelerometer platform is continuously rotated or precessed about an axis parallel to the earth's axis of rotation; a sidereal clock is employed for this purpose. The view in the figure is taken with respect to the earth and hence the gyroscopically stabilized platform (which actually remains fixed in its direction with respect to inertial space) is shown as rotating to the left, as indicated by the successive positions of the diamond-shaped indicator.

The methods for correcting for the centrifugal (i.e. gravity deflection) and Coriolis effects associated with the rotation of the earth are not shown. (Reproduced by permission of the author and the publisher, from Klass, (1956).)

itself mounted on a gyroscopically stabilized platform in such a way that the accelerometer can be rotated with respect to the stabilized platform. As the vehicle moves, the accelerometer base is continuously rotated at an angular rate that is given by the linear velocity of the vehicle divided by the distance to the center of the earth, the linear velocity itself being determined, in turn, from the integrated output of the rectilinear accelerometers. The net result is that the accelerometer platform is rotated through an angle that is equal to the arc of travel (λ in Fig. 7) with respect to the earth's center. This condition, under which the output signal of the accelerometer is doubly integrated, converted to an angular displacement, and fed back to control the position of the mounting base for the accelerometer so that the latter remains horizontal, is called Schuler Tuning (cf. Draper, 1958), and the corresponding feedback loop (indicated by the arrows in Fig. 7) is called the Schuler loop.

It should be noted, however, that the Schuler feedback characteristic holds only for horizontal velocities less than orbital ones (i.e. the velocity of an earth satellite). For orbital velocities, by definition, the centrifugal force acting on the satellite just balances the force of gravitational attraction, and hence the feedback is no longer of a negative character. Accordingly, errors in the indicated local vertical may become large after orbital flight of more than a few minutes. (It is interesting to note that the period of time for one orbit of a satellite in a circular orbit at the earth's surface, assuming that the atmosphere were not present, would be just the Schuler period of eighty-four minutes, approximately.)

It is thus a remarkable aspect of inertial systems that, subsequent to their initial alignment (see below), the local direction of gravity (i.e. the local vertical, or the direction that would be indicated by a stationary plumb bob) is calculated rather than measured, and is continuously available. If the rotation of the earth is taken into account, the indicated local vertical is in fact unique for each point on the earth's surface (Draper, 1958).

The existence of the feedback loop provides the basis, on occasion, of sustained oscillations in the inertial system such that the indicated position oscillates, even if the vehicle itself is at rest; the period of this oscillation (the Schuler oscillation) is eighty-four minutes. Thus, in a manner analogous to the oscillations that a Schuler pendulum (Fig. 6(B)) would undergo if its bob were displaced from its equilibrium position, the mounting base of the accelerometer shown in Fig. 7 will also exhibit a tendency to oscillate if initially it is not correctly aligned with the local vertical. Under the conditions of such a misalignment the accelerometer will sense a component arising from the acceleration due to gravity. However, as the misaligned accelerometer does not distinguish between the sensed component acceleration due

to gravity and acceleration arising from non-uniform rectilinear motion with respect to the surface of the earth, the result will be that the output of the accelerometer is considered as a shifting of position on the earth's surface. Hence a corresponding tilting of the accelerometric platform results in such a manner as to diminish the component of gravity being sensed. The period of the resultant oscillations, which may persist unless they are damped in
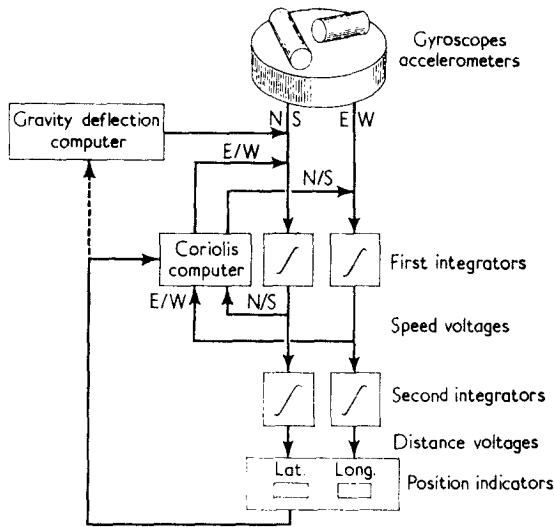

FIG. 8. Schematized indication of computation of Coriolis and gravity deflection corrections. Note that the Coriolis effect for north-south motion results in a correction to the east-west measured acceleration, and *vice versa*. The correction to the direction of gravity that arises by virtue of the earth's rotation is dependent only upon latitude. Quantitatively, the correction introduced into the output signals of the N–S accelerometer is given by $2\Omega V_{E-W}$ (sine λ), and for the E–W accelerometer is $2\Omega V_{N-S}$ (sine λ), where Ω represents the earth's angular velocity of rotation of 15°/hour, V_{E-W} and V_{N-S} are the east-west and north-south components of the ground velocity respectively, and λ is the latitude. The correction to the output of the N–S accelerometer for the deflection of the direction of gravity is given by $r\Omega^2$ (sine 2λ), in which r is the distance from the earth's center. (The illustration is reproduced, slightly modified, from Anderson (1958), by permission.)

some manner, is the period of the Schuler pendulum, i.e. eighty-four minutes. Since the accelerometer platform and the output signal of the accelerometer are oscillating, the indicated position oscillates also, even though the vehicle is actually at rest.

The fact that the navigation is being performed with respect to the earth which is itself rotating introduces additional correction factors that must be taken into account in inertial systems (cf. Klass, 1956; Anderson, 1958), corrections that arise in a straightforward manner from the generalized

equation of motion in theoretical physics (cf. Page, 1935, p. 105). Since the earth rotates on its axis at the rate of 15°/hr with respect to the "fixed stars" (i.e. once each sidereal day), the accelerometer platform must be rotated or precessed accordingly (see Fig. 7), even if the vehicle remains at rest with respect to the earth. By virtue of the centrifugal effect of its rotation, the earth is slightly flattened, and the local vertical (the direction of a plumb-line stationary with respect to the earth) is slightly inclined with respect to a line from the center of the earth. The latter effect is maximum at 45° (at which latitude it amounts to 11′ of arc) and is absent at the geographic poles and at the equator. Moreover, navigation performed with respect to a rotating earth necessitates that the Coriolis effect (cf. Fernandez & Macomber, 1962, pp. 35, 36, Figs. 2.20 to 2.22) be taken into account. Appropriate correction factors for these effects are accordingly computed and included in the calculations that are carried out automatically in the inertial navigation system. It is important to note that these corrections are not measured directly; rather, they are computed, as is indicated schematically in Fig. 8.

DETERMINATION OF ALTITUDE

The preceding discussion has been confined to that of determination of displacement parallel to the surface of the earth, and it has been evident that for this purpose the direction of the vertical, i.e. the direction of gravity, is computed. However, if appreciable motion occurs in the vertical direction (e.g. for a ballistic missile), the magnitude as well as the direction of gravity must be computed, and combined appropriately with the output of a vertical accelerometer, inasmuch as the latter cannot measure or sense acceleration relative to the earth arising from gravitational attraction. For example, a vertical accelerometer would have a zero output signal during free fall near the earth's surface, even though the vehicle is undergoing an actual acceleration downwards of 1 g, i.e. approximately 10 m/sec^2, or 32 ft/sec^2. The determination of altitude by inertial means is, however, basically unstable (cf. Anderson, 1958; Fernandez & Macomber, 1962, p. 349; Pitman, 1962, p. 5). Errors in the determination of altitude, or vertical displacement tend to increase as the square of time, and are therefore unbounded, in contrast to the errors in determination of horizontal displacement, which are oscillatory and therefore bounded, by virtue of the Schuler feedback characteristic. For this reason, determination of altitude by inertial means is generally impractical for time intervals of more than a few minutes (cf. Pitman, 1962, pp. 4, 5). Accordingly, for a cruise vehicle (i.e. a ship or a submarine, or a plane travelling at essentially constant height above the earth), determination of altitude must be carried out by some other means. For ballistic missiles, however, determination of vertical displacement can be carried out by

inertial means, since the duration of flight is of the order of a few minutes only.

INERTIAL NAVIGATION SYSTEMS WITHOUT STABILIZED PLATFORMS

Although it is frequently the case that inertial navigation systems are constructed with a stabilized platform in order to eliminate the moment-to-moment changes in the orientation of the vehicle from the inertial sensors, systems do exist in which the rectilinear and angular sensing elements are rigidly fixed to the vehicle; the terms Strapped-Down, Vehicle-Oriented Inertial Navigation (VOIN) System, and Gimballess System, have been used to describe these systems (Draper, Wrigley & Hovorka, 1960; McClure, 1960; Fernandez & Macomber, 1962). For this purpose, three rectilinear sensors (arranged mutually perpendicularly, for example, parallel to the longitudinal, lateral, and vertical axis of the vehicle), and two or three angular sensors with axes parallel to two or three of the same vehicle axes, are employed. In principle, such a system employs the above-mentioned sensors and a computer which determines, from the initial position and from the output signals of the sensing elements, the present position, relative velocity, and heading, irrespective of the changes in orientation of the vehicle itself.

The computer in such a system, however, must necessarily be of greater complexity than in systems in which an actual stabilized platform is employed, for the function of the latter must now be effected by the computer. For example, perturbations in the orientation of the vehicle may subject the different rectilinear accelerometers to varying components of gravity; for determination of horizontal position, therefore, the computer must, on the basis of information from the angular sensors, determine the horizontal component of acceleration by trigonometric resolution before integration to obtain velocity and distance is carried out. Moreover, it should be noted that angular motions of the vehicle may of themselves impose centrifugal forces on rectilinear sensors, for which appropriate corrections would have to be made by the computer. Accordingly, the requirements for the computer, as well as for the inertial sensing devices (e.g. their dynamic range, or range of measurable acceleration), are more stringent than those for these components in inertial systems that employ an actual stabilized platform. These requirements may be relaxed somewhat if the vehicle is approximately level most of the times, as are many aircraft, ships and submarines (McClure, 1960, p. 291).

Despite these limitations, it is possible in principle to design such inertial systems with an accuracy equal to that of systems employing a stabilized platform. Because the mechanical configuration of the mounting for the

sensing elements is simpler if no platform is used (Wiener, 1962; Powell, 1963), platformless systems are attractive for certain applications. Moreover, the advancements in computer technology in the last few years have facilitated the development of practical strapped-down or platformless systems.

It is interesting to note that the Schuler periodicity of eighty-four minutes may still occur in the indicated position with a platformless system. The feedback loop (cf. Fig. 7) for these oscillations appears within the computer itself (McClure, 1960, p. 290). Moreover, the basic instability of determination of vertical displacement or altitude by inertial means still obtains for strapped-down inertial systems, in which the vertical component of the output signals of the three mutually perpendicular rectilinear accelerometers that are affixed to the vehicle must be obtained by trigonometric resolution.
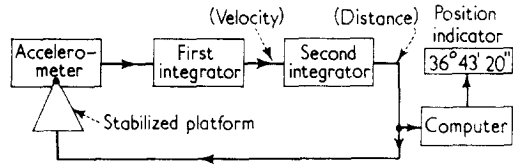
AIDS FOR INERTIAL SYSTEMS

The preceding discussion has been confined to those inertial systems that are entirely self-contained and hence utilize no external aids to navigation. In Fig. 9, two systems that do make use of ancillary aids are illustrated diagrammatically, in addition to the Pure Inertial System. For the former, the terms Hybrid, Aided, or Augmented, Inertial Systems have been used (Klass, 1956; O'Donnell, 1958; Pitman, 1962). In the Inertial-Doppler System, an ancillary radar system that utilized the principle of the Doppler effect gives an independent measure of the velocity with respect to the ground. In the Inertial-Celestial System, automatic star-tracking devices furnish an independent determination of position. In either the Inertial-Doppler or the Inertial-Celestial Systems, it is possible for the adjunct or ancillary system to be operated only intermittently. With the aid of a gyro-scopically stabilized platform, it is in fact possible to construct complete navigational systems based on either of the above two ancillary aids.

Any inertial navigation system may be recalibrated at intervals with the aid of position fixes obtained from an external reference. For this purpose, visual fixes (in which known landmarks are used), radio navigational aids, and celestial navigation can be employed.

CHRONOMETRY IN INERTIAL SYSTEMS

In the successful operation of inertial systems, accurate chronometry appears both intrinsically and extrinsically, since integration of acceleration with respect to time and the correction for rotation of the earth once each sidereal day both imply a stable time base. For a Pure Inertial System, or for an Inertial-Doppler System, the amount of time in sidereal units which has lapsed since the beginning of the journey suffices. However, Inertial-Celestial

(A) Pure inertial system
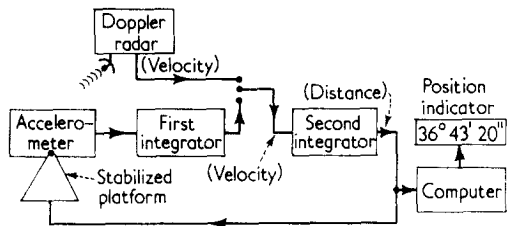
(B) Inertial–Doppler system
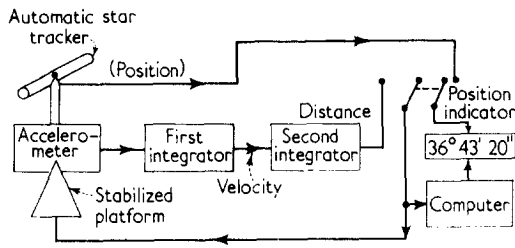
(C) Inertial celestial system

FIG. 9. Simplified diagrams of Pure, Inertial-Doppler, and Inertial-Celestial systems. The Pure Inertial system is entirely self-contained and requires no information from the outside. For the Inertial-Doppler system an independent check of ground velocity is afforded by means of a Doppler radar system. For the Inertial-Celestial system an independent check on position is afforded by means of automatic star-tracking devices. (Reproduced by permission of author and publisher, from Klass (1956).)

Systems require correct absolute, rather than lapsed, sidereal time (Stevens & Lynch, 1957; Stevens, 1958).

ALIGNMENT OF INERTIAL NAVIGATION SYSTEMS

In order to perform properly, inertial navigation systems must initially be aligned accurately. One practice is to utilize celestial information; should this not be available, the stable platform can be oriented parallel to the local vertical, the latter being determined from the direction of gravity, and the correct orientation in the horizontal plane can be achieved by means of an

azimuth accurately surveyed beforehand (Anderson, 1958). It is also possible to design an inertial system that is self-aligning, when the vehicle is at rest (O'Donnell, 1958). For Inertial-Celestial Systems, the clock of the system must be set to the correct sidereal time.

ACCURACIES AND ERRORS OF INERTIAL SYSTEMS

The accuracy obtainable with inertial systems is obviously dependent upon a number of factors, among which are the degree of precision of the sensing elements, their arrangement with respect to the vehicle, the precision of the computer, the time required for the journey, and the type of journey that is to be carried out. But the maximum attainable accuracy of a system will be determined by the performance characteristics of the angular and rectilinear sensing devices. Accordingly, the design of an inertial system with a specified accuracy necessitates the use of sensing elements of at least a certain level of precision.

As an example, it may be desirable in some cases to measure accelerations of up to ± 10 g with a resolution of 1×10^{-6} g, a dynamic range of 1×10^7 (Klass, 1956; Fernandez & Macomber, 1962, p. 195). For the angular sensing elements based on gyroscopes, the drift of the gyro axis is a principal source of errors in determination of position. For example it may be desirable to have a random drift rate of no more than $0.02°/hr$ (Fernandez & Macomber, 1962, p. 358). Moreover, a dynamic range of the order of 10^6 may be desirable for the angular sensing elements. For a strapped-down system, a dynamic range of nearly 10^9 may be necessary for the angular sensing element. (For comparison, one commercially available miniature angular accelerometer based on the principle of the torsional pendulum has a measurable range of angular acceleration from as low as $0.002°/sec^2$ to as high as $12,000°/sec^2$, a dynamic range of the order of 10^7 (Minneapolis-Honeywell, 1962).)

The estimation of overall system performance characteristics, including errors, of inertial systems is complex (cf. Fernandez & Macomber, 1962, p. 298 ff), and in fact it may necessitate simulation of the problem on a computer. The accuracy of an inertial system may be described in terms of the rate at which the position error builds up, or in terms of the error at some predetermined destination. For the latter, the term "Circular Probable Error" has been used, and refers to the radius of a circle inside of which 50% of the arrivals of a vehicle in a series of journeys would occur, from a given starting point (O'Donnell, 1958; Fernandez & Macomber, 1962). Correspondingly, 95% of arrivals, statistically speaking, would occur within a circle of twice the above radius.

More specifically, the errors in the determination of position which arise

from the sensing elements can be divided into those that are oscillatory and tend to be bounded (i.e. they do not exceed some maximum value), and those that tend to increase with time without limit. For travel at essentially constant height above the surface of the earth, the errors arising from rectilinear sensing devices fall into the former category (because of the Schuler tuning feedback characteristics), whereas those from the angular sensing elements fall into the latter category. In general, for relatively short-time journeys of this type the probable position error may be said to increase linearly with time, and for journeys long compared to the eighty-four-minute Schuler period it may be said to increase as the square root of time (O'Donnell, 1958). Errors in the determination of altitude, however, increase as the square of time, as previously mentioned.

As a specific example of the relationship between component accuracies and system errors, the Circular Probable Error for an airplane travelling at 614 nautical miles per hour (Mach 1, or the speed of sound) at an altitude of 20,000 feet for a one-hour flight along a great circle path, and utilizing an inertial system that employs rectilinear accelerometers with a bias (offset) error of 0·015 ft/sec² (i.e. 0·0005 g), and a scale-factor error of 1%, and gyroscopes with a drift rate (root-mean-square value) of 0·1° hr, is approximately 7·5 nautical miles (O'Donnell, 1958). This is a positional error of approximately 1%. In this particular example, the positional error due to gyro drift is about four times that due to the rectilinear accelerometer errors.

More recently mentioned figures for specifications of components include gyro drift rates of 0·02°/hr, rectilinear accelerometer bias (offset) errors of 1×10^{-5} g, and rectilinear accelerometer scale factor errors of 0·01%. These specifications would yield a Circular Probable Error of approximately ten miles after a four-hour flight of an airplane at 500 miles/hr at 20,000 feet, assuming that the errors are due only to the sensing elements (Fernandez & Macomber, 1962, p. 358).

The positional error of the Ship's Inertial Navigation System that was aboard the nuclear submarine, U.S.S. *Nautilus*, was reported to have been less than ten nautical miles after the transpolar submerged trip of 1,830 miles which lasted ninety-six hours, i.e. a positional error of 0·5%, after four days of travel (Anon., 1958).

It should be noted that the specifications and accuracies mentioned in these examples do not necessarily reflect the best currently attainable performances, especially since efforts are constantly being made to improve system accuracies. Moreover, as has already been mentioned, the design specifications of inertial systems for a given accuracy of performance over a given distance or time can be relaxed either by recalibration of the system at more frequent intervals, by the use of position fixes obtained in other ways,

or by the use of Doppler or Celestial aids to the Inertial System itself (cf. Pitman, 1962, p. 221).

Some Aspects of Animal Navigation

From the preceding discussion, it is evident that the man-made navigation systems that have been developed in the last few years are capable of controlling automatically and with remarkable precision the motion of a vehicle over appreciable distances by means of apparatus that is entirely self-contained. Some of these systems utilize on occasion external ancillary aids for navigation. The question then arises whether the feat of navigation as performed by a variety of animal species might also be carried out basically by inertial means. In the present context, animal navigation is taken to mean the ability of an animal to move intentionally from one location to another over territory that is at least in part previously unfamiliar to it. Although the present discussion is primarily concerned with the phenomenon of animal navigation as it has been the subject of experimental study, the discussion is also relevant to the problem of orientation and navigation by man, especially by the blind (cf. also Beritoff, 1961, p. 278).

The possibility that animals might navigate by means of a kind of dead reckoning system was raised by Charles Darwin in 1873 in the journal *Nature*. His remarks provoked a series of letters to the Editor of that journal; among these was one by Murphy (1873) who suggested, for the "faculty" mentioned by Darwin, a mechanical analogy, the principles of operation of which are remarkably prescient of those employed today in inertial navigation systems.

Subsequently, Exner (1893) suggested that the vestibular apparatus of animals could serve as the sensing element of a navigation system, and he observed that were the sensing apparatus fine enough the animal could evaluate sensory impressions from it so that the place of the animal in relation to its home would be determined at all times. In order to test this hypothesis, Exner then carried out a series of experiments with pigeons in which he employed rotation of the pigeons on the outbound journey, general anesthesia of the birds, and electrical stimulation of the vestibular apparatus. In none of these experiments did he find differences between the experimental birds and the controls. Subsequent experiments with anesthesia were carried out by Kluijver (1935) and by Griffin (1943); turntable experiments have been carried out by Rüppell (1936), Griffin (1940) and by Matthews (1951), all with negative results. Experiments with surgical interference with the vestibular apparatus were carried out by Hachet-Souplet (1911) and by Sobol (1930) and Huizinga (1935), all with negative results.

The above-mentioned hypotheses and experiments, as well as other

experiments of a similar type have been reviewed by Griffin (1944) and by Matthews (1955, pp. 74–77). With respect to the earlier experiments, including his own, Griffin observed that previous visual familiarity with the release territory or homing by random exploration could not be excluded. He concluded that the possibility of homing by memory of every twist and turn of the outward journey could not be said to be completely disproved, but he suggested that the accuracy and complexity of the required system would be so extreme that the hypothesis could not be seriously considered in the absence of direct supporting evidence. Matthews (1955) also concluded that it was highly improbable that recording and integration of displacement that were experienced during the outward journey could act as a basis for bird navigation, a conclusion that he felt to be supported by his own extensive series of rotation experiments (Matthews, 1951). He considered, however, that an absolutely final answer on this question would require similar critical releases of pigeons whose semicircular canals had been destroyed, but he suggested that such an operative procedure would be undesirable as the effects might be more widespread than anticipated, and that only negative results would be acceptable. His point may well be a valid one, in view of reports (Wendt, 1951) that the pigeon does not fly again after bilateral labyrinthectomy.

   An implicit assumption, however, in all of the above-mentioned experiments is that the vestibular apparatus provides the sole basis for homing, under the conditions in which the experiments were carried out. In particular, for example, visual aids to navigation either by means of previous familiarity with the territory of homing or by means of celestial aids have not been clearly excluded. The vestibular apparatus has therefore not been tested in the exclusion of other possible sensory aids. (In a subsequent section, specific suggestions for further experiments with this point in mind will be made.)

   It has generally been assumed that successful homing by animals transported while they are under general anesthesia is evidence against importance of the vestibular apparatus for homing. However, quite apart from the question of visual cues in such experiments, as mentioned above, this assumption must be re-examined in the light of the significant advances that have been made in recent years in the neurophysiology of the anesthetized state. In particular, it has been shown that anesthetic agents do not prevent primary sensory impulses from reaching the brain (cf. French, 1960), a general finding in which the vestibular system is no exception (Mickle & Ades, 1954). The effects of anesthetic agents have been shown to be primarily on the reticular activating system, which is also of great importance in natural sleep (French, 1960). Moreover, it should be noted that important physiological processes (e.g. respiration) continue under moderate doses of

anesthetic agents, as well as during natural sleep. It should also be recalled that it has been established in the last few years that some biological clocks, in addition to being remarkably precise, are remarkably resistant to external influences such as anesthesic agents and the lowering of body temperature (Rawson, 1960; Hastings, 1960). Particularly since a precise biological clock would be mandatory for the satisfactory operation of a physiological inertial navigation system, it may well be that the latter will also prove to be remarkably resistant to external influences. Thus, although it might seem logical that general anesthesia would render inoperative any central integrative mechanisms necessary for the establishment of the direction of home by means of sensory input from the vestibular apparatus, it is possible that this is not the case.

MEASUREMENT OF THE CORIOLIS EFFECT AS AN AID TO NAVIGATION

A possible role for the vestibular apparatus in animal navigation has been raised in a somewhat different way in theories of animal navigation based on a perception by animals of the Coriolis effect. By means of a perception of the Coriolis effect, it has been proposed that a determination could be made of geographic latitude (Yeagley, 1947, 1951), or of latitude as well as direction of motion (Ising, 1946). Both of these authors proposed a *direct measurement* by the animal of the Coriolis effect. Ising suggested the measurement of the Coriolis effect on a tube of fluid in motion (e.g. the motion of blood in the vascular bed), or the Coriolis effect upon a stationary torus of fluid that is rotated with respect to the earth's axis of rotation (e.g. the semicircular canals). Yeagley proposed a direct measurement, by means of unspecified organs, by a bird of the Coriolis effect upon itself while in flight. He proposed that the determination of velocity with respect to the ground, which would be necessary for this determination (cf. caption for Fig. 8) would be determined by visual means. The suggestion of a direct measurement of the Coriolis effect, which has been raised again by Beecher (1951, 1952, 1954), has been extensively criticized (de Vries, 1958; Wilkinson, 1948; Thorpe & Wilkinson, 1946; Griffin, 1952; Matthews, 1955), principally on the basis that calculations indicate that the sensitivity of the vestibular organ would not be sufficiently great for these determinations.

It was pointed out above that the Coriolis effect must be taken into account in inertial systems. It is to be emphasized, however, that inertial navigation systems are not based, even in part, on a direct measurement of the Coriolis effect. Rather, as is indicated in Fig. 8, the Coriolis effect appears as a correction factor computed on the basis of the present velocity (which is itself computed from the output of the accelerometers and position (latitude)), and is combined with the actual output of the rectilinear accelerometers. If,

therefore, birds navigate by inertial means, then the question of whether they are capable of *measuring* the Coriolis effect is irrelevant since the latter in inertial systems is a computed rather than a measured quantity. Nonetheless, the question of the basic sensitivity of the vestibular apparatus, which has been raised in the criticisms of the hypotheses of Ising and of Yeagley, are relevant to the present discussion. The question of sensitivity is therefore discussed below in some detail.

In view of the above discussion, the question of the importance of the vestibular apparatus in animal navigation must still be considered to be open. Moreover, the question of inertial navigation *per se* is especially relevant to vertebrates, in view of the well-established functions of the vestibular apparatus for the sensing of rectilinear acceleration (and of orientation with respect to the direction of gravity) and of angular acceleration, the utricle (and possibly, in some species, the saccule also) subserving the former, and the semicircular canals subserving the latter. (The possibility that some invertebrates might, by means of analogous structures (Pringle, 1957) also navigate by inertial means, will not be discussed here (cf., Pringle, 1963).)

SOME ASPECTS OF VESTIBULAR PHYSIOLOGY

A detailed discussion of vestibular physiology, which has been the subject of a number of recent reviews (cf. Wendt, 1951; Lowenstein, 1956a, b; Birukow, 1959; Gernandt, 1959), as well as of a conference monograph (Rasmussen & Windle, 1960), is beyond the scope of the present paper, but several points of direct relevance to the present discussion bear mentioning.

By virtue of the mounting of the otolith (as the inertial element) with respect to the supporting hair cells of the macula, the utricle can be considered in principle as the equivalent of a pendulous rectilinear accelerometer, displacements of the otoliths with respect to the macula occasioned by acceleration being signalled by a change in firing rate of many of the nerve fibers leading from the utricle. The operation of the cupula-endolymph system of the semicircular canals of vertebrates, as exemplified by the ray fish, can be described (Groen, Lowenstein & Vendrick, 1952) as that of a highly damped torsional pendulum (cf. Fig. 4). Further, the vestibular organs are paired, and hence they can be presumed to operate in push-pull fashion; the latter is attested to strikingly by the symptoms and signs that follow unilateral vestibular disorders (Gernandt, 1959).

The push-pull operation of the utricular macules (the otolith organs) as sensors for rectilinear acceleration, from which the acceleration due to gravity is indistinguishable (Einstein & Infeld, 1938; Einstein, 1945, p. 82) as was described in a preceding section (cf. also Jongkees & Groen, 1946), is

indicated schematically in Fig. 10 (cf. also Plate I of Lowenstein & Roberts, 1949). If the two organs are in the horizontal position the firing rate for the two sides in this idealized drawing is the same; an increase in the firing rate for one side which occurs during acceleratory motion (or after tilting) is accompanied by a decrease in the firing rate for the other side. For a given position the discharge rate of single fibers in the vestibular nerve may be remarkably constant (Groen, Lowenstein & Vendrick, 1952). It is of interest,
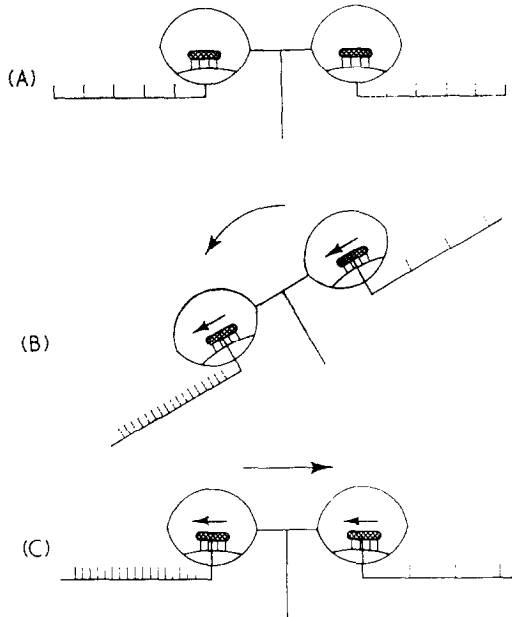

FIG. 10. Schema of the modulation of the pulse-interval by shearing of the utricular statoliths of the vertebrate vestibular organ. (A) horizontal position, at rest, (B) tilted to the left, (C) during linear acceleration to the right. (Reproduced by permission of author and publisher, from Birukow (1959).)

however, that the rate of firing of some fibers in the vestibular nerve remains constant irrespective of impressed accelerations (Lowenstein, 1956a), a phenomenon that could possibly form the basis for a central compensatory mechanism for changes in the input-output characteristics of the end-organ, due for example to changes in temperature of the latter.

In this connection, it is of interest that the cupulae of the lateral line organ, which bear a marked resemblance to those of the semicircular canals, and which share a common embryological origin with the latter, have been estimated to be sensitive to displacements of the overlying skin of the order of 25 Å (Kuiper, 1956, p. 140). Recent behavioral studies (Tavolga &

Wodinsky, 1963) suggest that the lateral line organs of certain fish may be sensitive to displacements of the order of 1 Å (W. van Bergeijk, pers. comm., 1963). Mention may also be made of the truly remarkable sensitivity of the electric receptors of certain fish (Machin & Lissmann, 1960), an organ whose evolutionary development may be linked (Lissmann, 1958) with that of the acoustico-lateralis system which includes the vestibular organ, the organ of Corti for hearing, and the lateral line organ. It is also relevant to note that the dynamic range for auditory stimuli of the organ of Corti (which shares a common embryological origin with the vestibular organ as well as a similar principle of operation of the primary sensory cells (Gernandt & Gilman, 1960; von Békésy, 1960)) has a dynamic range of 10^7 (Licklider, 1951).

From the above discussion it is apparent that the potential dynamic range and sensitivity of the vestibular organ may be very great, and the possibility must be considered that determinations of the threshold for acceleration which are based on observations of nystagmus of the head or eyes in animals, or of perception of acceleration by human subjects, may not indicate the potential capability of the vestibular organ itself for the measurement of acceleration. In a discussion of the operation of the semicircular canals, Lowenstein (1956b) suggested, in view of the fact that the response of many of the nerve fibers of the vestibular organ to acceleration is that of a change in an already existing firing rate, that whatever threshold exists for reflex responses to rotation (e.g. nystagmus) must be predominantly of central nervous origin.

Measurement of the minimum angular acceleration necessary to produce nystagmus of the head (e.g. in pigeons) or the eyes (e.g. in rabbits) have ranged from $0.1°/sec^2$ to $1.5°/sec^2$ (cf. Groen & Jongkees, 1948). Measurement of the threshold of perception of angular acceleration by human observers has ranged to as low as $0.2°/sec^2$ (Gernandt, 1959; de Vries, 1949). Von Békésy (1955) has remarked that the ratio between the minimal perceptible angular acceleration and the maximum that the organ can stand is of the order of 100, and he has contrasted this apparently small dynamic range with the large number of fibers in the vestibular nerve. A value of 6 cm/sec² (i.e. 0.006 g) has been reported by Jongkees & Groen (1946) for the minimum perceptible rectilinear acceleration by human subjects, lying on a parallel swing whose period was 2.5 seconds.

Determinations of the thresholds for perception of acceleration by human subjects, however, have not been carried out with the possibility of inertial navigation in mind, and it would be of interest to repeat these experiments but with those rare subjects whose "sense of direction" is said to be very good. It is possible, as has been suggested by Pumphrey (1948), that the

vestibular apparatus of the average human subject represents not a rudimentary, but a vestigial, system for precise orientation.

In view of the importance of feedback systems for extending the dynamic range of the sensing elements of inertial systems, as discussed in an earlier section, it is of interest to note that nerve fibers coursing from the brain to the vestibular end-organs have been demonstrated anatomically (cf. Carpenter, 1960; Gacek, 1960). Although the functional significance of this system of nerve fibers has not been worked out experimentally (Carpenter, 1960; Gernandt, 1963, personal communication), it has been suggested that the endings of nerve fibers on the primary hair cells of the vestibular receptors might form the basis of a feedback system of considerable importance for the vestibular system (Engström, 1958; Wersäll, 1960). In other sensory systems (i.e. auditory, visual, olfactory, and in the muscle stretch receptor system), such centrifugal fibers are known to constitute the elements of a feedback loop that serves to modulate the output of the sensory end-organs themselves (Brazier, 1958; Livingston, 1959).

CENTRAL INTEGRATIVE MECHANISMS

The possibility that analogies might exist between the central integrative mechanisms of the brain for the sensory information that is provided by the vestibular apparatus, and the computational procedures that form a part of inertial guidance systems, is an intriguing and relevant one (cf. also Beritoff (1961), p. 253 ff), but such a discussion is beyond the scope of the present paper. Prolonged post-rotatory spindle-like electrical discharges have, however, been recorded from implanted electrodes in or overlying the cerebellum in homing pigeons and migratory doves, but not in domestic pigeons or sedentary doves (Gualtierotti, Schreiber, Mainardi & Passerini, 1959; Schreiber, Gualtierotti & Mainardi, 1962).

THE VESTIBULAR APPARATUS AND SHORT-DISTANCE NAVIGATION

The role of the vestibular apparatus in the navigation of cats and dogs over a distance of a few meters has been extensively investigated in the last few years by Beritoff (1957, 1959, 1961), who has also reviewed earlier writings on the relationship of the vestibular apparatus to spatial perception (Beritoff, 1959, Chapter II), a field that is closely related to that of animal navigation. In one series of Beritoff's experiments, blindfolded animals were placed initially at one side of an experimental room and were then led on foot by a right-angle path to a food reward in another part of the room. The animals were then led from the original starting point to different release points in the room and set free. Beritoff found that the control animals could quite readily locate the feeding trough after being released, irrespective of

the location of the release. Several other possible sensory cues (auditory, olfactory, tactile) were examined, but only after bilateral labyrinthectomy was the performance of the animals seriously impaired. For the control animals, it was found that the feeding troughs were equally well located even if during the initial training period the animals were transported instead of led on foot to the food reward; these results appeared thus to exclude kinesthesis (by which is implied muscle, tendon and joint sense) as a sensory cue. Beritoff (1961) found similar results in analogous experiments with deaf-mute children with and without functioning vestibular organs.

Obviously the paths followed by Beritoff's animals to the food reward were arbitrary; a somewhat analogous result was found by Dashiell (1930) in his studies of the behavior of mice in an open-alley maze that permitted a large number of different paths of equal length. Dashiell found that, in a series of trials, an animal would follow a variety of different routes from entrance to exit.

"SPATIAL MEMORY", GENERALIZATION OF DIRECTION, AND ORIENTATION AT A DISTANCE

That animals can make a generalization of direction from the specific turns in the maze has been commented upon on a number of occasions (e.g. Lashley, 1929, p. 138). This has its counterpart in larger animals in the ability to return home over distances of several kilometers by the most direct path, even if the outgoing path has been a more devious one (cf. Schmid, 1932).

Although the path that an animal follows from its release to a goal may be arbitrary, the location in space of the destination at least in many instances is not, and the term "spatial memory" has been employed to describe the ability of animals to return repeatedly to precisely the same point in space, even if different paths have been followed in previous trips. In at least some instances this ability was not altered by appreciable changes in the immediate environment. For example, Watson & Lashley (1915) found that noddy and sooty terns were able to localize the site of their nests even if the visual environment, including the nest itself, were markedly altered. Hahn (1908), and later Möhres and zu Oettingen-Spielberg (1949), found a remarkable ability of bats to return repeatedly to the same point in space, an ability that may be dependent only initially on the well-known echo-location mechanism that bats possess inasmuch as it is known that they may collide headlong into obstacles newly placed in their accustomed paths of flight (Blatchley, 1896), even though their echo-location mechanisms may be operative at the time (Griffin, 1958, p. 164).

Several experimental studies have been concerned with the ability of

animals to orient themselves in the direction of home upon being released at a distance; for this purpose, displaced animals have been released in darkness in labyrinths offering exits in several possible directions (cf. Precht & Lindenlaub, 1952, 1954; Lindenlaub, 1955, 1960; Bovet, 1960). Although the results from this type of experiment have not always been unambiguous, on many occasions animals showed a clear preference for the homeward direction under conditions in which all visual cues were eliminated, and if the displacements (of the order of several hundreds of meters or a few kilometers) were not too great. Analogous observations have been made for salamanders (Twitty, 1959) and for toads (H. Kleinsteuber, 1961, personal communication).

TIME-COMPENSATED SUN ORIENTATION—CHRONOMETRY IN ANIMAL NAVIGATION

The ability of a number of species of vertebrates as well as invertebrates to utilize the position of the sun as information from which to derive direction has been firmly established in recent years (cf. Gould, 1959; Birukow, 1960; Braemer, 1960; Hoffman, 1960), and orientation by means of the stars at night has also been demonstrated for birds (Sauer & Sauer, 1960). It has long been apparent (Darwin, 1873), however, that information on direction alone does not suffice for successful navigation. This point is implicit in the map-and-compass concept of navigation which was outlined by Kramer (1953, 1959, 1960), and which has been re-emphasized by Schmidt-Koenig (1960).

In relation to the earlier discussion of chronometry in Inertial-Celestial Systems, experiments in which the orientational (i.e. choice of homeward direction) and homing ability of birds was tested after their internal chronometer had been reset (cf. Schmidt-Koenig, 1960) are of particular interest. In such experiments it has been found that the initial direction chosen by many released homing pigeons could be altered predictably (in some instances, even at a distance of a few kilometers from the home loft), although there was a noticeable increase in the scatter among the directions chosen by the experimental birds as compared with that for controls. Moreover, some of the experimental birds were able to reach home, a result that indicated that the initial erroneous orientation had been corrected *en route*. These latter two findings indeed suggested that other mechanisms might be operative as well as that of sun-compass orientation (Schmidt-Koenig, 1960); the results further raise the possibility that orientation information from the latter was in conflict with that from other mechanisms. When these findings are considered in relation to a possible inertial-celestial hybrid navigation system, it is conceivable that inertial and celestial factors might be weighed differently by different birds. Accordingly, those birds that were able to correct for the initial erroneous orientation might be presumed to have given greater weight to inertial information.

Correct directional orientation under conditions such that celestial cues were completely excluded has been reported to occur during the period of migratory unrest of birds (Merkel & Fromme, 1958), as well as for birds that had been displaced (Precht, 1956a, b, 1961; Gerdes, 1960, 1962). It is of interest that, from other experiments in which visual (i.e. celestial) cues were excluded, it was reported that the choice of direction at the time of migratory unrest had been unaltered by a resetting of the birds' internal chronometers (Fromme, 1961).

It seems clear then that although the importance of sun-compass orientation has been well established in recent years it by no means provides a complete explanation of animal navigation, even for those species that make use of it. In fact, Wallraff (1960) suggested that sun-compass orientation may only serve as ". . . a compass with whose help the bird can transfer the relative home direction, obtained in some other still unknown way, on to the absolute earth co-ordinates ". Wallraff, from a consideration of results of experiments with homing pigeons further concluded: "We are forced to recognize the existence of a non-celestial mechanism of establishing location which is superior to that of celestial navigation and which would make the latter practically superfluous" (Wallraff (1960), pp. 454, 459).

The importance of "biological clocks" in animal orientation and navigation is implicit in the demonstration of time-compensated sun orientation, for the very term, time-compensated, implies that the animal must have a kind of biological clock with which it is able to compensate for the sun's motion, in order to determine orientation with respect to the sun. That biological clocks may be of remarkable precision (for example, 0.3%) has been amply demonstrated experimentally (Rawson, 1956; DeCoursey, 1960), a finding that has been considered in direct relation to the problem of animal navigation (Rawson, 1956). The existence of a biological timing mechanism is implicit in all of the suggestions that animal navigation may be based in part on the vestibular apparatus, an assumption that was made explicit by Möhres & zu Oettingen-Spielberg (1949). That the brain itself might be the location of a biological clock has been suggested from theoretical (Wiener, 1961, p. 197), as well as experimental (Rawson, 1956) considerations, and the possibility has been raised that intrinsic rhythms of the electrical activity of the brain might be of importance for the chronometry necessary for bird navigation (Holubář, 1961).

Other Sensory Cues

The existence of hybrid forms of inertial navigation systems in which ancillary aids may assist, or on some occasions assume entirely, the solution of the problem of navigation, particularly raises the possibility that other

sensory cues may be of importance in experiments in the past that were designed to test the role of the vestibular apparatus. In addition to visual and auditory cues as ancillary aids for navigation, it is clear that supplementary information may be available from other primary senses, such as touch, smell, kinesthesis (muscle, joint and tendon sense) (cf. also, Pringle, 1963) and even taste. However, as suggested by Beritoff (1959), it may be that the localization in space of specific sensory stimuli from the above modalities is referred to spatial coordinates that are derived basically from the vestibular system. It is apparent, therefore, that there is a need for greater care in the experimental design of tests on the role of the various possible sensory cues in animal navigation, so that the experimental results will not be ambiguous.

Animal Navigation in Relation to Inertial Navigation

From the preceding discussion, it is apparent that the essence of the hypothesis that animals might find their way about by what would today be termed inertial navigation has long been entertained. Moreover, the suggestion that the vestibular apparatus of vertebrates might serve as the prime sensing element for animal navigation has existed for some time. Experiments specifically designed to test this possibility have not yielded positive results except for those of Beritoff which were cited above. At the same time, the experiments of Beritoff have apparently been the only ones in which the role of the vestibular apparatus has been tested specifically and unambiguously, although his experiments involved distances of only a few meters. The whole question of the role of the vestibular apparatus in animal navigation therefore merits further consideration.

Since the vestibular apparatus, of course, moves with the head a comparison of animal navigation with inertial navigation is, strictly speaking, a comparison with the Strapped-Down or Vehicle Oriented Inertial Navigation (VOIN) systems that were discussed earlier. All of the general concepts of inertial navigation, however, apply to the Strapped-Down Systems; for example, the stabilized platform appears analytically or computationally rather than actually. The maintenance of the indicated local vertical and the precession of the local vertical, determinations of which in Strapped-Down Systems are carried out by the computer of the system, would then be presumed to be determined physiologically in the brain, from neuronal information derived from the accelerometric sensors, i.e. the vestibular apparatus.

The detailed analysis of errors in inertial systems is quite complex, as has already been indicated and, to the author's knowledge, a detailed analysis of the errors of a Strapped-Down System utilizing an angular accelerometer as the angular sensing element is not available, and hence it is difficult to

make exact estimates concerning the accuracy that might be possible with an animal inertial navigation system. However, from some preliminary calculations it seems clear that the threshold levels for perception of angular acceleration and for linear acceleration which have been mentioned earlier (i.e. $0.2°/sec^2$ and 6 cm/sec^2, respectively) would not permit accurate navigation (e.g. errors of position of, say, 5%) for travel times longer than the order of a few minutes. Precision inertial sensing elements possess a threshold of some 10^3 or 10^4 greater than the above-mentioned values.

As has already been mentioned, it seems possible that the potential thresholds of the vestibular apparatus may be much greater than the above-mentioned values, and it would seem clear that the question of whether or not the actual capabilities of the vestibular system for accurate navigation over much greater distances and times can only be established by direct experimental tests of this phenomenon, under conditions in which other possible sensory clues for orientation and navigation are clearly excluded. At the same time it appears appropriate to examine in detail some of the aspects of animal navigation to determine if these may appear to be consistent with the possibility of inertial navigation. It should be clear that positive findings from such a comparison do not necessarily prove the existence of animal navigation.

DISCUSSION OF OTHER EXPERIMENTAL RESULTS

Although the only available experimental results that may be considered a specific test of a pure form of inertial navigation by animals are those of Beritoff, the results of a number of experiments appear to be consistent with an inertial basis for animal navigation. Moreover, some experimental phenomena that in the past have been considered extraordinary are not surprising if the results are viewed from an inertial standpoint. Among these phenomena are the variability of paths that animals may follow to a fixed goal, and the remarkable "spatial memory" for goals, which was described above. Both of these would be consistent with navigation on an inertial basis, as is apparent from consideration of Fig. 2. In this figure, the arbitrariness of the paths to reach the goals is in contrast to the exact localization of the goals themselves. The latter considerations would suggest that further studies on the ability of animals to localize their home (cf., for example, Watson & Lashley, 1915; Meise, 1933; Böhringer, 1960), might be carried out.

At the same time, from consideration of Fig. 2 it is apparent that the direction of departure of the animal from the release point (as well as the direction from which the animal arrives at its home) is entirely arbitrary, from an inertial navigation standpoint. Accordingly, it may well be that the

choice by an animal of the direction of departure depends entirely on the experimental conditions. Thus, in some instances the home direction may well be preferred from the start (cf. Lindenlaub, 1960), whereas under other circumstances, local environmental conditions may result in a choice of another initial direction (cf. Rawson, 1956; v. Lehmann, 1956; Bovet, 1962). Indeed, the fact that the direction of departure as well as the return path can be entirely arbitrary might suggest a re-evaluation of experimental results on homing behavior which appeared to indicate a "random search" type of homing.

Certain apparent peculiarities of animal behavior in the navigation process may assume some significance if they are viewed in the context of possible inertial navigation. Among the more obvious of these is the phenomenon of sun-orientation itself; for the possibility suggests itself that sun-orientation provides the compass element of a map-and-compass navigation, whereas an inertial system, possibly constituting the unknown mechanism of orientation suggested by Kramer (1960), Schmidt-Koenig (1960), and Wallraff (1960), furnishes the basis of the map itself for those species for which an external azimuthal reference is necessary.

In this instance one might consider the analogy of an inertial navigation system that is mounted in an airplane and provides a continuing indication of position; the system, however, is not directly linked with the controls of the aircraft, and hence it is not employed directly for automatic guidance of the flight. From information on position obtained from the inertial system, the necessary direction with respect to the points of the compass for flight from one place to another could be established, but the actual determination of the flight program itself would necessitate the additional availability of a compass *per se* (a gyrocompass, for example). However, were no compass available, the desired direction of flight could be established by trial-and-error during the initial portion of the flight, by taking note of the successive changes in indicated position (with respect to that of the destination) which would be provided by the inertial system. It is conceivable that the circling flights of some birds upon release, and prior to homing, might serve in a similar way to establish the direction of home.

In the above analogy, it is evident that the availability of a compass would immensely facilitate the establishment of the correct direction for flight, but it would not be absolutely essential for this purpose. Were a compass available but reading erroneously, then some minimal distance of flight would be necessary in order to establish that the direction of flight, selected with the aid of the inertial navigation system and referred to the compass for the actual flight path, did not agree with that indicated by the inertial system while the plane was in actual flight. It is in this context that information on

direction obtained from inertial and from celestial sources might be in conflict for birds whose internal chronometers had been reset.

The importance of the local vertical for inertial systems has already been emphasized, and it was apparent that the indication of the local vertical must be precessed as the inertial system moves about the surface of the earth. If the local vertical is not precessed properly, errors in the indicated position
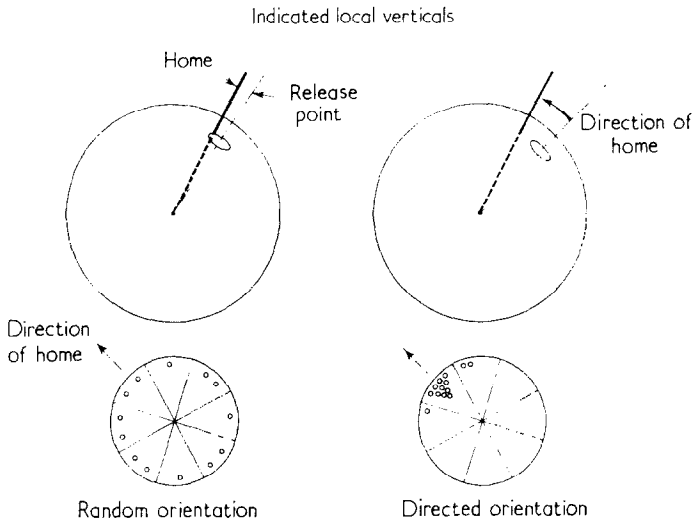

FIG. 11. Hypothetical effect of "circle of confusion" in the perception by animals of changes in the indicated local vertical. The upper part of the figure shows the local verticals for the home position and for two different release points. For the first, the displacement is insufficient for the perception by the animals that the direction of the local vertical has changed. Accordingly, a group of animals displaced by this distance from home would exhibit no preference for the homeward direction, as is indicated diagrammatically in the lower left. However, if the amount of displacement exceeds the radius of the circle of confusion (upper right), then a comparison of the two local verticals is possible, from which the direction of home can be determined. Accordingly, animals at this distance would exhibit a preference for the home direction (lower right).

build up very rapidly. It might be speculated whether the loss of ability for choosing the home direction if the distance of the displacement is too great, as shown for instance by cats and mice (Lindenlaub, 1955, 1960; Bovet, 1960), or too small, as shown in some instances by pigeons (Matthews, 1955), may be related to a failure of the mechanism for proper precession of the indicated local vertical.

Another possible explanation of the fact that pigeons may not choose the homeward direction unless the displacement is greater than some minimum is suggested in Fig. 11. In the figure, the assumption is made that the establishment of the direction of home is made by comparing a memory of the direc-

tion of the local vertical for home with that for the point of release, a technique that is well-established in inertial systems of certain types (Anderson, 1958; Draper, 1958). As suggested in Fig. 11, the possible existence of a "circle of confusion", however, might render the comparison impossible unless the displacement is greater than some minimum distance that corresponds to the radius of the circle. (Such a circle of course might exist for other modes of navigation.)

An observation with respect to the ability of birds to localize the site of their nests is perhaps of interest in relation to inertial navigation. In experiments in which the nests of terns were displaced, Watson & Lashley (1915) found that considerable changes could be made in the vertical position of the nest without affecting the birds' reaction in the slightest, whereas even minimal displacements of the nest in the horizontal plane (for example, displacements of a few inches) markedly affected the behavior of the birds. These results appear to suggest that horizontal localization of the nest site was carried out much more precisely than vertical localization, a difference that was unaffected by pronounced alterations in the immediate and nearby visual environment of the nests. Some of these experiments appeared to suggest, however, that vertical localization of the nests was carried out more accurately if the birds first alighted on a perch near the nest before flying on to it, instead of flying directly to the nest from a distance. In this connection it will be recalled that the determination of height above the earth by an inertial system is subject to much greater errors than the determination of horizontal displacement and, correspondingly, for the same degree of accuracy of determination of displacement in the vertical direction the vertical system would require much more frequent recalibration than the horizontal one. It is conceivable that the above-described relative insensitivity of the birds to vertical displacements of their nests might have an analogous explanation.

A curious feature of experiments in which the preferred direction of birds after displacement is examined is that on occasion the direction opposite to that of home is preferred (cf. Gerdes, 1962); in view of the existence under certain circumstances of Schuler oscillations in the indicated position in inertial navigation systems, as discussed in an earlier section, it might be of interest to examine whether the times of occurrence of choice of the opposite direction from home tends to exhibit an eighty-four-minute periodicity, so that the direction tendency would change approximately every forty-two minutes.

It seems clear (Möhres & zu Oettingen-Spielberg, 1949; Griffin, 1958) that the echo-location mechanism of bats plays an essential part in the building up of a spatial memory. It would seem possible that information concerning the immediate environment which is obtained by echo-location is referred,

for subsequent recall, to spatial coordinates based on information from the vestibular apparatus, in the manner suggested by Beritoff for other sensory modalities. In view of the existence of Doppler-Inertial Navigation Systems, as described in an earlier section, the possibility suggests itself that the echo-location mechanisms might in addition constitute an element of a Doppler-Inertial Navigation System for bats. A detailed comparison of the specifications for small portable navigational systems that employ ultrasonic Doppler techniques (cf. Galbraith, 1962) with the physiological details of the echo-location system of bats (Griffin, 1958; Grinnell, 1963) might help to elucidate this possibility (cf. also Kay, 1962). It is conceivable that the electrical mechanism employed by certain fish for the perception of surrounding objects in the water (Machin & Lissmann, 1960) might also form the basis of a Doppler-Inertial System.

The ability of some animals to retain their training to a particular compass direction (Neuhaus, 1950), even after they have been transported over some distance (Vogelberg & Krüger, 1951), has given rise to the suggestion that they may possess some type of absolute non-visual innate compass-direction preference (Thorpe, 1956). These experimental results are of interest when they are viewed in the light of the process of storage of a reference direction that is characteristic of all pure inertial systems (cf. also Fig. 4).

It was pointed out in a preceding section that the proper operation of inertial navigation systems requires that the corrections that arise by virtue of the rotation of the earth (i.e. the Coriolis and centrifugal effects) be taken into account; a failure of the system to include these corrections would therefore result in predictable errors in the indicated position after travel for some distance. Thus, for motion with respect to the earth in the northern hemisphere, the Coriolis effect results in an apparent deflection of the direction of motion to the right, irrespective of the compass direction of the motion; the magnitude of the effect is dependent upon the geographic latitude as well as on the velocity with respect to the earth and the duration of the journey (Page, 1935, p. 107). Accordingly, for a journey that is presumed to be due north, a failure of an inertial navigation system to take into account the Coriolis effect would result in a westward error in the indicated longitude of the current position. Reports that the homing ability of pigeons may be dependent on the direction of homing (cf. Kramer, Pratt & St. Paul, 1957; Kramer, 1960) might be examined in detail from the above standpoint.

Some Further Experimental Tests

From the previous sections it is evident that there is a need for specific tests of animal inertial navigation and of the role of the vestibular system in

it. In this connection it is noteworthy that newer techniques permit the effective inactivation of the semicircular canals without affecting the resting nervous discharge from them (Money & Scott, 1962). Consideration might also be given to the older technique of cocainization of the vestibular apparatus for short-time experiments.

Several lines of investigation could be carried out with animals in which the vestibular system has been at least in part disabled (for example, by means of the above-mentioned technique), and with normal animals as controls. It is, of course, essential in such experiments that other known sensory cues (especially visual ones) be excluded, so that the question of hybrid or aided inertial navigation does not enter in the experiments. Since it may be questioned whether birds can fly after total interference with the vestibular system if visual cues are excluded, experiments with birds could be confined to those in which orientational tendencies in a confined space are studied after the birds have been displaced, or at the time of migratory unrest.

Similar experiments could be carried out with cats or mice or other rodents, displaced over small distances. In addition, however, since it is well established that such animals can walk even after total labyrinthectomy in the absence of visual cues, the ability of a choice of the homeward direction as well as that of the homing behavior itself could be studied. Such experiments would in effect be an extension of the type of studies carried out by Beritoff, which have been described above, but with the use of much greater distances (e.g. several hundred meters, or a few kilometers, instead of a few meters).

It has been observed that dogs who had previously been lying quietly in an automobile during a trip, may become alerted when a familiar location is approached (E. Booth, 1963, personal communication). Although it is entirely possible that familiar odors, or other common sensory stimuli, may be the cause of the alerting response, it would seem that this observation might merit experimental investigation from the standpoint of whether or not the vestibular organ might be the basis of the alerting response.

The fact that information concerning motion with respect to the earth is continuously available from an inertial navigation system suggests some interesting tests of the possibility that animals might be able to navigate inertially. The subjective experience is not an uncommon one of being seated in a railway car alongside another one in a station, and of experiencing momentary confusion when one of the two begins to move; it is only when a glance is cast at a third, stationary object that it is possible to be certain which train has actually begun to move. However, if an animal had a truly functional inertial system, it would have no difficulty deciding which train was beginning to move, for its own inertial sensors would furnish the essential information. Whether or not satisfactory experiments could be

designed to test this possibility by means of conditioned reflexes, for example, can only be speculated, but in experiments employing conditioned reflexes, Beritoff (1961, p. 246) has reported the perception by animals of extremely subtle passive motion.

Analogous experiments on the behavior of bats accustomed to flying about in an enclosure to which motion is then imparted (e.g. in an elevator) might also be proposed. In the testing of whether or not the flight of the bat was carried out with respect to the earth, or with respect to the moving enclosure, such an experiment would also help to determine whether or not the spatial orientation of bats is carried out by means of the total pattern of echoes within the enclosure (Griffin, 1958, p. 165).

The current availability of orbiting earth satellites suggests a particularly interesting test of the possibility that animals (especially those that navigate over great distances) might employ a physiological inertial navigation system. If a species regularly navigates in a geocentric (head-upright) position on earth, then from a purely inertial standpoint, it might also exhibit a preference for a geocentric orientation during its free movements inside a satellite that is in an approximately circular orbit. In this instance, it would be assumed that the orientation of the head would be approximately that of the "indicated local vertical", the latter being precessed about the earth in a manner similar to that for the accelerometer base shown in Fig. 7. For this experiment, either flying or swimming species would be preferable to those that navigate entirely on land, since in an enclosure of the customary medium of the former (i.e. air or water), an unimpeded preference for a geocentric orientation could be manifested by the animal. It should be noted, however, if an animal did in fact exhibit a tendency to maintain a geocentric orientation while in a satellite, the tendency might well be manifest only during the minutes immediately following the launch into orbit since, as has been pointed out above, the stabilizing influence on the indication of the local vertical that is provided by Schuler tuning no longer obtains for orbital velocities.

Although the possibility seems rather remote, an alternative might be that the animal, once in orbit, would maintain an orientation that is fixed with respect to the fixed stars (i.e. with respect to inertial space), an analogy being made with the so-called "true inertia" systems (Anderson, 1958), in which the accelerometers as well as the stabilized platform are maintained fixed with respect to inertial space.

A tendency for animals to maintain their orientation in either one of the ways described above, during the period following launching of the satellite into orbit, would indeed constitute strong presumptive evidence for the existence of a physiological inertial navigation system. Analogous experi-

ments could be carried out in the so-called zero-gravity conditions attainable by aircraft in curved flight, but the time duration of the latter experiments would necessarily be very limited.

The Senses of Direction and Distance

The term "sense of direction" has in the past been more often used than it has been defined. From the preceding sections it is evident that in the context of inertial navigation, the term can be given a quite specific meaning, for inertial navigation systems can truly be said to possess a "sense of direction", inasmuch as the direction with reference to any arbitrary point or an absolute direction can be made continuously available.

At the same time, it is apparent that it is appropriate also to speak of a "sense of distance" which is complementary to the sense of direction, the two together constituting the "sense of space". Physiologically speaking, the sense of space, and its components, sense of direction and distance, may be considered as derived (or more strictly, perhaps, integrated) senses, rather than primary ones such as hearing, sight, and touch. In turn, the respective primary sense might be termed the "sense of inertia", if further investigation shows that inertial navigation is in fact employed extensively by animals, for it is upon the inertia of the otoliths and the cupula-endolymph system that the operation of the vestibular end-organs is based.

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