

= Animal navigation =

Animal navigation is the ability of many animals to find their way accurately without maps or instruments . Birds such as the Arctic tern , insects such as the monarch butterfly and fish such as the salmon regularly migrate thousands of miles to and from their breeding grounds , and many other species navigate effectively over shorter distances .

Dead reckoning , navigating from a known position using only information about one 's own speed and direction , was suggested by Charles Darwin in 1873 as a possible mechanism . In the 20th century , Karl von Frisch showed that honey bees can navigate by the sun , by the polarization pattern of the blue sky , and by the earth 's magnetic field ; of these , they rely on the sun when possible . William Tinsley Keeton showed that homing pigeons could similarly make use of a range of navigational cues , including the sun , earth 's magnetic field , olfaction and vision . Ronald Lockley demonstrated that a species of small seabird , the Manx shearwater , could orient themselves and fly home at full speed , when released far from home , provided either the sun or the stars were visible .

Several species of animal can integrate cues of different types to orient themselves and navigate effectively . Insects and birds are able to combine learned landmarks with sensed direction ( from the earth 's magnetic field or from the sky ) to identify where they are and so to navigate . Internal ' maps ' are often formed using vision , but other senses including olfaction and echolocation may also be used .

The ability of wild animals to navigate may be adversely affected by products of human activity . For example , there is evidence that pesticides may interfere with bee navigation , and that lights may harm turtle navigation .

= = Early research = =

In 1873 , Charles Darwin wrote a letter to Nature magazine , arguing that animals including man have the ability to navigate by dead reckoning , even if a magnetic ' compass ' sense and the ability to navigate by the stars is present :

With regard to the question of the means by which animals find their way home from a long distance , a striking account , in relation to man , will be found in the English translation of the Expedition to North Siberia , by Von Wrangell . He there describes the wonderful manner in which the natives kept a true course towards a particular spot , whilst passing for a long distance through hummocky ice , with incessant changes of direction , and with no guide in the heavens or on the frozen sea . He states ( but I quote only from memory of many years standing ) that he , an experienced surveyor , and using a compass , failed to do that which these savages easily effected . Yet no one will suppose that they possessed any special sense which is quite absent in us . We must bear in mind that neither a compass , nor the north star , nor any other such sign , suffices to guide a man to a particular spot through an intricate country , or through hummocky ice , when many deviations from a straight course are inevitable , unless the deviations are allowed for , or a sort of " dead reckoning " is kept . All men are able to do this in a greater or less degree , and the natives of Siberia apparently to a wonderful extent , though probably in an unconscious manner . This is effected chiefly , no doubt , by eyesight , but partly , perhaps , by the sense of muscular movement , in the same manner as a man with his eyes blinded can proceed ( and some men much better than others ) for a short distance in a nearly straight line , or turn at right angles , or back again . The manner in which the sense of direction is sometimes suddenly disarranged in very old and feeble persons , and the feeling of strong distress which , as I know , has been experienced by persons when they have suddenly found out that they have been proceeding in a wholly unexpected and wrong direction , leads to the suspicion that some part of the brain is specialised for the function of direction .

Later in 1873 , Joseph John Murphy replied to Darwin , writing back to Nature with a description of how he , Murphy , believed animals carried out dead reckoning , by what is now called inertial navigation :

If a ball is freely suspended from the roof of a railway carriage it will receive a shock sufficient to move it , when the carriage is set in motion : and the magnitude and direction of the shock ? will depend on the magnitude and direction of the force with which the carriage begins to move ? [ and so ] ? every change in ? the motion of the carriage ? will give a shock of corresponding magnitude and direction to the ball . Now , it is conceivably quite possible , though such delicacy of mechanism is not to be hoped for , that a machine should be constructed ? for registering the magnitude and direction of all these shocks , with the time at which each occurred ? from these data the position of the carriage ? might be calculated at any moment .

Karl von Frisch ( 1886 ? 1982 ) studied the European honey bee , demonstrating that bees can recognize a desired compass direction in three different ways : by the sun , by the polarization pattern of the blue sky , and by the earth ' s magnetic field . He showed that the sun is the preferred or main compass ; the other mechanisms are used under cloudy skies or inside a dark beehive .

William Tinsley Keeton ( 1933 ? 1980 ) studied homing pigeons , showing that they were able to navigate using the earth ' s magnetic field , the sun , as well as both olfactory and visual cues .

Donald Griffin ( 1915 ? 2003 ) studied echolocation in bats , demonstrating that it was possible and that bats used this mechanism to detect and track prey , and to " see " and thus navigate through the world around them .

Ronald Lockley ( 1903 ? 2000 ) , among many studies of birds in over fifty books , pioneered the science of bird migration . He made a twelve @-@ year study of shearwaters such as the Manx shearwater , living on the remote island of Skokholm . These small seabirds make one of the longest migrations of any bird ? 10 @,@ 000 kilometres ? but return to the exact nesting burrow on Skokholm year after year . This behaviour led to the question of how they navigated .

= = Mechanisms = =

Lockley began his book Animal Navigation with the words :

How do animals find their way over apparently trackless country , through pathless forests , across empty deserts , over and under featureless seas ? ... They do so , of course , without any visible compass , sextant , chronometer or chart ...

Many mechanisms have been proposed for animal navigation : there is evidence for a number of them . Investigators have often been forced to discard the simplest hypotheses - for example , some animals can navigate on a dark and cloudy night , when neither landmarks nor celestial cues like sun , moon , or stars are visible . The major mechanisms known or hypothesized are described in turn below .

= = Remembered landmarks = = =

Animals including mammals , birds and insects such as bees and wasps ( *Ammophila* and *Sphex* ) , are capable of learning landmarks in their environment , and of using these in navigation .

= = Orientation by the sun = = =

Some animals can navigate using celestial cues such as the position of the sun . Since the sun moves in the sky , navigation by this means also requires an internal clock . Many animals depend on such a clock to maintain their circadian rhythm . Animals that use sun compass orientation are fish , birds , sea @-@ turtles , butterflies , bees , sandhoppers , reptiles , and ants .

When sandhoppers ( such as *Talitrus saltator* ) are taken up a beach , they easily find their way back down to the sea . It has been shown that this is not simply by moving downhill or towards the sight or sound of the sea . A group of sandhoppers were acclimatised to a day / night cycle under artificial lighting , whose timing was gradually changed until it was 12 hours out of phase with the natural cycle . Then , the sandhoppers were placed on the beach in natural sunlight . They moved away from the sea , up the beach . The experiment implied that the sandhoppers use the sun and their internal clock to determine their heading , and that they had learnt the actual direction down to

the sea on their particular beach .

Experiments with Manx shearwaters showed that when released " under a clear sky " far from their nests , the seabirds first oriented themselves and then flew off in the correct direction . But if the sky was overcast at the time of release , the shearwaters flew around in circles .

Monarch butterflies use the sun as a compass to guide their southwesterly autumn migration from Canada to Mexico .

### = = = Orientation by the night sky = = =

In a pioneering experiment , Lockley showed that warblers placed in a planetarium showing the night sky oriented themselves towards the south ; when the planetarium sky was then very slowly rotated , the birds maintained their orientation with respect to the displayed stars . Lockley observes that to navigate by the stars , birds would need both a " sextant and chronometer " : a built @-@ in ability to read patterns of stars and to navigate by them , which also requires an accurate time @-@ of @-@ day clock .

In 2003 , the African dung beetle *Scarabaeus zambesianus* was shown to navigate using polarization patterns in moonlight , making it the first animal known to use polarized moonlight for orientation . In 2013 , it was shown that dung beetles can navigate when only the Milky Way or clusters of bright stars are visible , making dung beetles the only insects known to orient themselves by the galaxy .

### = = = Orientation by polarised light = = =

Some animals , notably insects such as the honey bee , are sensitive to the polarisation of light . Honey bees can use polarized light on overcast days to estimate the position of the sun in the sky , relative to the compass direction they intend to travel . Karl von Frisch 's work established that bees can accurately identify the direction and range from the hive to a food source ( typically a patch of nectar @-@ bearing flowers ) . A worker bee returns to the hive and signals to other workers the range and direction relative to the sun of the food source by means of a waggle dance . The observing bees are then able to locate the food by flying the implied distance in the given direction , though other biologists have questioned whether they necessarily do so , or are simply stimulated to go and search for food . However , bees are certainly able to remember the location of food , and to navigate back to it accurately , whether the weather is sunny ( in which case navigation may be by the sun or remembered visual landmarks ) or largely overcast ( when polarised light may be used ) .

### = = = Magnetoreception = = =

Some animals , including mammals such as blind mole rats ( *Spalax* ) and birds such as pigeons , are sensitive to the earth 's magnetic field .

Homing pigeons use magnetic field information with other navigational cues . Pioneering researcher William Keeton showed that time @-@ shifted homing pigeons could not orient themselves correctly on a clear sunny day , but could do so on an overcast day , suggesting that the birds prefer to rely on the direction of the sun , but switch to using a magnetic field cue when the sun is not visible . This was confirmed by experiments with magnets : the pigeons could not orient correctly on an overcast day when the magnetic field was disrupted .

### = = = Olfaction = = =

Olfactory navigation has been suggested as a possible mechanism in pigeons . Papi 's ' mosaic ' model argues that pigeons build and remember a mental map of the odours in their area , recognizing where they are by the local odour . Wallraff 's ' gradient ' model argues that there is a steady , large @-@ scale gradient of odour which remains stable for long periods . If there were two or more such gradients in different directions , pigeons could locate themselves in two dimensions

by the intensities of the odours . However it is not clear that such stable gradients exist . Papi did find evidence that anosmic pigeons ( unable to detect odours ) were much less able to orient and navigate than normal pigeons , so olfaction does seem to be important in pigeon navigation . However , it is not clear how olfactory cues are used .

Olfactory cues may be important in salmon , which are known to return to the exact river where they hatched . Lockley reports experimental evidence that fish such as minnows can accurately tell the difference between the waters of different rivers . Salmon may use their magnetic sense to navigate to within reach of their river , and then use olfaction to identify the river at close range .

= = = Other senses = = =

Biologists have considered other senses that may contribute to animal navigation . Many marine animals such as seals are capable of hydrodynamic reception , enabling them to track and catch prey such as fish by sensing the disturbances their passage leaves behind in the water . Marine mammals such as dolphins , and many species of bat , are capable of echolocation , which they use both for detecting prey and for orientation by sensing their environment .

= = Path integration = =

Dead reckoning , in animals usually known as path integration , means the putting together of cues from different sensory sources within the body , without reference to visual or other external landmarks , to estimate position relative to a known starting point continuously while travelling on a path that is not necessarily straight . Seen as a problem in geometry , the task is to compute the vector to a starting point by adding the vectors for each leg of the journey from that point .

Since Darwin 's *On the Origins of Certain Instincts* ( quoted above ) in 1873 , path integration has been shown to be important to navigation in animals including ants , rodents and birds . When vision ( and hence the use of remembered landmarks ) is not available , such as when animals are navigating on a cloudy night , in the open ocean , or in relatively featureless areas such as sandy deserts , path integration must rely on idiothetic cues from within the body .

Studies by Wehner in the Sahara desert ant ( *Cataglyphis bicolor* ) demonstrate effective path integration to determine directional heading ( by polarized light or sun position ) and to compute distance ( by monitoring leg movement or optical flow ) .

Path integration in mammals makes use of the vestibular organs , which detect accelerations in the three dimensions , together with motor efference , where the motor system tells the rest of the brain which movements were commanded , and optic flow , where the visual system signals how fast the visual world moves past the eyes . Information from other senses such as echolocation and magnetoreception may also be integrated in certain animals . The hippocampus is the part of the brain that integrates linear and angular motion to encode a mammal 's relative position in space .

David Redish states that " The carefully controlled experiments of Mittelstaedt and Mittelstaedt ( 1980 ) and Etienne ( 1987 ) have demonstrated conclusively that [ path integration in mammals ] is a consequence of integrating internal cues from vestibular signals and motor efferent copy " .

= = Effects of human activity = =

Neonicotinoid pesticides may impair the ability of bees to navigate . Bees exposed to low levels of thiamethoxam were less likely to return to their colony , to an extent sufficient to compromise a colony 's survival .

Light pollution attracts and disorients photophilic animals , those that follow light . For example , hatchling sea turtles follow bright light , particularly bluish light , altering their navigation . Disrupted navigation in moths can easily be observed around bright lamps on summer nights . Insects gather around these lamps at high densities instead of navigating naturally .