they responded well to flashing or moving slits of a given orientation and poorly to other orientations. Orientation-selective neurons were classified as direction selective if thin slits moving in the presumptive preferred direction evoked at least twice as many spikes per presentation as slits moving in the nonpreferred direction. In initial experiments, we assessed direction selectivity simply by listening to unit responses over a loudspeaker, but in later experiments an averaging computer was used.

Orientation selectivity was a common feature in both normally reared cats and those reared in the stroboscopic light, although it was rarely found in those reared in the dark (Fig. 1). The breadth of orientation tuning for individual units was comparable in the strobe-reared and normal groups. By contrast, the occurrence of cells with direction selectivity was much rarer in the strobe-reared group than in normal cats and did not differ significantly from the proportion found in cats reared in the dark. The reduction of direction selectivity for the strobe-reared group was observed among both the simple and complex classes of cortical neurons. We also compared responses to visual stimuli moving at different velocities in cortical neurons of strobe-reared and normal cats. No differences either in preferred stimulus velocities or in breadth of velocity tuning were observed; slowly moving visual stimuli were most effective in activating striate cortex neurons in both groups of cats.

We were concerned about the permanence of the changes in cortical organization brought about by the restricted environment. In most situations, alterations caused by early deprivation are largely irreversible, once the "critical period" has passed (*2*, *6*). Because a number of exceptions have been reported (*5*, *7*), however, we assessed the consequences of a recovery period in a normally lit animal colony room. We recorded repeatedly from the same animal at varying intervals after allowing it normal exposure. There was little additional direction selectivity after 6 months in the normal environment (Fig. 2). Thus, the deprivation effects were largely irreversible, although further experiments would be required to establish whether any small residual plasticity remains.

Three main conclusions may be drawn. (i) It seems necessary to expose the retina to motion during postnatal development in order to develop mature direction selectivity among cortical neurons. (ii) The ability to preferentially deprive a major facet of cortical selectivity while leaving intact other properties, such as orientation selectivity and velocity specificity, implies that these properties of cortical cells are determined by largely independent mechanisms. (iii) The deprivation effects cannot be reversed by normal visual exposure if the initial deprivation is maintained for the first few months of life. The preparation described above may prove a useful tool for behavioral and structural studies by providing a system in which a specific part of the cortical circuit has been altered.

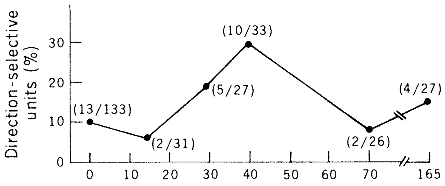

Fig. 2. Percentage of direction-selective units encountered in successive recording sessions from the visual cortex of strobe-reared cats as a function of time after introduction to the normal environment. The numbers in parentheses represent the number of direction-selective units over the total units for that recording session. The $T = 0$ point includes data collected from all five cats. In normal cats, 83 percent of the neurons found are direction-selective.

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26 January 1976; revised 19 April 1976

Magnetic Direction Finding: Evidence for Its Use in Migratory Indigo Buntings

Abstract. *The orientational capabilities of caged migratory indigo buntings were studied under differing magnetic field conditions. When tested in a situation allowing minimal exposure to visual cues but in the presence of the normal geomagnetic field, the birds demonstrated a significant orientation in the appropriate migratory direction (to the north). When the horizontal component of the magnetic field was deflected clockwise 120° by activation of Helmholtz coils surrounding the cage, the orientation of the buntings shifted accordingly (clockwise to geographic east-southeast). These results suggest that indigo buntings are not only able to detect the geomagnetic field, but also can use this information in the finalization of their migratory direction.*

In recent years there has emerged a growing body of evidence that birds might detect, and their behavior be altered by, changes in the earth's magnetic field. These range from cases where errors or disruptions of orientation are correlated with magnetic storm activity (*1*), through experiments where homing abilities of pigeons and gulls are altered when miniature Helmholtz coils or disk or bar magnets are attached to their bodies (*2*), to cases where nocturnal migratory orientation of caged songbirds shifts predictably when the direction of the surrounding magnetic field is altered (*3*, *4*). Experiments with migratory birds are of especial theoretical importance since, by predictably altering the birds' orientations, they stand practically alone in demonstrating that magnetic information not only can disrupt normal orientation, but also can be used actively in the finalization of the appropriate direction.

The principal studies of migratory orientation in artificial magnetic fields come from the laboratories of Merkel and Wiltschko at the University of Frankfurt am Main (Germany). They have reported that European robins (*Erithacus rubicula*) and three species of European warbler (genus *Sylvia*) will orient their spontaneous nocturnal migratory activity (zugunruhe) in a seasonally appropriate direction when deprived of all meaningful visual cues but in the presence of normal geomagnetic information (*3*). Further, when the magnetic field is altered by means of Helmholtz coils, the directions

Table 1. Analysis of migratory orientation tests with indigo buntings under magentic normal and magnetic deflected conditions; **r**, mean vector; mN, magnetic north.

Seasonal division	Runs (No.)	Mean direction	Length of **r**	Rayleigh probability	V probability*
Normal geomagnetic field (mN = 10°)					
24 April–15 May	29	5°	0.45	0.002	
16 May–31 May	24	347°	0.40	0.020	
1 June–16 June	23	273°	0.27	0.189	
Deflected magnetic field (mN = 130°)					
24 April–15 May	24	110°	0.38	0.029	0.006
16 May–31 May	22	95°	0.33	0.084	0.015
1 June–16 June	25	1°	0.17	0.480	0.151

*The "expected" direction for the V test was calculated by adding 120° to the observed mean direction under normal magnetic conditions for each seasonal division.

selected by the migrants shift in such a manner as to preserve the magnetic bearing of the migratory direction (*4*).

These data have produced both considerable excitement and skepticism. The skepticism stems primarily from two considerations. (i) The degree of concentration of orientation in the Frankfurt studies is low, frequently demonstrable only by pooling the results of many tests from many individual birds. Howland (*5*) cautioned that slight inequalities of cage design, artifacts in the experimental environment, or unconscious biases on the part of investigators could all combine to produce weak, spurious concentrations. (ii) Attempts to replicate the first phase of these experiments, to obtain meaningfully oriented behavior under "visually cueless" conditions, have only been successful when performed in the radial-perch cage design developed and used at Frankfurt (*6*). Numerous attempts to obtain similar results in cages equipped with tangentially arranged perches, including one by Merkel himself, have been unsuccessful (*7*).

In the spring of 1974, we collaborated on a study to determine whether indigo buntings (*Passerina cyanea*) could use magnetic cues for direction finding. This North American migrant bird has been shown to be able to select its migratory direction by using stellar cues (*8*) when tested in a funnel-shaped cage (*9*). Being aware of the methodological problems mentioned above, we used both the funnel cages employed by Emlen in his previous studies and the radial-perch cages used by the Frankfurt group.

The experimental birds, nine adult indigo buntings, were mist-netted on their breeding territories near Ithaca, New York, in August 1973. The birds were housed in a large flight room (2.5 by 2.5 m) in the local geomagnetic field for Ithaca and exposed to photoperiod conditions that simulated those which a bunting normally would experience during the autumn and winter. Seven of the birds came into migratory condition (as determined by the termination of the prenuptial molt, the appearance of subcutaneous fat deposits, and the initiation of intense nocturnal activity) in late April. Two additional birds failed to display nocturnal activity in both cage types and are not included in the analyses reported here.

Six days before the first experiments commenced, all birds were moved to a wooden building where they were housed in individual wooden cages. This building was located immediately adjacent to the experimental chambers; the birds were exposed to natural geomagnetic and environmental cues so that any trauma they might associate with sudden changes in conditions or any effect of displacement or transport should have been minimized. Light was provided by incandescent bulbs controlled by an astronomical timer. We adjusted the timer at 2-week intervals to simulate the latitudinal increases in photoperiod that would be experienced by migrating buntings as they moved north from wintering grounds at 18°N latitude to breeding grounds at 42°N (Ithaca, New York).

The experiments were conducted in four wooden buildings, located 12 m apart, and each measuring 4 by 4 by 2 m in size. The magnetic field in these houses was the local geomagnetic field with total intensity of 0.57 gauss, inclination of 72°, and declination of mN (magnetic north) of 10° (360° = 0° represents geographic north). In each building we constructed a pair of Helmholtz coils [2 m in diameter with 1-m clearance (*10*)], which were aligned such that, when activated, they produced a magnetic field that preserved about the same total intensity and dip angle as the earth's field but with the horizontal component deflected clockwise 120° to the east-southeast (geographic 130°).

Two of the houses were equipped with octagonal, automatic registering cages used in previous experiments by Merkel and the Wiltschkos and shipped to Cornell for use in these experiments (*10*). These are wooden cages (1 m in diameter and 35 cm high) equipped with a series of eight radially oriented perches. As a bird moves through this cage it depresses the sensitive perches, thereby making an electrical record that is automatically recorded on paper-punch tape. The remaining two houses contained "funnel" cages of a type used in previous studies of migratory orientation by Emlen (*9*). These consist of a funnel or cone of white blotting paper (14 cm high, 35 cm upper diameter) that is mounted over an aluminum pan to which an ink pad has been secured. The record of orientation is produced by ink footprints that a bird leaves on the sloping side of the cage during its nocturnal activity. Each cage type was positioned in the geometric center of the Helmholtz coils to minimize inhomogeneity of the artificial magnetic field during the experiments.

We took great care to minimize potential visual artifacts in the test environment, including within the cages themselves. The sole nocturnal light for each house came from a dim frosted bulb, the light of which passed through two different sets of highly effective diffusers before reaching the experimental birds in the test cages. The light level at the position of the bird was 0.28 lux. To ensure that this illumination was devoid of any directional bias, each orientation cage was centered directly beneath the light source prior to each nightly experiment.

Interiors of orientation cages themselves are never completely homogeneous; hence they could provide visual cues or other interior inequalities that might serve to attract birds preferentially to one perch or zone over another. We attempted to eliminate any consistency in this possible source of error by (i) leveling the cages prior to each experiment and (ii) rotating each cage nightly according to a predetermined, pseudorandom sequence (*11*). One remaining source of possible bias concerns the selection of individual birds to be tested on any given night or in any particular test situation. To guard against unconscious weighting of the results in favor of particular individual birds, we prepared and adhered to a programmed sequence of experimental runs for each bird (*12*).

All four experimental conditions (two magnetic conditions and two cage types) were run simultaneously every night. A random drawing determined which birds would be run on a given night. The prearranged sequence of test conditions for these individual birds then determined the placement of individuals in the specific cages and magnetic field conditions.

All four test birds were put in their assigned cages approximately 1 hour before "sunset." The photoperiod clock that controlled daylight in the experimental rooms also controlled the paper-punch registration machine. Consequently, all perch activity that occurred during the hours of darkness was automatically recorded for the birds in the radial-perch cages from Frankfurt.

With the funnel cages, registration occurs whenever a bird with inked feet jumps up the side of the cage. To avoid unwanted daytime recording (since buntings are entirely nocturnal migrants), a piece of waxed paper was placed on top of the ink pad. Approximately 2 hours after the birds were put into the cages we removed the waxed paper and thus activated the funnel. Birds in funnel cages were removed 1 to 3 hours before dawn.

In analyzing the data from the radial-perch cages, the number of jumps recorded in each of the eight sectors was totaled and a mean bearing was calculated for each night by vector analysis (*13*). The nightly bearings were then pooled for different test conditions. The data from the funnel cages were analyzed by quantifying the footprint densities in each of 24 equal sectors (15° each) (*9*). Through appropriate conversions (*14*) these were transformed into an estimate of the actual number of jumps. Nightly mean bearings were calculated and pooled as described above. In all analyses, any bird night showing less than 50 jumps total activity was excluded from consideration.

The pooled sets of bearings were tested for deviations from a uniform distribution by the Rayleigh test and for agreement with a predicted direction by the V test (*13*). The behavior in the two magnetic conditions was compared by using the F test of Watson and Williams (*15*).

Figure 1 and Table 1 present the pooled nightly bearings of seven indigo buntings under different magnetic conditions. The season is arbitrarily divided into three periods of approximately equal length. During the early and middle experimental periods (Fig. 1, A and B, left), buntings tested in the absence of directional visual cues but in the presence of the normal geomagnetic field displayed a significant orientation to the north. When the horizontal component of the magnetic field was deflected by 120° (Fig. 1, A and B, right) the buntings continued to show oriented behavior, with the mean direction shifting to geographic east or east-southeast. The orientation in the two magnetic conditions is significantly different by the F test in each of these periods ($F_{1,50} = 13.9$, $P < .01$; $F_{1,44} = 10.5, P < .01$).

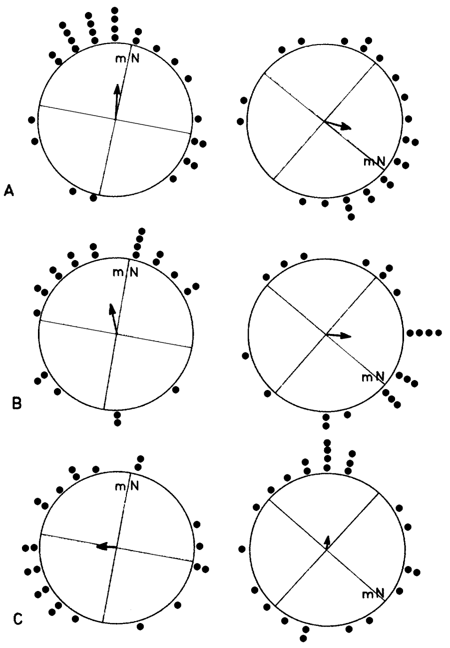

Fig. 1. Orientation of caged indigo buntings. (Left) Behavior in the normal geomagnetic field (mN = 10°). (Right) Behavior under magnetically deflected conditions (mN = 130°). Arbitrary subdivisions of the experimental season are represented as follows. (A) Results obtained between 24 April and 15 May; (B) between 16 May and 31 May; and (C) between 1 June and 16 June. In the figure, 0°, or 360° represents geographic north; mN denotes magnetic north. Each dot represents the mean bearing of one bird on one test night. The arrow in the center of each figure is the mean vector for that sample; its direction is the mean direction and its length is a measure of the consistency of orientation (see Table 1).

Late in the season the consistency of orientation deteriorated considerably. Neither in the natural nor in the deflected magnetic field did the data deviate significantly from uniform.

The concentration of orientation for most birds on any given night was extremely low, with a median vector length of only 0.06 for the radial-perch cages and 0.22 for the funnel cages. Only 21 percent of the individual bird nights deviated significantly from uniform distributions. But the consistency of the pooled nightly bearings of different birds on different nights was great enough to give a clear statistical separation under the two magnetic conditions. Examination of the pooled behavior of individual birds under the two magnetic situations showed that the bearings of six (out of seven) birds were deflected in the predicted direction and, in three instances, these differences were statistically significant. A detailed discussion of the behavior of individual birds, the general low degree of concentration, and a comparison of orientation behavior observed in the two different cage designs is in preparation (*16*).

Emlen (*17*) reported that indigo buntings did not show significant directional tendencies when deprived of visual cues but allowed exposure to the normal geomagnetic field during an autumn migration season. In that study, the behavior of numerous individuals was investigated but the results were not pooled. When reanalyzed in accordance with the statistical procedures applied here, in which results from all birds are pooled and a "grand mean" is calculated, a significant trend does emerge for the birds to orient southward (mean direction, 173°; Rayleigh probability < 0.001) (*18*). Together with our findings, these results suggest that indigo buntings can determine their appropriate direction by nonvisual means during both migration seasons. These results strengthen the growing body of evidence that birds can detect magnetic fields approximating the earth's in strength. Of even greater importance, they indicate that indigo buntings, like the European robin and some European warblers (*4*), can use this information to help finalize the appropriate seasonal direction for migration.

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12. The sequence of test conditions for each bird was determined as follows: cards representing the four conditions (two cage types and two magnetic conditions) were made up. These were drawn at random with the constraint that no single condition be repeated more than three times in any set of 12 test runs.
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29 March 1976; revised 7 June 1976

Biogeography of Free-Living Soil Nematodes from the Perspective of Plate Tectonics

Abstract. *In this first biogeographical synthesis based on the morphology and known distribution of a group of free-living soil nematodes, data indicate a pre-Jurassic origin followed by West Gondwanaland radiation for some genera and Laurasian radiation for others.*

Raven and Axelrod (*1*) presented a convincing case that West Gondwanaland was a primary area of evolution for many orders of angiosperms (possibly the earliest angiosperms) and reviewed the data leading to a similar conclusion for birds, marsupials, snakes, and anurans. Edmunds (*2*) suggested a probable sequence of breakup of Gondwanaland based on the distribution of mayflies and a minimum of geological evidence. It has been variously postulated that the Nematoda constitute an ancient phylum that evolved in upper Proterozoic or early Cambrian time, and, conversely, that the phylum is of fairly recent origin like the Lepidoptera or passerine birds (*3*). We have recently clarified the systematics of the superfamily Leptonchoidea of the Dorylaimida (*4*) so that a reasonable analysis of the biogeography and history of the group can now be made. Our data on this group of free-living soil nematodes point to a pre-Jurassic origin followed by West Gondwanaland radiation for some genera and a Laurasian radiation for others. We now present data for three genera from our larger study of the entire superfamily.

The Dorylaimida occur mainly as part of a diverse soil and freshwater nematode fauna of relatively natural habitats (Fig. 1). Dorylaimid nematodes reach a high diversity in uncultivated areas, but their diversity and numbers decline rapidly in cultivated fields (except for a few species that are plant parasites), and the dorylaimid fauna can be used as an indicator of degree of disturbance in deciduous forests (*5*).

Generally speaking, man is the most effective dispersal agent for nematodes, and many species that are plant parasites (usually of the order Tylenchida) have been widely spread by movements of plant parts and soil by humans. The Dorylaimida as a whole have poor dispersion characteristics. They do not seem to have a drought-resistant stage, as do some of the successful plant parasites, and they must rely mainly on fresh water or chance adherence in moist soil to the feet or bodies of animals for dispersal. Since in natural areas most dorylaimid species are rare in relative numbers with few or no predominant species, the chances of new colonies becoming established at distant points must be low (*6*).

Insufficient collecting on many continents made a biogeographic study impossible until recently. However, large collections have now been made in many areas of the world (*7*), and distributions of genera and species of Leptonchoidea on a worldwide basis show patterns that can be interpreted in relation to geological events now known to have occurred at various times (*1*). Our approach is closest to the vicariance model (*8*), in which biotic distribution is thought to result mainly from subdivisions (vicariance) of ancestral biotas with secondary emphasis on pathways of dispersal and migration. The vicariance model facilitates generalizations regarding entire biotas.

The Leptonchoidea show various combinations of plesiomorphic (or primitive) and apomorphic (or advanced) character states (*9*). Species of the genus *Dorylaimoides* have the most plesiomorphic characters, including a relatively elongated basal esophageal bulb (Fig. 2, a and b). Modifications of the esophagus and female gonads are represented among the species of *Dorylaimoides*, which can be ordered into two groups, one plesiomorphic and the other relatively apomorphic. Species of the plesiomorphic group, all of which have an unconstricted esophagus (Fig. 2a), have been found in many of the Laurasian countries (with several species on more than one continent) and also in India, Africa, South America, and Puerto Rico. India has several species in common with Laurasian areas and shares one species with South America only. On the basis of these data alone, *Dorylaimoides* might appear to be a northern group with recent dispersal to the south. However, data from the apomorphic forms indicate a different history. India has one species with an apomorphic constricted esophagus (Fig. 2b). All four Australian species also have this character. Elsewhere in the world this character is possessed by one species found only in South America and another species found only in Puerto Rico. The fact that all four Australian species have the constricted esophagus and that this characteristic is found elsewhere only in India, South America, and Puerto Rico tells us that an ancestor of these species was present in West Gondwanaland prior to India's passage to the north, and that a nematode fauna of some antiquity may be present on Puerto Rico.

It follows from these data for apomorphic forms that ancestors of plesiomorphic *Dorylaimoides* present today in India and elsewhere had evolved and become well distributed prior to the breakup of Pangaea, 180 million years ago. After the breakup, those species now shared only by Laurasian continents may have evolved. On the basis of present data it is not possible to decide whether those plesiomorphic species which India shares with the Laurasian countries are Pangaean survivors or