# Effect of Ecological Pressures on Brains: Examples from Avian Neuroethology and General Meanings*

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Z. Naturforsch. **53c,** 560–581 (1998); received April 2, 1998

Neural Computation, Vision, Audition, Comparative, Sensory

Comparative neuroethological research emphasizes that brains of animals have been shaped by the specific demands and constraints imposed by the ecological niche that a species occupies. Since avian species have developed very diverse life styles and occupy extreme ecological niches, bird brains should show many specializations, which may be revealed in species that have survived under high ecological pressures. In this paper, we will give several examples of adaptations, in which we are able to correlate structural and physiological specializations to the specific ecological demands: adaptations found to nocturnal hunting in barn owls, the characteristics of bird song and its underlying neurobiological correlates, retinopetal projections and their relation to peripheral attentional switching, looming detection, and adaptations related to memory capacities of food-storing birds. We stress especially that the analysis of the animal's ecological situation is important in understanding the factors that shaped both behavior and the neuronal substrate.

## Introduction

Research on avian mental capabilities has shown achievements rivaling those observed in mammals. The grey parrot "Alex" is able to identify many different objects, to work with numbers up to 6, and has a concept of yes or no (Pepperberg, 1987). Pigeons and other migrating birds display such a versatility in navigation that researchers have not been able to thoroughly understand the underlying mechanisms (Walcott, 1996). Some song birds exhibit amazing variability in their songs, and are able to modify their repertoire life long (Konishi, 1985). Food storing birds surprise researchers with respect to both, searching strategies and memory capabilities (Shettleworth, 1983).

We shall examine in the following what enables birds with their seemingly small brains that lacks a layered neocortex to behave so intelligently. How is the behavioral complexity just mentioned implemented in the brains of birds? We shall try to put our statements also into a broader perspective: how do brains reflect ecological pressures? Is it possible to correlate specific ecological situations and pressures with central nervous specialization?

By and large, ecological pressures are comparable for all animals: major demands are the acquisition of food, the avoidance of predators, reproduction and locomotion. In this respect, the enormous variability of ecological niches occupied by bird species is of advantage, because we find specialists for various tasks. By choosing a species that is specialized for a particular niche, we can then attempt to correlate the structural and physiological adaptations of its central nervous system with ecological requirements. For birds, additional constraints stem from the fact that the animal has to be capable of flying during all of its reproductive cycle which imposes certain problems for the animal's reproduction and development. We shall first describe in the following the organization of a bird's brain and compare this brain with other vertebrate brains. Then, we will introduce in some detail the neuronal specializations found in birds for a) sensory processing for the acquisition of food (auditory system of the barn owl, food storing and retrieval by memory), b) song production (songbirds), and c) specializations of the visual system that are directly correlated to the species' ecological situation (attentional switching

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* This communication is a contribution to the workshop on "Natural Organisms, Artificial Organisms, and Their Brains" at the Zentrum für interdisziplinäre Forschung (ZiF) in Bielefeld (Germany) on March 8–12, 1998.

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and looming detection). Thus, this review is by no means exhaustive. We have instead chosen a few examples that clearly illustrate the points we want to make.

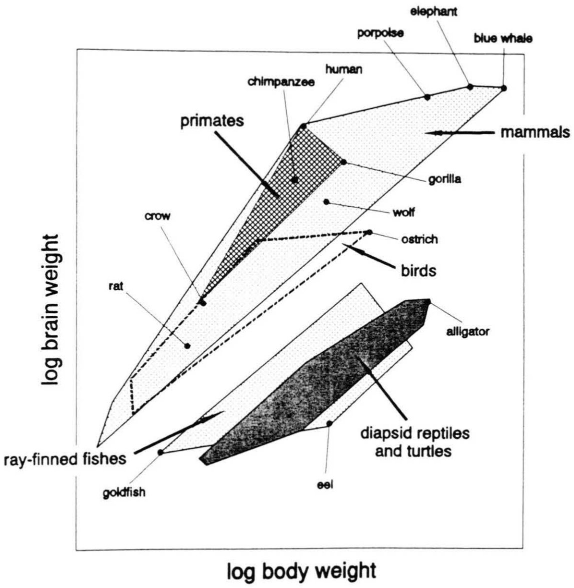

Fig. 1. Allometric analyses of vertebrate brains. The geometrical figures are the minimum convex polygons that will enclose all data points. From Butler and Hodos (1996) with permission.

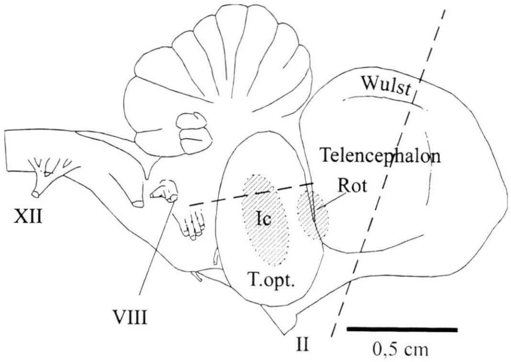

Fig. 2. Brain of a chicken in sagittal view. Anterior is to the left. Structures mentioned in the article are named and/or indicated by dotted lines. Wulst: visual Wulst; Rot: nucleus rotundus; Ic: colliculus inferior; T. opt.: optic tectum; II: nervus opticus (second brain nerve); VIII: nervus statoacousticus; XII: nervus hypoglossus. Broken lines indicate planes of sections shown in Fig. 4. Mark corresponds to 5 mm.

## Overview over the Bird Brain

Allometric measurements are a means for the comparison of brains of animals having different sizes. Body size varies considerably within the vertebrate phylum. According to allometric analyses, bird brains are on average larger than brains of fishes, amphibia, and reptilia, and resemble the brain sizes found in mammals (Jerison, 1973) (Fig. 1). Some birds have even larger brains than primates of the same body weight. Irrespective of the inherent problems of allometric analyses, these data clearly show that the sizes of avian and mammalian brains form a continuum. These data also render false opinions that postulate a linear increase of brain size, behavioral complexity and intelligence along the line of the „phylogenetic scale“, leading from fish to mammals and, of course, to primates and man.

The avian central nervous system displays the typical features of a vertebrate brain and may be subdivided in 7 major parts, i.e. spinal cord, myelencephalon (medulla oblongata), metencephalon (pons and cerebellum), mesencephalon, diencephalon and telencephalon (Fig. 2). We shall briefly describe some of these subdivisions to provide the background for the specific discussion of specializations related to ecological and behavioral adaptations. A more detailed overview may be found in Butler and Hodos (1996) that served as reference for the following summary.

In the medulla oblongata, the auditory and vestibular pathways are well developed. Both superior and inferior olive are distinguishable. In general, the organization of nuclei and fiber tracts resembles the mammalian pattern (Shimizu and Karten, 1993). Unlike reptiles, birds have a pontine enlargement that extends ventrally over the rostral rhombencephalon and comprises the pontine and reticular formations.

The mesencephalon of birds is dominated by the extensive development of the optic tecta (homologue to the colliculi superiores in mammals) that bulge far out to form prominent lateral hemispheres. The size of the tecta already points towards the predominance of the visual system in many birds. The optic tecta are laminated; fourteen to 16 different laminae may be discriminated. The superficial layers receive a direct topographical projection from the contralateral retina. In spite of its name, the optic tectum is a multisensory center that also receives an afferent auditory projection from the auditory midbrain (Knudsen and Knudsen, 1983) and contains a motor map for head movements (duLac and Knudsen, 1990). The auditory midbrain lies within the tectal protrusion below the fourth ventricle. Referring to research in owls, we shall use the term inferior colliculus for the main auditory-midbrain nucleus, while researchers from other fields will also term this nucleus mesencephalicus lateralis dorsalis. In addition to the optic tectum and the tectal nuclei (inferior colliculus and isthmic complex), the midbrain contains the tegmental nuclei which consist of the oculomotor complex, the red nucleus, the nucleus of the basal optic root and the tegmental reticular formation.

The high differentiation of the avian diencephalon resembles the mammalian counterpart. The major sensory-relay nuclei of the dorsal thalamus have a different nomenclature in birds. The lateral geniculate complex of mammals is termed nuclei optici principales and consists of several subnuclei with varying nomenclature according to different authors (reviewed in Güntürkün *et al.* (1993)). The thalamic nucleus of the tectofugal visual pathway (the "pulvinar" in mammals) is a very prominent structure in birds called nucleus rotundus. The mammalian medial geniculate body has been compared to the avian nucleus ovoidalis, because it receives the ascending auditory projections from the inferior colliculus.

The telencephalon of birds is composed of two large hemispheres, the internal organization of which is considerably different from the organization of the mammalian telencephalon. The telencephalon in mammals is characterized by a six-layered isocortex (or neocortex); this term refers to the uniform appearance of the structure independent of its function. The telencephalon in birds does not have a prominent isocortex but is rather arranged in large nuclear masses. The basal telencephalon consists of the septum and the paraolfactory lobe. Medial to the ventricles, a thin hippocampal and entorhinal area can be found. The ventricles themselves are almost obliterated by the protrusion of the lateral cell masses. These nuclear masses have been termed striatal complex in early descriptions and can be differentiated on the basis of histological data into five major divisions: archistriatum, ectostriatum, paleostriatum, neostriatum and hyperstriatum. Note that the term striatum refers to a different structure in mammals. The dorsal part of the hyperstriatum is often separated from the remainder by a longitudinal groove, the vallecula, and forms the so-called visual Wulst that consists of a caudal visual, a medial hippocampal, and a rostral somatosensory area. In the caudal neostriatum, an auditory area is found that is called Field L. This region has been compared to the auditory cortex.

## Sensory Specializations

### *General comments*

To illustrate adaptations in response to ecological pressures, the processing of sensory stimuli yields excellent examples. Animals have often refined detection of stimuli to the physical limit: in vision we find sensitivity to a single photon; in olfaction receptors respond to the binding of a single molecule; in hearing the threshold is often close to the thermal noise. However, not only thresholds become quite low in response to ecological pressures, neural hardware and the implementation of neural algorithms also change, as will be outlined in the following case study on the neural adaptations in the barn owl.

### *A case study: the adaptations of the barn owl's brain to hunting*

Barn owls have particularly variable hunting strategies (Bunn *et al.*, 1982; Brandt and Seebass, 1994). They may hunt when there is still enough light to use the visual sense for prey localization, but typically they hunt at dawn and dusk or during the night, when their prey, mainly small mammals, are active and their own risk of being preyed upon is minimal. While an adult owl lives on 2 mice per night, the situation for an adult during the breeding season gets quite exceptional, as the animal has to catch some 25–30 mice a night to feed the rapidly growing offspring. Since localization is mainly achieved by listening to the sounds of prey, and since the offspring's survival depends directly on the sensory processing capacity of the parent, specializations of the auditory system have developed.

In order to localize prey, the owl has to determine two angles: azimuth, the horizontal angular deviation from the midsagittal plane, and elevation, the vertical angular deviation from the horizontal plane. The distance between the predator and the prey is the third parameter necessary to give the exact spatial location of the prey in three-dimensional space. Little is known about the distance measurement in the barn owl beyond the fact that this parameter is measured passively (Payne, 1971). Therefore, we shall concentrate in the following on describing the mechanisms for the auditory computation of azimuth and elevation of stationary sounds.

### Peripheral adaptations of barn owls

Since acoustic signals play an important role during hunting, the noise produced during flight has to be reduced, and the sound coming from a potential prey has to be amplified. This is achieved by several adaptations in the morphology of the wing feathers (Sick, 1937; Neuhaus *et al.*, 1973) and the ruff feathers (Koch, 1997). There are two important morphological types of feathers in the ruff, the conch or ruff feathers that form the edge of the ruff (Fig. 3A, inset top right) and the auricle feathers (Fig. 3A, inset top left). The ruff feathers are densely ramified and have a closed vane. They reflect the sound and direct it to the ear canals. The auricle feathers, on the other hand, have a less dense ramification and an open vane. They are transparent for sound and have a mere protective function. The ruff has the function to amplify sounds (Coles and Guppy, 1988), and provides the basis of the very low hearing threshold (−15 to −20 dB SPL (Konishi, 1973; Wagner, 1993). The hearing threshold of the barn owl is, thus, about ten times lower than the hearing threshold in humans and is in the range or below the thermal noise. The auricle feathers conceal a further spe-

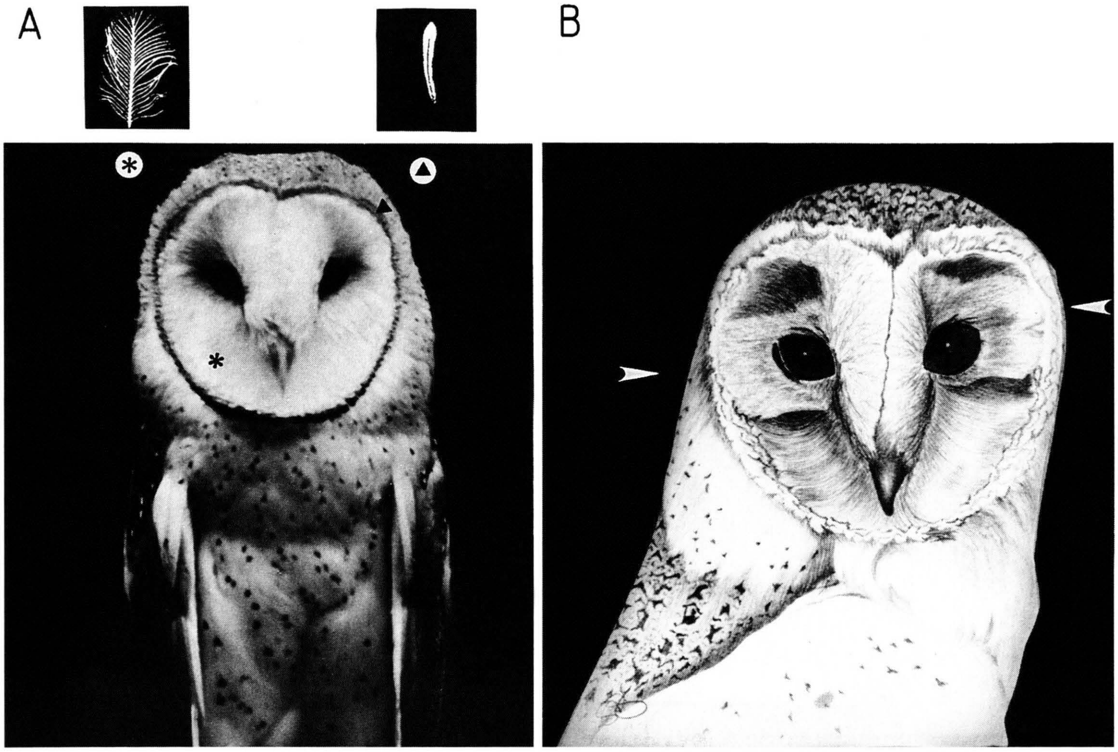

Fig. 3. Barn owl head and plumage. A) Frontal view in full plumage. The asterisk is located in the facial disc, where auricle feathers (top left) are found. The triangle points to the edge of the ruff, where densely packed ruff feathers abound (top right). B) Face after removal of the auricle feathers. Note the asymmetrically arranged pre-aural flaps (arrowheads) that conceal the ear openings. Reprinted with permission after Volman (1994).

cialization: asymmetrically arranged pre-aural flaps (Fig. 3B). The left flap is located higher on the head than the right one. This anatomical asymmetry is the basis of a physiological asymmetry: high frequency sounds from below the horizon are louder in the left ear, and those from above the horizon louder in the right ear. In animals with symmetrical ears the differences in the sound level in the two ears, the interaural amplitude difference (ILD), varies with azimuth. In contrast, due to the asymmetric ears in the barn owl, the ILD varies more with elevation than with azimuth (Moiseff, 1989a; Brainard *et al.*, 1992). Indeed, barn owls associated changes in ILD with changes in elevation (Moiseff, 1989b). The cue that varies with azimuth is interaural time difference (ITD) (Moiseff, 1989a), and barn owls use ITD to localize the azimuthal position of a sound source. Thus, the ear asymmetry leads to a separation of the coordinates along which ITD and ILD vary and generates a

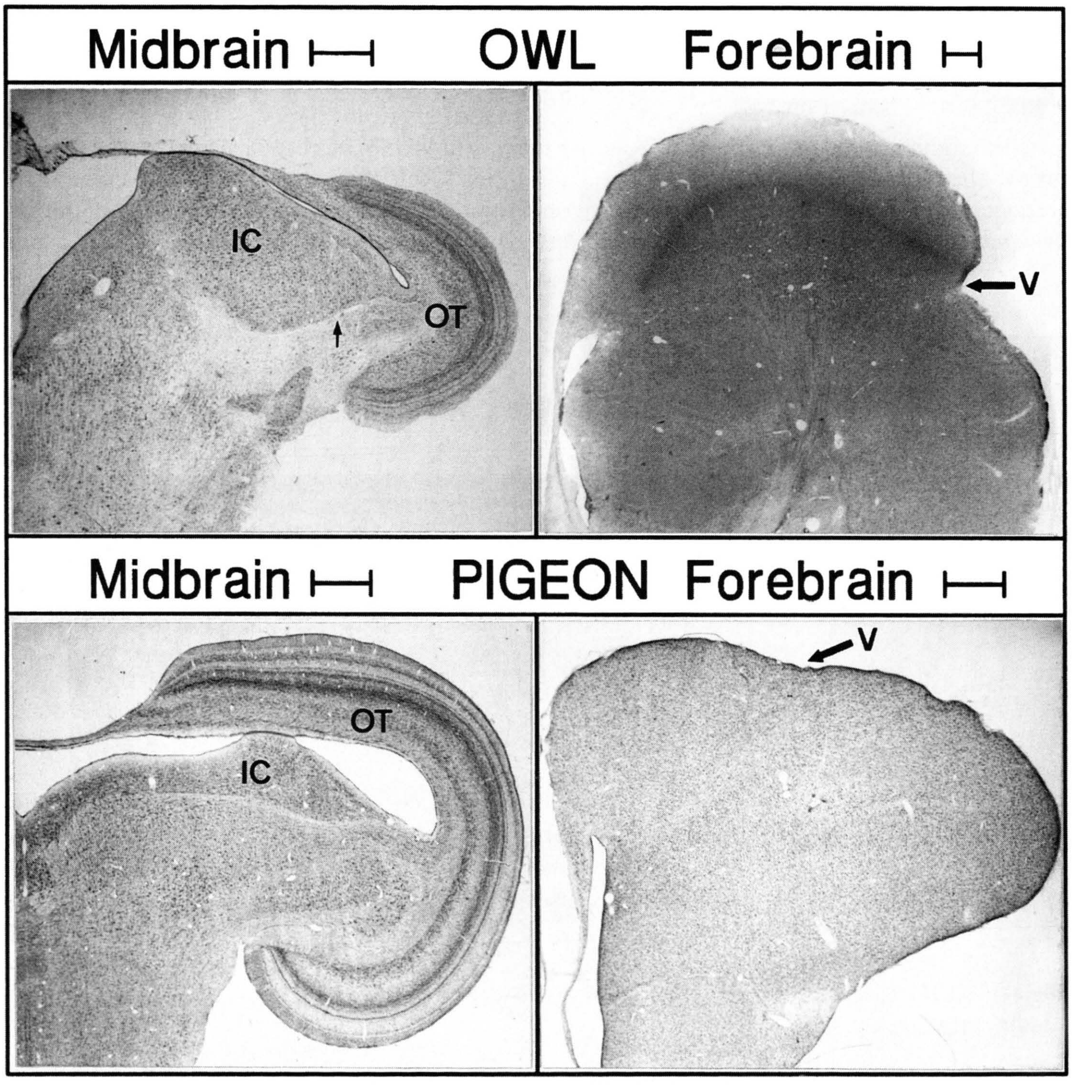

Fig 4. Comparison of owl and pigeon midbrains and telencephalons. The optic tectum (OT) is larger in the pigeon than in the owl, while the colliculus inferior (IC) is larger in the owl than in the pigeon. The visual Wulst and the vallecula (V) are much more prominent in the owl than in the pigeon. The arrow in the upper left picture points to the region that separates the laterally lying ICx from the medial ICc. Marks correspond to 1 mm.

two-dimensional grid, one coordinate of which is ILD, while the other coordinate is ITD. Since both cues are good localization cues, this two-dimensional grid allows the owl to simultaneously determine the location of sounds in azimuth and elevation with high accuracy. The spatial resolution is between 1 and 2 degrees in azimuth and elevation (Knudsen, 1984).

### *The barn owl's brain*

The gross morphology of the owl's brain looks much like that of other birds. However, some extrusions are more conspicuous than in other birds. The visual Wulst is particularly large in barn owls (Fig. 4). A substantial part of the Wulst is involved in the processing of binocular information, another sensory specialization in barn owls, that we can not discuss in detail in this review. Likewise, the dorsal hindbrain has a big vault close to the pons caused by the nucleus laminaris, an auditory hindbrain nucleus. In the following we shall describe some of these specializations in the brain in more detail. Two kinds of specializations are of interest here: morphological specializations in nerve cells and nuclei and physiological specializations such as effective implementation of neural algorithms.

## Morphological adaptations of the owl's brain

The barn owl possesses the longest basilar papilla of any bird studied so far (Köppl *et al.*, 1993). This hearing organ contains some 30,000 hair cells (Köppl, 1997), much more than other species of a comparable size like the chicken or the pigeon.

The general auditory pathway is not different from that of other birds (Fig. 5). A sub-pathway (stream) that processes ITD and its precursors ("time pathway") can be separated from a sub-pathway that processes ILD and its precursors ("intensity pathway") (Moiseff and Konishi, 1983; Takahashi *et al.*, 1984). Important stages in the initial time pathway are the cochlear nucleus magnocellularis (NM) and the nucleus laminaris in the pontine region. The nucleus laminaris (NL) is the first station of binaural interaction. Further up, the anterior part of the auditory nucleus in the lateral lemniscus (VLVa), and the core of the central nucleus of the inferior colliculus (ICccore) (Takahashi and Konishi, 1988) are part of the time pathway. The intensity pathway starts at the second cochlear nucleus, the nucleus angularis (NA), which projects to the posterior part of the auditory nucleus in the lateral lemniscus (VLVp). In the lateral shell of the central nucleus of the inferior colliculus (ICcls), the convergence of the hitherto separated pathways begins. The convergence and neural computation of ILD and ITD is completed in the next station, the external nucleus of the inferior colliculus (ICx). As mentioned above, the organization of the auditory pathway is identical for all birds. The only connection not reported in other birds is the commissural projection from the ICccore to the ICcls in the barn owl (Takahashi *et al.*, 1989, Fig. 5).

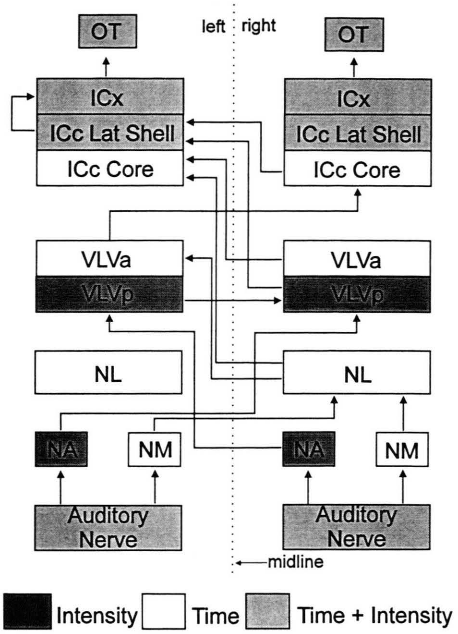

Fig. 5. The auditory pathway of the barn owl. There are two parallel pathways, the time pathway and the intensity pathway, that separate at the level of the cochlear nucleus and converge at the level of the lateral shell of the central nucleus of the inferior colliculus (ICc Lat Shell). Note that in most cases only connections originating on one brain side are shown. Abbreviations are explained in the text.

While the auditory pathway in the barn owl is equivalent to the auditory pathway in other birds, the volume of the nuclei that process auditory information is enlarged in the barn owl. This holds for all nuclei of the auditory pathway, indicating that more cells take part in the computation of a certain parameter. This hypertrophy of the nuclei can best be demonstrated by comparing the size of the auditory midbrain, the inferior colliculus (IC), of the owl with that of a generalist of comparable size, the pigeon (Fig. 4 left). The photographs show a frontal section at the largest cross-section of the IC in both species. The owl's IC is quite conspicuous compared with the pigeon's IC, and the volume of the owl's IC is at least 5 times larger than that of the pigeon (Wagner and Güntürkün, unpublished). In the lateral third of the nucleus a region of low cell density can be seen in Nissl stains (see arrow Fig. 4, top left). This region lies just medial to the ICx (Knudsen and Konishi, 1978; Knudsen and Knudsen, 1983). The ICx plays an important role in sound localization as will be discussed below.

Similar enlargements in brain areas are found in parts of the visual pathway, e.g., the visual Wulst (Fig. 4, bottom row). If we compare this structure in the barn owl and the pigeon, we see that the owl's Wulst is large and sits on top of the brain forming an additional ridge, while the pigeon's Wulst is much smaller. This structure contains neurons sensitive to horizontal disparities (Pettigrew and Konishi, 1976; Wagner and Frost, 1993) necessary for the visual computation of depth.

In conclusion, the anatomical specializations introduced in the last section suggest that the owl's brain is especially suited to process acoustic information related to sound loci and to visual information conveying depth. The hypertrophy of the nuclei points towards a specialized implementation of some algorithms. Such algorithms will be introduced in the following section.

## Physiological adaptations

Physiological specializations are found along the entire auditory pathway. These specializations have increased the effectivity of neural algorithms that also exist in generalists. We shall discuss three of these mechanisms that are important for sound localization. The first, phase-locking, depends mainly on the properties of hair cells and may thus be regarded as a simple mechanism. More requirements are necessary for the second algorithm, coincidence detection. The last algorithm, across-frequency integration, is even more complex, binding together the responses of many coincidence-detecting cells in a specific manner that may be influenced by behavioral feedback. Complexity of computation thus increases as we move from phase locking to across-frequency integration.

*Phase locking.* As described above, barn owls and other animals use ITD to determine the azimuthal position of a sound source. To be able to compute ITD, i.e., the relative arrival time of the

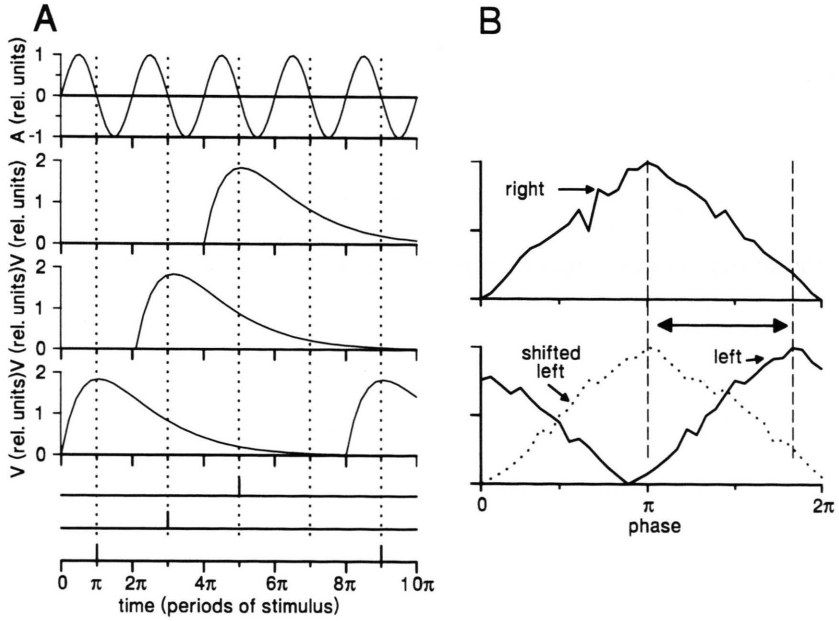

Fig. 6. Phase-locking. When the stimulus is a tone (A), spikes are found preferably at certain phases of the stimulus. If spike arrival time is plotted with respect to the period of the stimulus one arrives at a period histogram (B). In this simulation, a stimulation with 4761 Hz was assumed, and the maxima of the period histograms obtained by stimulating the left ear (left) and the right ear (right) have been separated by some 150 degrees, corresponding to 90 μs. If the left period histogram is advanced by 150 degrees, it parallels the right one.

sound at the two ears, the animals must be equipped with a mechanism to represent time in some way in the first place. In theory, this could be accomplished by an internal clock, in analogy to other internal clocks (e.g. the diurnal clock). However, 1 degree in azimuth corresponds to some 2–2.5 μs in ITD. Therefore, the precision of time measurements lies in the range of some 2–5 microseconds (Moiseff and Konishi, 1981; Knudsen, 1984; Brainard *et al.*, 1992), which is beyond the precision that can be achieved with internal clock mechanisms. Rather, the computation of timing is accomplished by a mechanism termed phase locking.

To explain phase locking, let us regard a simple auditory stimulus, a tone (Fig. 6A). The amplitude of a tonal stimulus changes in a sinusoidal way, reaching the same value after a full period or 360 degrees of phase. If cells now could preferably respond at the highest amplitude (90 degrees of phase) or at the time when the amplitude decreases fastest (180 degrees of phase), then the cells could represent time relative to an external event, the tone. This can be determined by measuring a cell's response relative to the period of the external stimulus (Fig. 6A). By plotting the arrival time of many action potentials, a so-called period histogram can be generated (Fig. 6B). This period histogram can be statistically analyzed to determine whether a neuron's response is locked to the phase of a stimulus.

Phase locking is first seen in hair cell responses. These cells respond to acoustic stimulation with a change in their membrane potential. The change has two components, a DC component and an AC component. Phase-locking seems to be correlated with a detectable AC response of a cell (Russel and Sellick, 1983). As it is easier to change the membrane potential slowly, phase locking is best for low frequencies, because these frequencies have a long period (10 ms for a 100 Hz tone). The higher the frequency, the more difficult phase locking gets. Research in the last 30 years has shown that hair cells in normal laboratory animals such as guinea pigs are able to exhibit phase locking up to frequencies of some 4–5 kHz (Russell and Selick, 1983). In the barn owl, phase locking is seen at frequencies one octave or more higher than in other laboratory animals. In terms of temporal precision, a single auditory nerve fiber in the barn owl can represent time with a precision of some 22 microseconds at 9–10 kHz, while the precision is about 100 μs at 2 kHz in the chick (Warchol and Dallos, 1990) and the owl. This observation supports the claim made above that existing algorithms have become more effective in specialists. To achieve this, the owl must have some specializations – for example fast ion channels – that allow high-frequency phase locking. However, the underlying molecular and biochemical mechanisms are unresolved and a challenging issue for further research.

Why is the ability to phase-lock to high frequencies so important for barn owls? From a functional point of view, it is a precondition for the simultaneous analysis of both parameters for sound localization (i.e., ITD and ILD) in the same frequency range. Distinct ILDs only appear above 5 kHz (Brainard *et al.*, 1992), because the animal's head does not cast an acoustic shadow for sounds having lower frequencies and, therefore, no ILDs arise. Thus, phase locking must extend above 5 kHz and indeed does so. This extension of phase-locking has been directly correlated with the evolutionary pressures operating on a nocturnal hunter (Volman, 1994).

Phase-locking in the range of 20 microseconds presents a formidable problem for the nervous system, because the neural signals used for information processing (postsynaptic potentials and action potentials) are some 10–100-fold longer in cells like the pyramidal cells of the mammalian cortex. With such potentials, phase-locking in the microsecond range would be impossible. Experiments in both mammals and birds have revealed a mechanism that shortens action potentials and especially postsynaptic potentials (Reyes *et al.*, 1996). The clue lies in a voltage-dependent outward-rectifying $K^+$-channel (Manis and Marx, 1991). Measurements in the chicken have shown that by activation of this channel postsynaptic potentials can be reduced in duration to some 500 μs (Reyes *et al.*, 1996), while postsynaptic potentials in cells that lack such specialized channels, like the pyramidal cells of the mammalian cortex, have a duration of some 5 ms. Simulations show that phase locking at 5 kHz can be explained if we assume cellular mechanisms that are about twice as fast as in the chicken (Gerstner *et al.*, 1996).

Thus, with the processes underlying phase locking, the auditory system has "invented" a means to represent time which can be used for further computations. We shall discuss one of these – coincidence detection – in the following paragraph, but it should be kept in mind that the importance of time measurement goes far beyond this, since, for example, speech perception also depends on the precise encoding of temporal events.

*Coincidence detection.* A neuron may be called a coincidence detector if its response depends on the temporal difference in the time of arrival of its inputs. Simultaneously arriving spikes elicit simultaneous excitatory post-synaptic potentials that sum up to exceed firing threshold, while randomly arriving spikes are not as effective (König *et al.*, 1996; Kempter *et al.*, 1998). In this way, a neuron's response is an indicator of binding together two inputs. First we shall briefly mention the general meaning of coincidence detection and then turn to the special mechanisms found in the owl's brain.

Coincidence detection plays a role not only in the measurement of ITD for sound localization but in many other neural processes that occur in different neural substrates and on a large range of time scales: learning (Kandel and Schwartz, 1982), motion detection (Borst and Egelhaaf, 1989), long-term potentiation (Konnerth *et al.*, 1996), synchronization of neural activity (Singer and Gray, 1995), range detection in bats (Suga, 1988), depth vision by spatial or temporal disparity (Carney *et al.*, 1989; Wagner and Frost, 1993), and coordination of cerebellar activity (Heck, 1993). The computation of coincidence detection is performed by neurons having quite different morphology: from pyramidal cells in the mammalian cortex to dendrite-lacking cells in the nucleus laminaris of the owl. Likewise, several different molecular mechanisms are involved: for example, NMDA-receptors in the hippocampus (Konnerth *et al.*, 1996), outward-rectification of potassium currents in the auditory system (Manis and Marx, 1991; Reyes *et al.*, 1996), or 5-hydroxy-tryptamine receptors in conjunction with G-protein-dependent intracellular cascades in sensitization in the snail (Kandel and Schwartz, 1982). The different computational speeds of the molecular processes together with neural gross morphology and conduction times account for the wide range in relevant time scales: from microseconds in measuring interaural time differences to seconds in associative learning. Nevertheless, the formal description, the algorithm, is always the same.

Coincidence detection in the microsecond range in the auditory system is used to represent ITDs. It depends on the high precision phase-locking described in the last section and on several further conditions. First, a special neural circuitry is necessary. Secondly, some regulatory mechanism has to bind together inputs with similar delays. In addition, the coincidence-detecting cells have to be similarly sensitive to time as the input cells and the cells must be able to segregate inputs from the left brain side from inputs from the right brain side.

The principal idea for the realization of an adequate neural circuit dates back some 50 years (Fig. 7 (top); Jeffress, 1948). According to Jeffress (1948) the cells that measure these small time differences act as coincidence detectors, and the neural network innervating the coincidence detectors

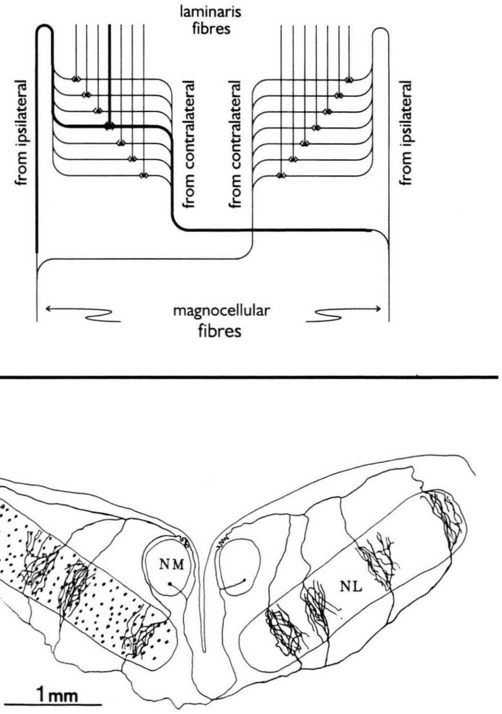

Fig. 7. Binaural interaction in nucleus laminaris. A) A model of the interaction as proposed by Jeffress (1948). The thick lines show terminals from the left and right nucleus magnocellularis that synapse on the soma of a coincidence-detecting neuron in nucleus laminaris. The axon of the laminaris neurons leaves the nucleus. B) Frontal section through owl hindbrain with two magnocellular cells and their axonal arborisations (courtesy Carr). The somata of the neurons are indicated by the black dots. NM: nucleus magnocellularis; NL: nucleus laminaris.

is built of cables that act as delay lines. Jeffress' proposal is realized in remarkable detail in the owl (Fig. 7 (bottom); Carr and Konishi, 1990). It is also obvious in the anatomy of the chick nucleus laminaris, but the structural similarity and clearness are not as outstanding as in the owl (Parks and Rubel, 1975). The coincidence-detecting neurons are the neurons in the nucleus laminaris, the first station of binaural convergence in the auditory pathway. The delay lines are formed by axon collaterals of the cells of the nucleus magnocellularis (Figs. 5, 7).

A regulatory mechanism to establish the correct wiring of the system is necessary, because the times that have to be measured are in the range of microseconds, while the total delay from the ear drum to the coincidence detector lies in the range of 2–4 milliseconds. Gerstner *et al.* (1996) proposed that Hebbian mechanisms might allow the cells to select inputs with the correct delay.

The cells seem not only to use Hebbian mechanisms, but we also see morphological specializations in the coincidence-detecting neurons. While, in principle, binding by a Hebbian mechanism may also work via axo-dendritic synapses and passive or active conductances in a complex dendritic tree, in cells of nucleus laminaris a correlation between frequency tuning and dendritic arborisation exists. Cells tuned to frequencies above some 4 kHz do not have dendritic trees at all, but the afferent axon terminals synapse on the soma (Carr and Boudreau, 1993). Thus, the reduction of the dendritic tree is a further specialization that underlies temporal sensitivity in the microsecond range.

Coincidence-detection is a neuronal computation that may be used for the binding of events. Coincidence detections may be the basis for many cognitive functions like speech perception (Sussman, 1989; Sussman *et al.*, 1998) or the synchronization of brain activity that is supposed to underlie "higher" brain functions (Singer and Gray, 1995) and even consciousness (Crick, 1993).

*Across-frequency integration.* A biological stimulus within a given modality is often very complex, and the brain processes these stimuli by decomposing the separate qualities and processing them separately. There are, for example, the separate time and intensity pathways in the peripheral auditory pathway of birds (Fig. 5). Still, in order to generate adequate behavior, there is a necessity for an organism to bind the different components of a stimulus together again. Coincidence detection is a first mechanism to achieve this. However, the neural responses representing a stimulus after a first coincidence-detection computation are often ambiguous. As an example, the response shown in Fig. 8 depends in a periodic manner on ITD. This precludes the representation of one location in space, and, thus, false targets or target attributes appear. If a hunting animal wants to avoid futile hunting attempts, it must try to reduce false targets as much as possible. We can therefore expect additional algorithms after the stage of primary coincidence detection that remove such ambiguity. Such an algorithm has indeed been found in the auditory pathway, and in the following we will describe the algorithm in some detail. This computation takes place in the external nucleus of the inferior colliculus, three synapses after the computation of coincidence detection (Fig. 5). We shall first outline what the ambiguity looks like in the responses of the coincidence-detecting cells, then show how the ambiguity arises, and finally introduce a solution to the ambiguity problem.

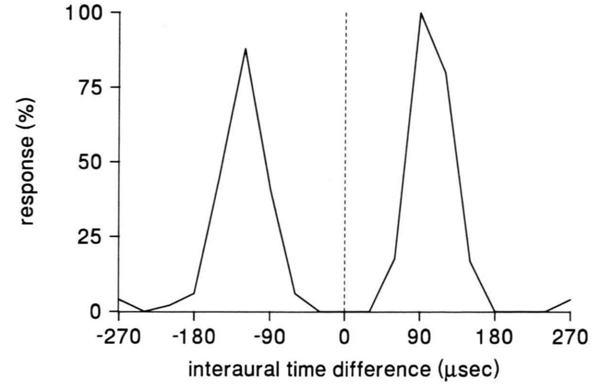

Fig. 8. ITD-curve. The cyclic response function has a period of 210 µs that is equivalent to the period belonging to the stimulating frequency (4761 Hz). The peaks thus occur at interaural phase differences of 90/270 = 0.43 and −120/270 = −0.57.

Cells in nucleus laminaris are the first that exhibit sensitivity to ITD. ITD-sensitivity might be measured by counting the number of spikes occurring in a certain time interval after stimulus onset. The spike counts for the responses to different ITDs constitute the so-called ITD-curve (Fig. 8). Coincidence detectors respond best when the spikes arrive together, as can be seen in the period histograms (Fig. 6B). If we shift the period histogram obtained by stimulating the left ear by 90 μs to the right, it coincides with the period histogram obtained by stimulating the right ear. Consequently, 90 μs ITD elicited the highest response in the ITD-curve (Fig. 8). Since ITD-curves in nucleus laminaris are periodic to both small-band and broad-band stimuli, such laminaris neurons cannot represent a single ITD, but they represent more than one ITD. The response shown here is very regular. Within the range of ITDs tested, the curve exhibits two response peaks and three response minima. The response changes almost follow a sinusoid.

Why are the neurons unable to represent the correct ITD unambiguously? As has been mentioned before, the representation of ITD is a binaural process. Since there are signals to the left and right ears, the correct match of the sounds has to be determined. The solution of this false-target problem is easy if the sound is broad-band as indicated in the upper curves of Fig. 9A. The correct match can always be found. For the tones shown in the lower part of Fig. 9A, several matches are possible, if the onset of the sound is not known. Then it cannot be decided which troughs on the left and right sides correspond to each other. Even if the stimulus consists of noise, narrow-band neu-

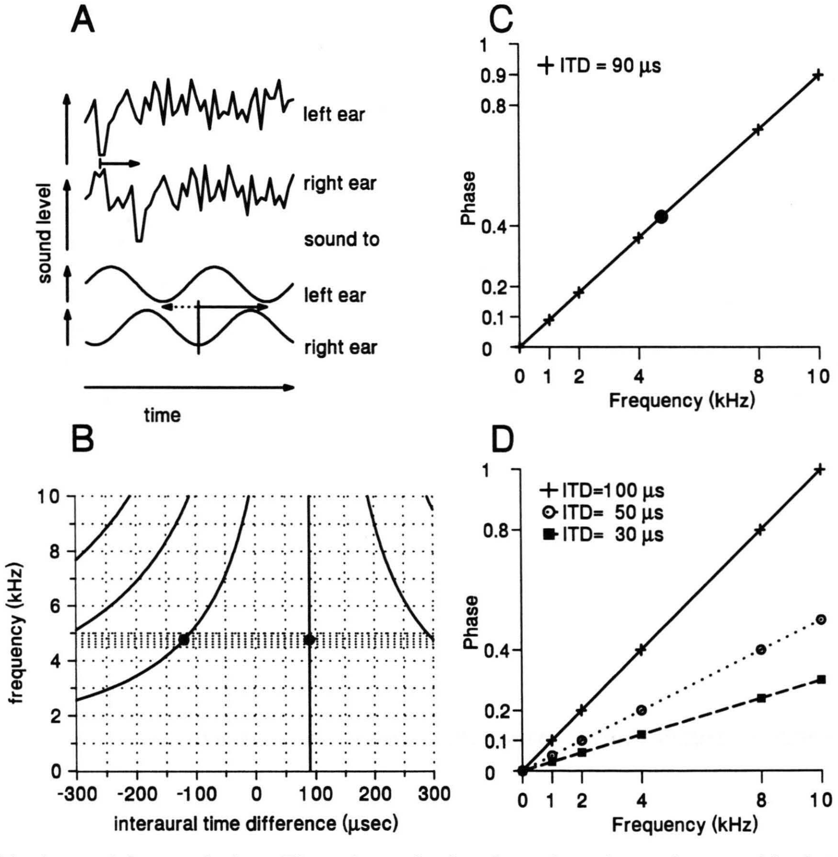

Fig. 9. Phase-ambiguity and its resolution. The schematic drawings show how phase ambiguity may arise if the stimulus is a tone (A, bottom). Phase ambiguity is absent if the stimulus is broad-band noise (A, top). B) Graph showing the appearance of response peaks in ITD-curves as a function of frequency. The dots and the tiny dashes take the example shown in Fig. 7. The regions marked by the tiny dashes center around 4761 Hz. The dots denote the locations of the response peaks. The thick lines show a theoretical construct under the assumption that one response peak occurs at 90 μs for all frequencies. The locations of the neighboring peaks change as functions of frequency. C) The phase of the response (0.43 from the example of Fig. 4) is plotted as a function of frequency (4.761 kHz from the example of Fig. 7) (dot). The phase-frequency pairs of neurons having a common response peak at 90 μs but being tuned to different frequencies (1, 2, 4, 8, 10 kHz) lie on a straight line. The slope of the straight line corresponds to the common response peak. D) Differently sloped lines represent different ITDs.

rons receive inputs from a small frequency range. Therefore, the ITD-curves of narrow-band neurons (Fig. 8, 10A) are periodic. The temporal difference of the response peaks in the ITD-curve corresponds to one period of the stimulus tone. Since these narrow-band neurons respond maximally to more than one ITD, they cannot signal ITD unambiguously but only the phase equivalent of the ITD. In technical terms, the neuron's response shows maxima at

$$\text{ITD} = \text{interaural phase difference/frequency} + k^{*}2\pi; \quad k = 0, \pm 1, \pm 2, \ldots \qquad (1)$$

This equation is shown graphically in Fig. 9B for frequencies from 1 to 10 kHz and for ITDs from −300 to +300 µs. One peak occurs for all frequencies at +90 µs. For a frequency of 4800 Hz, the best frequency of the neuron with the ITD-curve shown in Fig. 8, a second peak around −120 µs is expected (Fig. 9B). Fig. 8 shows a second peak at exactly this time difference. Note also that for other frequencies similar phase ambiguities occur (Fig. 9B).

While the Jeffress model mentioned in the last section explains the principle of binaural interaction by coincidence detection, this model cannot explain the representation of one sound location by the brain without further assumptions. One reason is that this model is formulated without taking the frequency dependence of the responses into account. As has just been described, narrow-frequency tuning in concert with phase-locking may create problems for sound localization, because a coincidence-detecting neuron will be unable to discriminate inputs that are exactly one period apart.

There are two ways to solve this problem. The first one is to restrict analysis of behaviorally relevant ITDs to a range of frequencies at which the ambiguity problem does not occur. This would be 90 µs for the response shown in Fig. 8. If we take the range of physiological ITDs into account, the limit would be at some 750 Hz in humans, and at some 3000 Hz in the barn owl. Thus, the barn owl cannot make use of this solution, because it has to analyze ITDs in a frequency range at which its head creates measurable ILDs. This is, as mentioned above, the frequency range above some 5 kHz. Therefore, the barn owl needs to employ a different solution to the ambiguity problem. It resolves the ambiguity occurring in the upper frequency range by integrating over several frequencies. Thus, an additional concept is necessary for the representation of auditory space. This concept will be referred to as across-frequency integration.

Equation (1) is plotted in Fig. 9C for an ITD of 90 µs and different frequencies. If we take an ITD of 90 µs, we have a corresponding phase of 0.09 cycles at 1 kHz (1 kHz has a period of 1000 µs), a corresponding phase difference of 0.36 cycles at 4 kHz and of 0.9 cycles at 10 kHz. Thus, if we keep time constant, phase changes linearly with frequency. In this plot ITD is the slope of the regression line in Fig. 9C. If we look at Fig. 9B, we see that there is only one ITD for which the response is constant over all frequencies. This is the correct ITD of the signal, marked by a vertical line that connects the ITD-curves at the different frequencies. If we change ITD by one period to the left or right and connect responses that have the same values, we get curved lines (Fig. 9B). The straight line connects responses of equal relative height. Since the slope of the regression line in the phase-frequency plots indicates the ITD, different slopes represent different ITDs (Fig. 9D). Note that this is not the only way how across-frequency integration may take place. Neuronal responses of any equal height, not only at the maximal response as was assumed in the generation of the graphs of Fig. 9B-D, might be combined (Yin and Kuwada, 1983).

We have seen from a theoretical analysis that across-frequency integration might solve the phase-ambiguity problem. Do mechanisms of across-frequency integration exist in the owl's brain? For across-frequency integration cells tuned to different frequencies have to be combined in a specific way: the best combination would be in the way sketched in the mathematics of Fig. 9B and C. Such across-frequency integration was observed (Fig. 10, see also Wagner *et al.*, 1987). ITD-curves of neurons in the lateral shell of the central nucleus of the inferior colliculus (ICcls) are still multi-peaked. These neurons also have a narrow frequency tuning. ITD-curves from 7 recordings obtained at different depths (and therefore frequency) are shown in Fig. 10A. This array of neurons possesses one ITD at which the relative response is stimulus-independent as shown by statistical analysis (Fig. 10B). This array of neurons projects to one neuron in the next higher station of the auditory pathway, the ICx. By this across-frequency integration a new property – unambiguous representation of ITD – emerges in the ICx neuron (Wagner *et al.*, 1987). One might say that the ITD associated with the straight line is characteristic for a cell, and therefore, the term 'characteristic delay' was coined (Rose *et al.*, 1966), and, indeed, ICx neurons exhibit characteristic delays (Takahashi and Konishi, 1986).

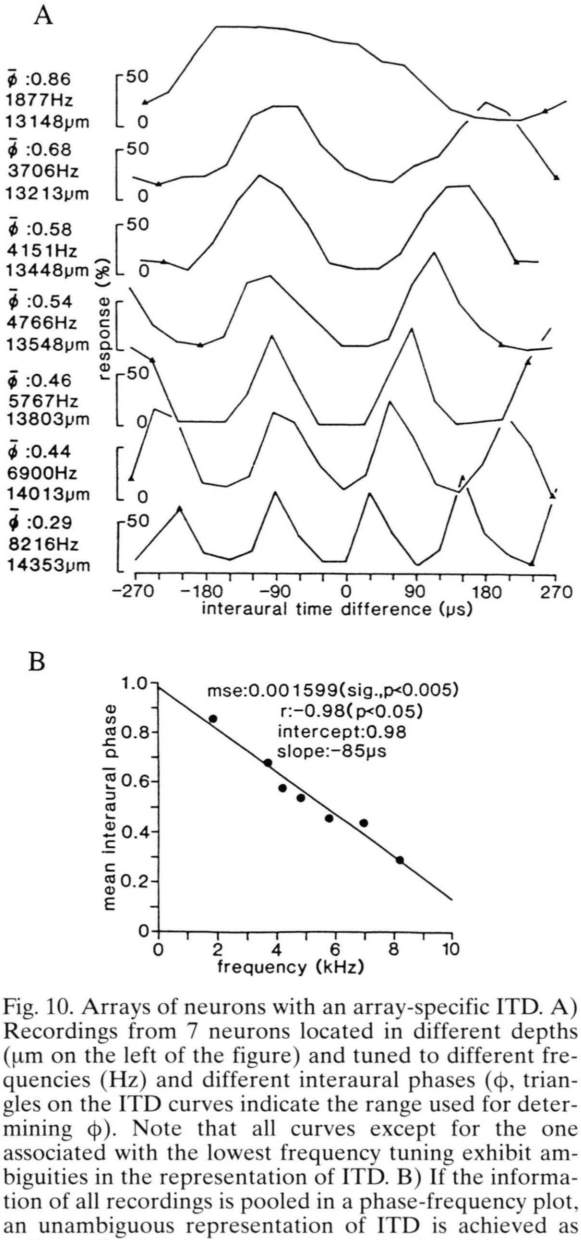

Fig. 10. Arrays of neurons with an array-specific ITD. A) Recordings from 7 neurons located in different depths (μm on the left of the figure) and tuned to different frequencies (Hz) and different interaural phases (ϕ, triangles on the ITD curves indicate the range used for determining ϕ). Note that all curves except for the one associated with the lowest frequency tuning exhibit ambiguities in the representation of ITD. B) If the information of all recordings is pooled in a phase-frequency plot, an unambiguous representation of ITD is achieved as indicated by the mean square error (mse) and the correlation coefficient (r).

Thus, the neural algorithm for the transformation of an ambiguous code to an invariant code in the sound-localization pathway of the owl is across-frequency integration. This algorithm follows the rule that cells tuned to different frequencies but having a constant relation of phase and frequency project onto one cell in the next station. By this integration, and the addition of a tuning to ILD, the cell in a hierarchically higher station becomes not only broadly tuned to frequency, but can also unambiguously represent one location in auditory space. This mechanism is similar to mechanisms of binding discussed in the visual literature (Singer and Gray, 1995), because features of a signal (different frequencies, ITD and ILD) are bound together. Likewise, Sussman *et al.* (1998) have used this algorithm together with coincidence detection to explain the extraction of elements in human speech.

In Fig. 9 and Eqn. (1), we have outlined a theory that combines neurons responding to phase-frequency combinations that are linearly related. This was motivated by the good correlation between theory and observations made with stimuli presented via earphones (Figs. 9, 10). Indeed, if the phase-frequency relationship is measured for sources at loci in frontal auditory space, linear relationships result (Brainard *et al.*, 1992). For lateral auditory space, however, the relation is no longer linear (Brainard *et al.*, 1992). Therefore, a linear relationship would not represent one locus in space, but many of them in a frequency-dependent way. Thus, the linear theory is a good approximation for frontal space only. For other locations in auditory space, the theory must be extended. The wiring is most likely achieved by behavioral feedback, i.e. those phase-frequency combinations are bound together that lead to the best localization or hunting success.

## Song System

Birds have developed songs for territorial behavior and as social signals. Bird songs have many interesting features that link them to human speech like a regular structure (syntax), ontogenetic acquisition, and appearance of dialects

(Konishi, 1985). The seasonal variation suggests hormonal influences on song production. For all these reasons, the neurobiology of song and the adaptations in the brain to song production has interested neurobiologists for a long time.

We first describe some important characteristics of bird songs before we turn to the neural mechanisms underlying these specializations. Songs are different from calls. The song is usually longer and more complex than a call, it is usually only produced by sexual mature males in a particular body posture during the breeding season, and in most cases the main components of songs are learned during ontogeny and are not genetically fixed (for a review see Konishi, 1985).

Bird songs have a structure. The most elementary units have been termed "notes". Several notes may group together to form a "syllable", and syllables can be combined for a "phrase". Many birds produce several different phrases in a fixed sequence as a unit, called the "song". Some birds like thrushes are able to deliver syllables in variable sequences. The rules underlying the timing and sequencing of phrases and syllables are called the syntactical rules and are usually species-specific. The song repertoire, the whole set of different songs a bird is able to produce, can be as large as several hundred different songs (Kroodsma, 1980).

Song learning consists of perceptual and sensorimotor phases. Songbirds are predisposed to learn the song of their own species. Young nestlings hear other birds sing. During the perceptual phase of learning, they commit an acceptable song, usually the song of their father, to memory. In this phase the nestlings only hear the song; they do not vocally reproduce it. During the second phase, the sensorimotor phase, the bird practices. Practising means that the bird sings what is called a plastic song. In this phase of song acquisition the bird has to hear itself vocalize in order to match the vocal output with the memory trace of the tutor song. In most species the song crystallizes after the sensorimotor phase into a "full song", and these birds often sing very stereotyped songs. In contrast, other song birds (e.g., mocking birds, some warblers and starlings) acquire new song elements life long. Starlings for example are able to mimic the squeaking sound of an opening door. Usually, females do not sing, but song can be induced in females if they are treated with steroid hormones.

The song of a bird is so specific that it can be used by naturalists for the identification of the species. In addition to these species-specific features, many songs show distinct geographical variations, known as song dialects (Marler and Tamura, 1962). Dialects occur in certain breeding habitats. All males in a given habitat sing a song typical for the local dialect. These dialects are inherited culturally: nestlings hear the father or neighboring males sing, and will later sing a song of the same dialect. Dialects have been found to be stable for over 10 years (Payne *et al.*, 1981).

In the last two decades, the neural basis of these behavioral observations has been worked out in great detail. A breakthrough in the study of the neural representation of song was the description of a circuit devoted to the production of songs, the song system (Nottebohm *et al.*, 1976; Fig. 11). The song system receives input from the auditory system (Field L). The output of the song system is to a part of the hypoglossus nucleus that innervates the musculature of the vocal organ, the syrinx. Central elements of this circuit are the nucleus HVc and the nucleus RA (Fig. 11). The nuclei be-

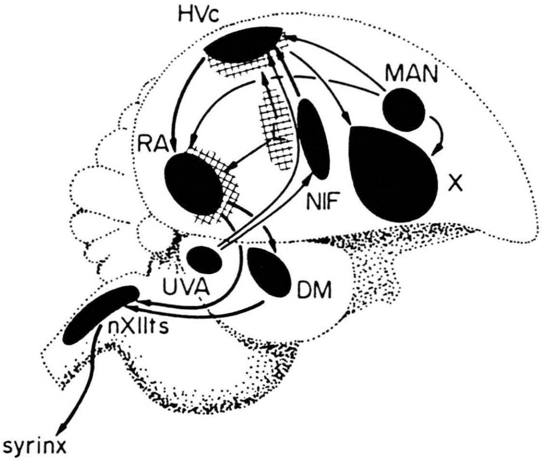

Fig. 11. Song system. The arrows indicate anterograde connections. NIF: Nucleus interface; L: Field L; X: Area X; MAN: magnocellular nucleus of the anterior neostriatum; HVc: Nucleus hyperstriatum ventrale, pars caudale; RA: nucleus robustus archistriatalis; DM: dorsomedial nucleus of nucleus intercollicularis; nXII: nucleus hypoglossus, pars tracheosyringealis); UVA: nucleus uva; Syrinx: vocal organ of birds. Hatched areas indicate sensory centers, dark areas motor and premotor centers. Reprinted with permission after Konishi (1985).

longing to the song system have only been found in song birds (passerines) and parrots, but not in other bird orders. Thus, it seems that these nuclei are a special adaptation of the bird brain to produce complex vocalizations.

The nucleus HVc receives input from the auditory forebrain nucleus, Field L, and neurons in HVc respond to complex auditory stimuli. Interestingly, the HVc contains neurons that respond predominantly or even exclusively to the bird's own song. These highly selective neurons were called song-specific neurons (Margoliash, 1983). Their selectivity develops while the bird sings the plastic song and is completed when the song crystallizes (Volman, 1993). These song-specific neurons play a role during song development and also in song recognition. They are not the memory trace, the template, that is used in the phase of sensorimotor learning to establish the full song, because song-specific neurons develop in parallel with the full song. The location and nature of the memory trace in the brain is still a matter of debate (Konishi, 1985).

As outlined above, songs can be subdivided into notes and syllables. Zebrafinches produce stereotyped songs. Yu and Margoliash (1996) found that changes in the activity of neurons in HVc could be associated with syllables, while the activity of neurons in the nucleus robustus archistriatalis (RA) could be related to notes. RA receives input from HVc. Since association with syllable identity does not require as tight a temporal structuring as association with note identity, this observation means that during the production of a song larger entities with less temporal precision are established first and then refined in a hierarchical network.

Song changes seasonally, and seasonal changes have also been demonstrated in song nuclei and their neurons. A small number of neurons seems to be born at the beginning of a new season in adult canaries, but the majority of the neurons only change dendritic and somatic shape (review in Gahr, 1997). These changes can be directly correlated to the action of hormones. Estrogen receptors have been found in the shelf that surrounds the HVc. If a female of a white-crowned sparrow (that normally does not sing) is implanted with a small pellet of hormone, it starts to sing within some 4 weeks of hormone action. In parallel, the dendritic arborisation of neurons in HVc changes: neurons resemble those found in males in respect to both size and complexity of dendritic arborisation, whereas untreated females have smaller and less complex neurons (Konishi and Gurney, 1982).

Bird song has been claimed to be lateralized in the song birds' brains (Nottebohm and Nottebohm, 1976). However, the site of lateralization may be in the syrinx and not in the song system. The syringeal musculature on the left side is more voluminous than that on the right in the canary (Nottebohm, 1980). So far, no clear central asymmetry has been demonstrated (McCasland, 1987), but further studies are necessary to settle this point. Since the issue of lateralization is unresolved, we have not added lateralization as a further similarity of bird song with human speech.

## Adaptations to Ecological Demands in the Visual System

### *General remarks*

The visual system is very well developed in almost all birds. This is reflected in the size of the nuclei dedicated to visual processing, e.g., the optic tectum and the visual Wulst. Especially in those avian species that are able to fly, the demands on the visual capacities are tremendous and involve the computation of flow-fields, the precise estimation of approaching objects, and the orientation in three-dimensional space. Most birds have laterally-positioned eyes. The binocular overlap is small so that each eye sees its own world. The eyes can be moved some 30 degrees, but usually head turning is more conspicuous than eye movement. Some birds turn the head when they look at things so that one eye fixates the object of interest. There is some evidence that birds may use the left and right eyes in different behavioral situations (Andrew, 1982).

The visual system of all vertebrates has at least three pathways that work in parallel (Karten, 1979). In mammals, the pathway that has been studied most thoroughly is the projection from the retina via the lateral geniculate body to the visual cortex. This thalamofugal pathway has been divided in two streams in primates, the parvo- and the magnocellular stream. A thalamofugal pathway is present in birds, but it is not as prominent as in primates and separated magno- and parvocellular streams have not been observed in birds. The second (tectofugal) pathway connects the retina with the superior colliculus, and leads via the pulvinar to several cortical areas like MT. Birds possess a prominent tectofugal pathway that comprises the optic tectum, the nucleus rotundus in the diencephalon and the ectostriatum in the telencephalon. Finally, the third pathway originates from special displaced ganglion cells, and ends in the nucleus of the optic tract in mammals or the nucleus of the basal optic root in birds, respectively. There seems to be a division of labor between the three pathways, with the third pathway clearly being sensitive to large-field motion for the control of the optokinetic response. All three pathways eventually project to the telencephalon. The current assumptions on the function of these pathways are largely derived from research in mammals like cats and primates. According to data from these animals, the thalamofugal pathway is involved in the detailed analysis of objects, whereas the function of the tectofugal pathway involves sensorimotor tasks like orienting reactions towards objects. Data from studies on birds show that this division of labor is not consistent among various species. Rather, it seems that species with frontal eyes and large binocular overlap (e.g. owls) have a strongly developed thalamofugal system, whereas species with lateral eyes and mostly monocular fields of vision have a strongly developed tectofugal system. As this seems to hold true for mammals as well, the contributions of each system to visual processing might be directly correlated to the ecological situation of a given species.

### *Attentional switching*

Since most birds are active during the day, they have a well developed color system with three different cones. The visual world gets even more colorful, because the incoming light is filtered by oil droplets. Oil droplets of different color are clustered in different parts of the eye in the pigeon so that a red field and a yellow field can be separated. If the head is in upright position, the red field views the ground while the yellow field views the sky. Concomitant with the different eye fields, the optimal viewing distance for the lower visual hemifield and the upper visual hemifield also differs: Chickens are myopic in the lower hemifield, while they are emmetropic in the upper visual hemifield. This peculiarity develops during ontogeny, and depends on the fact that different regions of the eye can be induced to develop emmetropization (Fitzke *et al.*, 1985). These differences make sense for ground feeding birds, because the lower and upper visual hemifield have different ecological functions. The lower field is important for the selection of food grains, while the upper field is important for the detection of possible predators. Ground-feeding birds can be observed to often switch attention from pecking to watching at a distance.

It has been proposed that a neural circuit found especially in grain-feeding birds mediates this attentional switching. This neural loop originates in the retina and projects onto a specific subset of neurons in the optic tectum. The tectal neurons project onto the isthmo-optic nucleus (ION) that

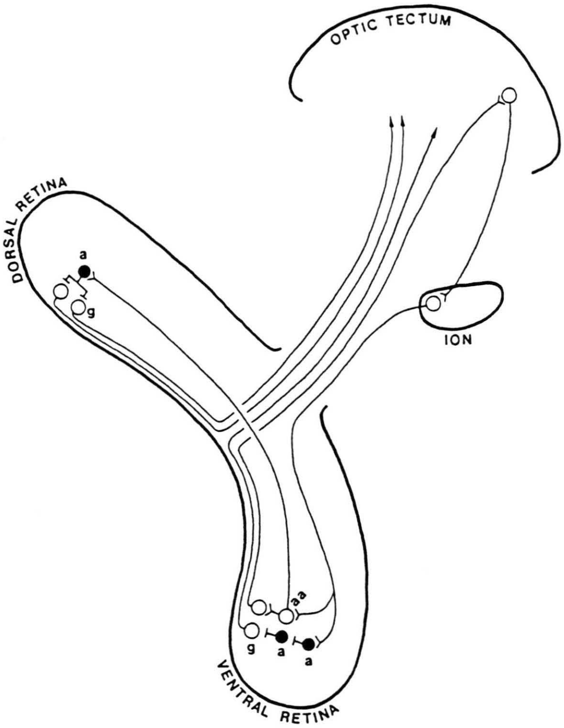

Fig. 12. Circuit for attentional switching. ION: isthmo-optic nucleus; g: retinal ganglion cells; a: ordinary amacrine cells; aa: association amacrines; open circles: excitatory neurons; filled circles: inhibitory neurons. Reprinted with permission after Clarke *et al.* (1996).

finally projects back to the retina. In the retina, efferents from the ION form specific types of terminals (Woodson *et al.*, 1995) that contact a subset of amacrine cells and displaced ganglion cells, and make widespread arborisations in the inner plexiform layer (Catsicas *et al.*, 1987; Uchiyama and Ito, 1993). Whether this neural loop projects back onto the retinal ganglion cells of origin is not clear. Some authors suggest a heterotopic circuit that originates in the dorsal aspects of the retina (the fovea and the red field in pigeons) and projects to the inferior retina (Woodson *et al.*, 1995), others have suggested a homotopic connections that originates and terminates in the ventral retina (Clarke *et al.*, 1996). Undisputed, however, is the finding that birds of prey and birds that feed on the wing have a considerably smaller number of isthmo-optic neurons than grain-feeding birds (Feyerabend *et al.*, 1997). Birds of prey (strigiformes, falconiformes) have been shown to have 900–1400 efferent fibers to the contralateral retina, whereas in grain-feeding birds (chicks and pigeons) 8000–12,000 efferent fibers have been found.

What is the functional significance of this 10-fold difference? Clarke and coworkers (1996) have recently proposed an interesting explanation based on behavioral, physiological and anatomical findings. They argue that, for a ground-feeding bird like chick or quail, an essential task for the visual system is to switch between different areas of interest, e.g., the ground beneath the animal and the upper visual field where a predator might be expected. How do animals without a foveal organization of the retina shift the attention between these visual fields? Clarke *et al.* (1996) propose that this is achieved by switching the focus of computation from the ventral visual field (i.e., the dorsal retina) to the dorsal retinal field (i.e., the ventral retina). This switch is accomplished by the activity of the centrifugal pathway: The ION excites a specific type of amacrine cells in the ventral retina that had already been described by Ramon y Cajal and is termed association amacrines. These neurons project onto the dorsal aspect of the retina (Catsicas *et al.*, 1987). In addition to the association amacrines, another class of amacrines is activated by the ION, the overall effect of this being the enhancement of responses of retinal ganglion cells in the ventral retina and a decrease in the responses of retinal ganglion cells in the dorsal retina (Uchiyama and Barlow, 1994). Taken together, the stimulation of ganglion cells in the ventral retina (the dorsal visual field) would shift the focus of activity to the ventral retina (Fig. 12). Even though other hypotheses on the role of the centrifugal system in birds exist (Woodson *et al.*, 1995), the function hypothesized by Clarke and coworkers could explain various findings from behavioral studies, electrophysiology and comparative anatomy. However, as the behavioral and electrophysiological evidence is rather scarce, this hypothesis remains to be corroborated by more detailed studies. A peripheral mechanism to direct visual attention is quite different from the central concepts discussed in mammals, but might prove to be a fascinating and approachable circuit to reveal fundamental properties of attentional processes.

### *Looming detection*

While we have explained some adaptations to feeding on the ground in the last section, we shall now turn to one of the biggest ecological pressures on the birds' brain: the computation of visual flow fields and the need for sensorimotor reactions during fast flight. Flight is advantageous as a low-cost mode of locomotion over huge distances, as a way to escape predators and to exploit food sources otherwise inaccessible, but in return requires elaborate sensorimotor mechanisms.

The problems are similar to the problems faced by airplanes (or rather pilots). Flight control is especially important to guarantee crashless straight-on flight, safe landing or approaching or hovering in front of objects. Much of the necessary information is contained in the visual flow-field. Birds have a powerful optokinetic system, and looming systems are used especially during landing and hovering. In the following, we shall not try to give a detailed description of all neuronal adaptations of birds to flight, but shall only talk about the looming system.

The flow-field has a focus of expansion that lies in the direction of flight. The focus of expansion is in the point from which all the movement vectors seem to originate. If the bird can measure parameters of the flow-field, then it can control both approach and landing. In this respect, a particular interesting feature of (stationary) objects relative to the moving bird is the "time-to-collision" (TTC) associated with the object. The time-to-collision ($\tau(x)$) is defined as follows:

$$\tau(x) = \frac{x}{\mathrm{d}x/\mathrm{d}t}$$

with $x$ being the distance of the object to the bird, and $\mathrm{d}x/\mathrm{d}t$ the temporal derivative of the distance. The time derivative, $\mathrm{d}\,\tau(x)/\mathrm{d}t$, provides direct information for controlled stopping without the need to measure distance, speed and deceleration: to stop at a location, it is sufficient to keep $\mathrm{d}\,\tau(x)/\mathrm{d}t$ constant at a positive value not greater than 0.5 (Lee *et al.*, 1991).

Thus, by taking into account object size and object expansion, the bird can calculate how long it will take until it reaches the landing point or how to control flight to obtain a stable hovering position. Indeed, pigeons decrease their velocity during landing in a way that suggests that they control TTC (Lee *et al.*, 1993). Similarly, hummingbirds control their position in front of a flower during feeding nectar via time-to-collision information (Lee *et al.*, 1991). Flight control by TTC is also useful in other situations: during plunging in order to control the time when the wings have to be unfolded (Lee and Reddish, 1981). TTC also plays a role in the every day life of humans: car drivers start to brake when TTC reaches a certain threshold (Lee, 1980).

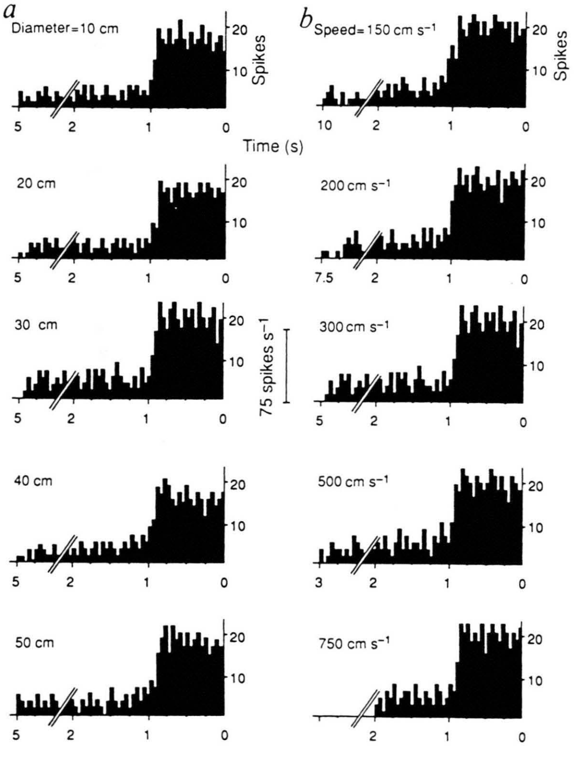

Fig. 13. Representation of time-to-collision in pigeon nucleus rotundus. A cell was stimulated with a series of approaching soccer-ball patterns having different sizes and different speeds. Note that the cell always started to respond at a certain time before impact independent of stimulus size and stimulus speed. Reprinted with permission after Wang and Frost (1992).

The neural implementation of the TTC-algorithm in birds has been partly worked out in the pigeon (Wang and Frost, 1992). What one would expect are cells that respond only if the time-to-collision is below a certain threshold independent of the velocity and the size of an object. Such cells have indeed been found in a nucleus of the tectofugal visual pathway. Wang and Frost (1992) recorded from cells in the nucleus rotundus of the diencephalon that responded selectively to objects moving on a collision course towards the bird. These neurons give their maximum response at a constant time before contact occurs, even when the size of the stimulus or its velocity is varied widely (Fig. 13). Thus, these cells seem to signal the time-to-collision of approaching objects. They do not signal self-motion. Therefore, these cells are probably involved in the detection of approaching objects like predators and not in flight control.

### *Visual spatial memory*

We have already spoken about memory when we described the song system. What we described there was a memory trace about the temporal sequence of complex auditory stimuli. However, there are many more examples where memory seems to play an important role in bird behavior, and we shall briefly discuss an aspect of visual spatial memory in the following.

Many birds store food in caches (for a review see Shettleworth, 1983), either as stock for times when food is scarce (Clark's nutcracker) or to hide it from competitors (black-capped chickadee, marsh tit). As the retrieval is better than chance, the birds must have some memory of the cache sites. In the first case, the bird needs a memory that lasts some months, while in the latter case, a memory of several minute up to several days is sufficient. This memory is of spatial nature, because a change of landmarks influences the searching pattern in a predictable way (Shettleworth, 1983).

From studies with mammals it is known that the hippocampal formation plays a role in spatial memory. Birds also possess a hippocampus. After ablation of the hippocampus in black-capped chickadees, the accuracy of cache recovery decreased (Sherry *et al.*, 1992). This points towards an involvement of the avian hippocampus in spatial memory tasks. In addition, the volume of the hippocampus and the adjacent area parahippocampalis is enlarged in bird families with food storing species compared to non-food-storing families (Fig. 14; Sherry *et al.*, 1992). Thus, hippocampal volume may have increased in response to ecological pressure to remember food caches. Similar adaptations are also found in pigeons that were selectively bred for homing. In those strains that are good homing pigeons, the hippocampal area is larger than in strains that are not selected for homing tasks. Data from woodpeckers, however, suggest that many factors apart from food storing may influence hippocampal size (Volman *et al.*, 1997).

## Conclusions

We have shown examples of how bird brains have been shaped by ecological pressures. The most consistent changes in brain gross anatomy were enlargements of volumina in nuclei. Such enlargements can, for example, be seen in the auditory system of the barn owl and the hippocampus of food storing birds. In these enlarged structures, the cellular arrangement may become more regular as can be seen in the nucleus laminaris and the inferior colliculus of the owl as compared to the nucleus laminaris in the chicken and the inferior colliculus of the cat, respectively. Likewise, altered connectional strengths or even the appearance of new connections may result as was discussed in the loop connecting the retina with the optic tectum and the isthmo-optic nucleus and is also observed in an prominent suprachiasmatic decussation in the owl to allow for the representation of both visual hemifields in binocular neurons. At a more intricate level, the shape of neurons may change: singing males of song birds have more complex dendritic arborisations than non singing males or females; neurons in nucleus laminaris of the owl loose their dendrites to guarantee representation of small temporal differences. Specific functional types of neurons may occur as with the song-specific neurons in song birds. Implementation of neural algorithms may become more effective as demonstrated in the examples of coincidence detection and across-frequency integration. The brain may also invent new implementations of algorithms, and the appearance of NMDA-receptors and their computational capacity in vertebrates may be seen in this context. However, invertebrates that lack NMDA-receptors are also able to perform computations that bind two stimuli together. In this respect the algorithms seem to be more conservative than brain anatomy and physiology.

Such changes are not restricted to birds. Insects use some 50% of their neurons for the processing of visual information, which seems to be closely related to the large information flow through flight (Borst and Egelhaaf, 1989). Similar adaptations are also seen in a variety of species from different vertebrate classes, e.g. electric fish, barn owl and bats. In these species this intricate interplay between ecology, behavior, and neuronal organization has been analyzed in great detail. Thus, the brain is plastic enough to react to evolutionary pressure and to shape brain anatomy accordingly.

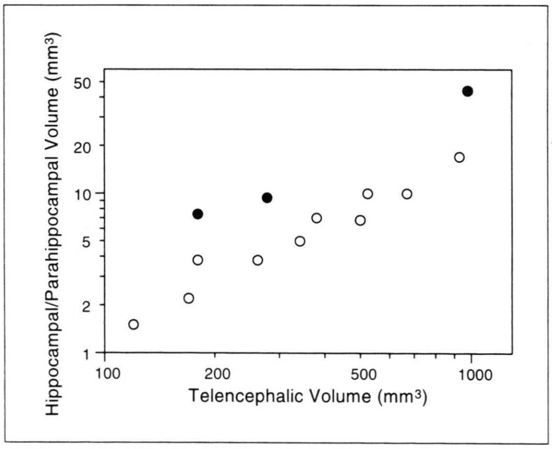

Fig. 14. Hippocampus enlargement in food-storing birds. Families of birds that have species that store food have a larger hippocampal volume than families without food-storing species. Reprinted with permission after Sherry *et al.* (1992).

The feature of the mammalian brain that makes it most different from other brains is the layered isocortex. This isocortex has often been related to the evolutionary success of the mammals – leading eventually to humans with their great cognitive abilities. However, birds with their seemingly small brains are not less intelligent than most mammals. Thus, one general insight might be that a layered structure as is found in the cortex of the mammals is not a necessary prerequisite of complex computations (Karten, 1997). A system that can do a certain job may be designed in different ways. Whether the layering of the cortex is the best way to do complex computations has to be determined. There is some evidence that the appearance of regularity may help in representing certain functions like in the inferior colliculus of the owl. On the other hand, the amazing capabilities of birds demonstrate that brain organizations other than layering may not only lead to evolutionary success but also be able to produce complex behavior.

## *Acknowledgments*

We thank S. Brill and M. Dohms for excellent help with preparing the figures. M. Konishi and D. Sherry advised us on issues on the song system and food storing, respectively. Martin Egelhaaf, Barrie Frost and Michael Koch read an earlier version of this manuscript and gave us a lot of helpful suggestions.

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