

INVITED REVIEW

Barn owl and sound localization

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Abstract: The barn owl is a nocturnal predator with excellent sound localization ability. Due to the asymmetric ears of this bird, the interaural time and level differences, respectively, provide information for the horizontal and vertical direction of a sound source. Forty years of behavioral, anatomical and physiological research on the owl's auditory system have revealed that these two acoustic cues are computed in parallel and hierarchical neural pathways, which converge at the midbrain to form an auditory space map. This neural representation of the acoustic world, calibrated with the visual system, underlies the highly precise sound localization behavior of the barn owl.

Keywords: Binaural hearing, Interaural differences, Neuroethology, Owl, Sound localization

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1. INTRODUCTION

The barn owl is a nocturnal hunter that can find and track its prey in the darkness solely relying on acoustic cues [1]. The owl hears rustling noise created by a small terrestrial animal and quickly locates the source of the sound using binaural acoustic information [2]. In the last 40 years, studies on owls' auditory system have revealed a number of specializations dedicated to this prompt, precise binaural information processing. These studies have also provided important insights on how adaptive and computational processes take place in the brain [3]. The main goal of this review is to provide (1) a comprehensive overview of the neuronal mechanisms that underlie the barn owl's sound localization and (2) pointers to articles that cover each specific topic in more detail. In the following sections, we first summarize owls' acoustical and behavioral performances, and then move forward to the parallel but hierarchical neural computation in their binaural auditory information processing pathways.

Barn owls are distributed widely in the world including Europe, Africa, South and West Asia, Australia, and North and South America [4]. For the study of the auditory system, common European species (*Tyto alba*) and American species (*Tyto furcata*) have been most frequently used. The American barn owl is slightly bigger than the European barn owl, but they have very similar hearing thresholds [5]. These two species can interbreed, and until recently both are often called *Tyto alba* (at least in the field

of neuroscience). In this review, we do not distinguish between these species.

2. BARN OWL AS AN AUDITORY SPECIALIST**2.1. Behavioral Performance**

Many animals orient their vision to an auditory target. This audio-visual behavior is called an auditory saccade. Barn owls, whose eyes are almost immobile [6], turn their heads to the direction of a sound source [2]. This head saccade of the barn owl is quick and reliable [7], and thus has served as a useful tool for characterizing owls' auditory behavioral performances. Anatomical studies showed that the owl's specialized S-shaped neck contributes to its head flexibility [8,9].

Among a number of mammalian species tested, humans show one of the lowest auditory threshold [10] and almost the best sound localization acuity [11] with a minimum resolvable angle of a few degrees. In avian species, owls have an excellent sensitivity to sounds between 200 and 10 kHz [5,10] (Fig. 1) and sound localization acuity of a few degrees [12]. Behavioral experiments showed that a probe sound of only 10-ms duration is sufficient for a barn owl to localize a sound source in azimuth [13]. This outstanding auditory performance has made the barn owl a unique model for the study of sound localization.

2.2. Sound Localization Cues

Several owl species including the barn owl have asymmetric ears [14]. The left ear of the barn owl is located higher and pointing downwards, whereas the right

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Table 1 List of abbreviations (and locations).

AAr: auditory arcopallium (forebrain)
AN: auditory nerve (periphery)
IC: inferior colliculus (midbrain)
ICcc: core of the central nucleus of the inferior colliculus (midbrain)
ICcl: lateral shell of the central nucleus of the inferior colliculus (midbrain)
ICx: external nucleus of the inferior colliculus (midbrain)
ILD: interaural level difference
ITD: interaural time difference
NA: nucleus angularis (brainstem)
NL: nucleus laminaris (brainstem)
NM: nucleus magnocellularis (brainstem)
LLDa: anterior part of the dorsal nucleus of the lateral lemniscus (brainstem)
LLDp: posterior part of the dorsal nucleus of the lateral lemniscus (brainstem)
OT: optic tectum (midbrain)
Ov: nucleus ovoidalis (thalamus)
SO: superior olivary nucleus (brainstem)

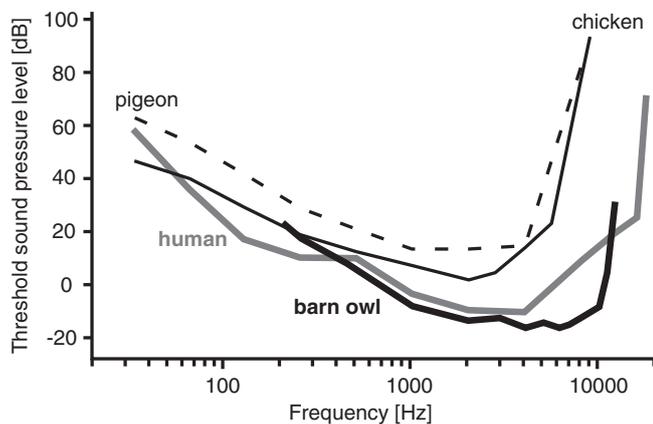


Fig. 1 Behavioral audiogram of the barn owl (thick line), chicken (thin line), pigeon (broken line) and human (gray line). Taken from [5,154] after permission.

ear is lower and pointing upwards [2,12]. Because of this ear asymmetry, the horizontal location of the sound source primarily affects the interaural time difference (ITD), whereas the vertical direction has a major effect on the interaural level difference (ILD) [15,16], making a sharp contrast to other animals, in which ITD and ILD, respectively, serve as low- and high-frequency cues for horizontal sound localization [17]. Since the ITD and ILD axes of the barn owl are not parallel but nearly orthogonal to each other, the combination of ITD and ILD gives a two-dimensional coordinate of the sound source [18].

Measurements of the owl's head-related transfer function revealed that the maximum ranges of ITD and ILD available for a barn owl are 500–600 μ s and 30–40 dB, respectively [19,20]. These values are significantly greater

than values estimated from the owl's typical skull size of \sim 4 cm, because the facial ruff serves as an acoustic amplifier and effectively increases the head size [21]. Indeed, removal of the facial ruff degrades the owl's sound localization ability [12,22].

Many non-mammalian animals have internally coupled ears, which may alter sound localization cues [23]. In the barn owl, however, high frequency sounds over 4 kHz are greatly attenuated in the interaural canal and thus the internal coupling has only limited effects on sound localization [24]. At lower frequencies, effects of internal coupling might be more salient [25] but remain poorly characterized.

2.3. Auditory Periphery

Birds have slightly different inner ears from mammals. The cochlea of a bird (or a reptile) does not form a spiral [26]. Hair cells in the avian cochlea are anatomically classified into two categories, tall hair cells with both afferents and efferents and short hair cells with only efferents [27]. Unlike mammalian inner and outer hair cells, distribution of tall and short hair cells in birds is not uniform along the basilar papilla [28,29]. Compared to other avian species, the barn owl has an exceptionally long basilar papilla of over 10 mm [30], probably reflecting the extended high frequency hearing of this bird [31].

The total number of hair cells in the owl's basilar papilla is estimated to be 16,000 [29], innervated about 30,000 auditory nerve (AN) afferents [32,33]. Unlike mammalian AN afferents, which are often divided into three distinct spontaneous rate categories, avian ANs do not have a multimodal distribution of spontaneous rates. In the barn owl, spontaneous rate of an AN afferent tend to decrease with its characteristic frequency [34,35].

2.4. Sound Localization Pathways

Coding of timing and intensity information of a sound starts at the AN level. Monaural sound pressure level is encoded by the average spiking rate of an AN [36], while monaural timing information is reflected by temporal patterns of AN action potentials. The barn owl's AN shows phase-locking to tonal frequencies up to 10 kHz, which greatly exceeds common phase-locking frequency limits of other animals [37]. This prominent temporal precision of less than 0.1 ms is far below the typical duration of an action potential (\sim 1 ms).

An AN fiber entering the brain branches into two pathways: one of the targets is the nucleus magnocellularis (NM) located on the dorsomedial edge of the brainstem, and the other target is nucleus angularis (NA) found more laterally [38]. Selective pharmacological blockade of these cochlear nuclei showed that ITDs and ILDs are processed in independent, parallel pathways [39]. Namely, the timing

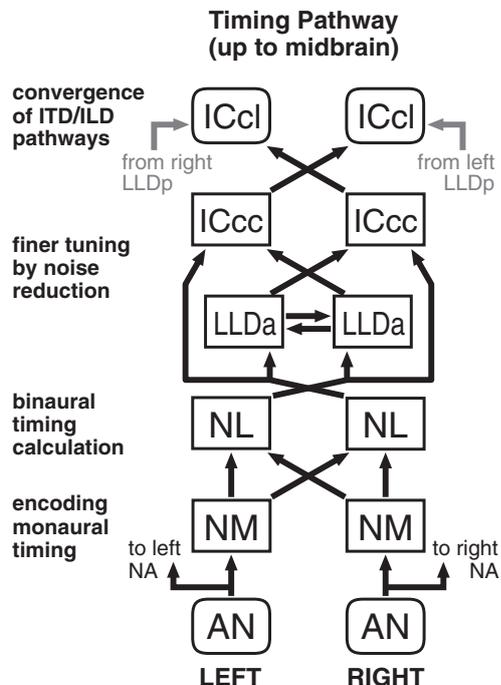


Fig. 2 Timing pathway for computing ITDs. Black arrows indicate excitatory inputs. Gray arrows indicate inhibitory inputs. Neural computation at each stage is shown on the left.

cue is computed in the pathway starting from the NM, whereas the intensity cue (as well as almost all other sound information [40]) is processed in NA and succeeding auditory stages. In the following two sections, we review stepwise auditory processing in these pathways. The ITD and ILD information converges in the midbrain of the barn owl, which will be discussed in Sect. 5.

3. ITD PATHWAY

3.1. Nucleus Magnocellularis

The primary function of the NM is to reliably convey temporal information to the binaural neurons in the nucleus laminaris (NL) (Fig. 2). A barn owl has about 28,000 NM neurons, far more than other bird species [41] and even more than other owl species with larger bodies [42]. An NM neuron receive 1–4 AN afferents with large synaptic endings [38] called the endbulbs of Held named after the German anatomist, Hans Held, who first reported these types of giant synapses in the cat auditory system [43]. Endbulb synapses are also found in mammalian spherical bushy cells in the anteroventral cochlear nucleus [44,45], which are assumed to have similar auditory functions to NM. The synaptic connection via the endbulb is so fast and strong that an incoming AN action potential almost always elicits a spike in NM [46], reliably transmitting neural signals phase-locked to tones over 8 kHz [37].

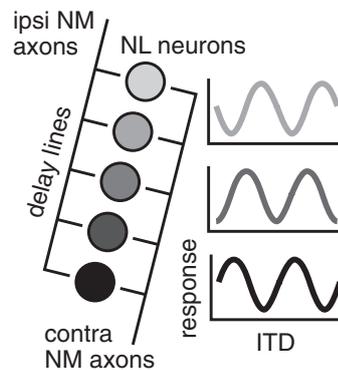


Fig. 3 Jeffress-type ITD map in NL. Peak positions of the ITD tuning curves gradually shift along the delay line.

3.2. Jeffress Model

An NM neuron tonotopically projects to both ipsi- and contralateral NL [47]. Axons from ipsilateral NM neurons enter NL from the dorsal border, whereas contralateral axons approach NL ventrally [48]. Oval-shaped neurons with short and stubby dendrites are distributed sparsely in the NL receiving inputs from both sides [47,49]. Since ipsilateral NM axons run from dorsal side to the ventral and contralateral axons run to the opposite direction, arrival timings of bilateral synaptic inputs vary systematically along the dorsoventral dimension of the NL [49]. Namely, an NL neuron located near the dorsal border receives ipsilateral input earlier and contralateral input later than a neuron near the ventral edge. Axonal conduction velocity is finely tuned so that neural maps of ITD appear dorsoventrally in the owl NL [49,50] (Fig. 3). Developmental adjustment of the axonal path length, internodal distance, and axonal diameter [47,49,51], as well as spike timing dependent plasticity [52], may contribute to the fine tuning of input timings from NM to NL. Cochlear delays were also suggested to affect ITD tuning [53,54], but this hypothesis was rejected in the barn owl [55,56].

The arrangements of owls' NM and NL conform to the Jeffress model of sound localization [57], with NM axons serving as delay lines and NL cell bodies as coincidence detectors [48,49] (Fig. 3). ITDs are represented by dorsoventral locations of NL neurons that receive synchronized bilateral synaptic input to show a maximized spiking activity. Similar Jeffress-type arrangements were also found in emus [58], chickens [59,60] and alligators [61]. In these animals, however, the ITD map extends mediolaterally along the cell layer of the NL, whereas the owl's NL has a multiple ITD maps in parallel to each other [49]. Existence of ITD maps in the mammalian medial superior olive (mammalian counterpart of avian NL) is still under debate [17,54,62].

3.3. Nucleus Laminaris

The NL is the earliest auditory stage where binaural inputs converge. The NL neuron varies its output spiking rate periodically with ITD, detecting changes in the bilateral input timings of far less than a millisecond [49,63]. Single unit responses in the NL are hidden in the background by the large extracellular field potential called the neurophonic [50,64], which hinder further analyses of synaptic inputs in NL. Application of the coaxial micro-electrode technique, however, enabled us to record intracellularly from NL neurons [65]. Convergence of phase-locked synaptic inputs from NM axons induces oscillating synaptic inputs in NL, as theoretically predicted [52,66,67]. Variations in ITD lead to changes in the oscillation amplitude, which the NL neuron senses to change its output spike rates [65,68].

A number of neuronal specializations contribute to the owl's precise ITD coding in NL. A barn owl has about 15,000 NL neurons; this number is greater than in any other bird species tested [41,42]. Dendritic length of NL neurons decreases with increasing characteristic frequency [69], which enables efficient coincidence detection of binaural inputs [70]. The owl's high frequency NL neuron has a spike initiation site away from the cell body [71], enhancing detection of high frequency signals [66]. Similar segregation of synaptic integration from the spike initiation site was also found in mammals [72]. See [62] for more about synaptic and cellular specializations of the owl NL. Neurons in NL receive inhibitory synaptic inputs [73], which will be discussed in Sect. 4.2.

3.4. Anterior Part of the Dorsal Nucleus of the Lateral Lemniscus

Afferent axons of the NL project to the anterior part of the dorsal lateral lemniscus (LLDa) [74] and to the core of the central nucleus of the inferior colliculus (ICcc) [75] on the contralateral side. LLDa used to be called VLVa in earlier literature (see [76] for the revised terminology). An LLDa neuron receives inputs from a smaller number of NL neurons tuned to similar ITDs (physiologically estimated as 2–10 inputs) [77]. The primary role of the LLDa is suggested to reduce spike count variability. An NL neuron requires repeated presentation of the same stimulus to obtain a reliable response, whereas for an LLDa neuron a single trial of sound stimulus presentation is sufficient to produce a robust ITD tuning curve [77].

3.5. Core of the Central Nucleus of the Inferior Colliculus

The ICcc in the midbrain receives afferents from the NL and LLDa on the contralateral side [75,78]. An ICcc neuron receives inputs from multiple neurons with similar ITD tunings to average out neuronal noise, and performs

reliable ITD computation [79] similarly to an LLDa neuron [77]. It is still unknown what benefits may accrue from the convergence of direct and indirect (via LLDa) projections from NL to ICcc. It is also unknown whether cells in LLDa and NL project to the same population of ICcc neurons. Direct and indirect projections from the medial superior olive to the inferior colliculus [17] and similar noise reduction in the lateral lemniscus [80] were also reported in mammals. Having both direct and indirect ITD pathways to the midbrain may thus constitute an unknown but shared computational principle between mammals and birds.

The ITD pathway terminates at the ICcc and will be integrated with the ILD pathway in the lateral shell of the central nucleus of the inferior colliculus (ICcl). It should be noted that, at the ICcc (as well as LLDa and NL) level, phase ambiguity in the ITD-tuning curve exists [77,81,82]. Multiple peaks in the ITD-tuning curve appear with a certain ITD step (which is the reciprocal of the frequency for tonal stimuli and reciprocal of the characteristic frequency of the unit for broadband noise stimuli). This phase ambiguity is due to the tonotopic tuning present in these auditory stages receiving only narrowband inputs and will be resolved later in the external nucleus of the inferior colliculus (ICx), where inputs from multiple frequency channels are integrated [81].

4. ILD PATHWAY

4.1. Nucleus Angularis

The intensity pathway starts at the NA, which receives tonotopic projections from the ipsilateral AN [83] (Fig. 4). An owl has about 17,000 NA neurons, which is again more than any other birds tested [41,42]. In contrast to NM neurons that show high temporal fidelity, NA neurons have longer time windows for synaptic integration, which are more suitable for processing intensity information coded by AN spike counts [84]. The NA is a heterogeneous nucleus: neurons in the NA can be classified into morphologically [85] and physiologically [86] distinct subgroups. In the mammalian cochlear nucleus, different types of neurons with different physiological properties project to different targets [87]. The avian NA also projects to multiple targets [74–76,78], but which NA neuron projects to which auditory areas is unclear. Nevertheless, these observations lead to a suggestion that the NA is involved not only in ILD coding but also in other sorts of sound information processing except ITD coding [40].

4.2. Superior Olivary Nucleus

The superior olivary nucleus (SO) contains inhibitory neurons that receive inputs from the NL, NA and contralateral SO, and project back to the ipsilateral NM, NL, NA and contralateral SO [74,76,78,88]. Note that the avian SO is different from the superior olivary complex in

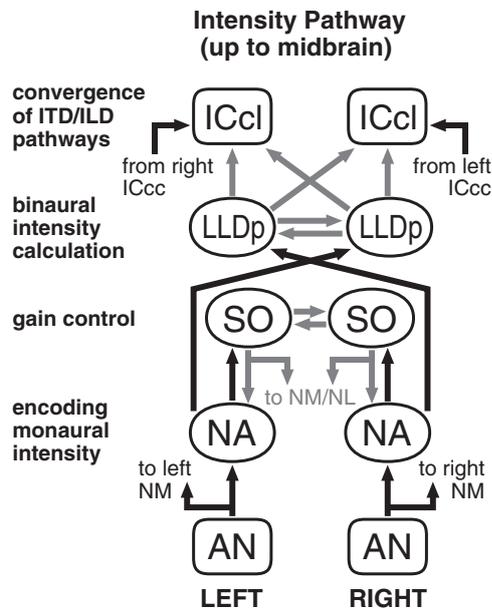


Fig. 4 Intensity pathway for computing ILDs. Black arrows indicate excitatory inputs. Gray arrows indicate inhibitory inputs. Neural computation at each stage is shown on the left.

mammals, although they share the same name. Since the SO sends inhibitory inputs to the ITD pathway (NM and NL), one of the primary suggested roles of the SO is to balance ipsilateral and contralateral inputs to eliminate possible effects of ILD on ITD coding [63,88]. Indeed, in the barn owl, ILD does not affect ITD coding in NL [89].

Inhibitory inputs in the sound localization circuit are provided primarily by SO and are mediated by GABA [73]. The slow GABAergic inhibition was reported to improve temporal coding along the sound localization circuit [90], accelerating the membrane response by shunting [91]. Fast glycinergic inhibition, which plays an important role in mammalian ITD coding [17], is also found in the chicken cochlear nuclei [92]. Possible roles for the newly-found inhibition in the owl's sound localization are yet to be investigated.

4.3. Posterior Part of the Dorsal Nucleus of the Lateral Lemniscus

The posterior part of the dorsal lateral lemniscus (LLDp) is the first location where binaural intensity difference is computed. LLDp was formerly called VLvp [76]. The LLDp receives excitatory inputs from the contralateral NA and inhibitory inputs from the contralateral LLDp [74,93]. Since the contralateral LLDp is driven by the ipsilateral NA, the LLDp is excited by contralateral inputs and inhibited by ipsilateral inputs, resulting in ILD-tuned responses [94–96]. LLDp neurons also show sensitivity to slow changes in the stimulus, reflecting the excitatory-inhibitory interaction [97]. LLDa sends its

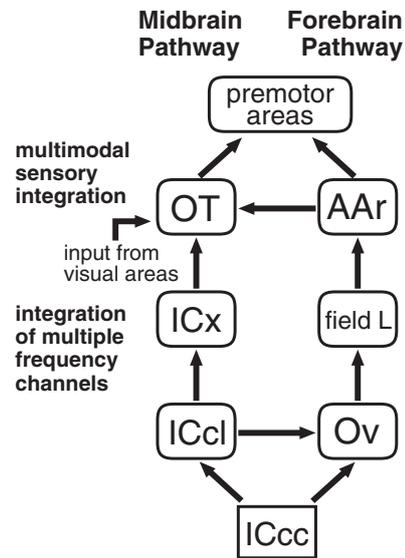


Fig. 5 Midbrain and forebrain auditory pathways. Neural computation in the midbrain pathway is shown on the left.

output to the ICcl in the midbrain, where both ITD and ILD pathways converge [78].

The avian lateral lemniscus contains two more auditory stations: intermediate nucleus and the ventral nucleus, whose functions are still unknown. These nuclei receive inputs from the NA [74,78], and are assumed to be monaural [98,99]. Direct projections from these nuclei to higher auditory areas bypassing the midbrain suggest that these nuclei may be mostly irrelevant to sound localization.

5. MIDBRAIN PATHWAY

5.1. Lateral Shell of the Central Nucleus of the Inferior Colliculus

Compared to other bird species, owls with asymmetric ears have substantially larger auditory midbrains [100], where sound localization cues are integrated and the external auditory space is internally represented. In some literature, the auditory midbrain is also referred to as the dorsal part of the lateral mesencephalon (mesencephalicus lateralis pars dorsalis: MLd). Ascending projections from the ITD and the ILD pathways systematically converge at the level of ICcl [101] (Fig. 5). Each ICcl neuron changes its output spiking rate according to a combination of ITD and ILD [102]. The spiking activity of an ICcl neuron can be predicted by a simple product of its ITD response and ILD response [102,103], as was first suggested from recording results in the ICx [104].

Auditory nuclei up to the ICcl are tonotopically organized. ICcl neurons tuned to different frequencies but to the same ITD projects to an ICx neuron [103]. Due to the across-frequency summation of ICcl inputs, sidebands of

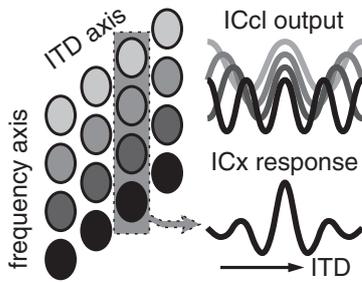


Fig. 6 Across-frequency convergence in the ICx. Summation of ITD tuning curves with different periods eliminates phase ambiguity.

the ITD tuning curves are suppressed and only the main peak is emphasized (Fig. 6), leading to the elimination of the phase ambiguity (see Sect. 3.5) in the ICx [81,105,106]. Behavioral and physiological experiments showed that a bandwidth of 3 kHz is sufficient for an owl to distinguish the correct sound source from an illusory target [107].

5.2. External Nucleus of the Inferior Colliculus

The ICx is the location where inputs from the ICcl converge over multiple-frequency channels [75,108] and the barn owl's auditory space map is established. An ICx neuron is excited only when the stimulus sound comes from a certain spatial direction [109], indicating that each ICx neuron has its own preference to a specific combination of ITD and ILD. The horizontal direction of a sound (represented by ITD) and the vertical direction (represented by ILD) are mapped two-dimensionally in the ICx [18,109]. Agreement between the owl's behavioral acuity and the coding performance of ICx neurons supports the hypothesis that ICx is the central location where the external auditory world is mapped internally [110]. Some ICx neurons also show sensitivity to moving sound sources [111], which may be suitable for tracking live targets. Adaptive processes in the midbrain will be discussed in Sect. 5.4.

For birds with symmetric ears, ITD and ILD do not change independently with the location of the sound source. In contrast to the barn owl, which has asymmetric ears, owls with symmetric ears have smaller cochlear nuclei with fewer neurons and also relatively smaller auditory midbrain (normalized to the total brain volume) [42]. ICx neurons of symmetric-eared owls are sensitive only to the azimuth but not to the elevation of the sound source [112]. Midbrain neurons in other birds of prey with symmetric ears, such as falcons and hawks, also show restricted tuning to the azimuthal sound location [113], indicating that these symmetric birds have only one-dimensional representation of the acoustic world.

5.3. Optic Tectum

ICx neurons project to the optic tectum (OT), the avian homologue of the mammalian superior colliculus. The OT is the location where auditory and visual information is integrated. The barn owl's OT not only inherits the auditory space map from the ICx [108,114,115] but also receives retinotopic inputs from the visual system [116]. The visual map shows an astonishingly clear agreement with the auditory map [117], and simultaneous audiovisual stimulation facilitates responses of OT neurons [118]. The barn owl has excellent sight [119], and the visual input to the OT is used for calibrating the auditory space map. A barn owl raised with a binocular prism that displaces the visual field turns its head not directly to the acoustic target but to the displaced direction imposed by the prism [120], and the auditory space map of the OT is aligned to the displaced visual map [121].

Neurons in the OT project to premotor neurons in the brainstem that control head and neck muscles [122]. Electrical stimulations to the OT [6] as well as to the premotor areas in the brainstem [123] induce owls' head turns. Thus computation of the sound localization cues completes at the OT and then corresponding behavior of the barn owl is finally produced. In the following (sub)sections, we discuss adaptive properties in the mid-brain and forebrain pathways.

5.4. Plasticity and Adaptation

Because of its clear functional organization and highly adaptive nature, the barn owl's auditory midbrain has been intensively used for the study of neuronal plasticity and development. Alteration of sound localization cues by plugging ears, for example, changes sound localization behavior [124] and the underlying auditory space map in the OT [125,126]. Owls lose developmental capability of adjusting abnormal auditory cues at about eight weeks of age [124], suggesting the importance of early experience. Active experience, such as hunting, however, extends the age window of plasticity where such audio-visual realignments are possible [127].

The ICx also show plastic changes to altered vision, although it does not receive direct visual inputs. Prism-induced visual displacement alters not only the auditory space map in the OT but also the map in the ICx [128]. Dynamical changes in axonal projection patterns to the ICx are suggested to be the underlying mechanisms of this experience-dependent plasticity of the auditory space map [129]. In contrast to ICx, the central nucleus (ICcl/ICcc), does not show plastic changes to vision [129]. Although earlier auditory stages were generally assumed to be robust to changes, adaptive changes have been found in the mammalian auditory brainstem [130], which suggests that owls' brainstem might also show stimulus-dependent plasticity.

6. FOREBRAIN PATHWAY

6.1. Nucleus Ovoidalis

Neurons in the ICcc and ICcl project to the nucleus ovoidalis (Ov) in the auditory thalamus [131], which is the entry point to the forebrain auditory pathway (Fig. 5). Similar to the central nucleus of the IC, the Ov is tonotopically organized [132]. The Ov contains multiple types of neurons: some neurons have sensitivity to either ITD or ILD, whereas other neurons are sensitive to both cues [132,133]. Ov neurons sensitive to both ITD and ILD show similar auditory spatial tuning to ICx neurons [134]. Neurons in the Ov, however, show broader frequency tuning than ICx neurons [133], and no topographic map of the auditory space is identified in the Ov [132,133]. Pharmacological inactivation of the Ov has only limited effects on the sound-induced head turning behavior [135]. These observations, along with the fact that Ov does not receive inputs from the ICx or OT [132], suggest that the auditory thalamus conveys to higher auditory areas different types of information from what is represented in the auditory space map.

6.2. Forebrain (Field L and Arcopallium)

The auditory thalamus Ov sends its output to the forebrain field L [136], which corresponds to the primary auditory cortex in mammals [137]. Although the field L is tonotopically organized [138], some neurons in the field L show spatial tuning and others do not [139], suggesting the complex nature of the cortical auditory information processing. The field L directly and indirectly (via other forebrain nuclei) projects to the auditory arcopallium (AAR), which was also called the archistriatum. The AAR sends descending projections to the auditory midbrain and the brainstem motor nuclei [136]. Since functions of the auditory cortex are, in general, broad and complex [140], we here focus on the contribution of the owl's forebrain pathway to sound localization.

Midbrain and forebrain auditory units show a number of differences. An AAR neuron has a broader frequency [141] and spatial tuning [142] than a midbrain neuron. Similar to the Ov, the AAR lacks clear topographic map of the auditory space [142]. The ITD-tuning curve of an AAR neuron is often asymmetric, whereas ICx neurons tend to have more symmetric ITD tuning [141]. In contrast to the ICx neuron, to which neurons with similar ITD tuning are assumed to converge, an AAR neuron is suggested to receive inputs from a neuronal population that have a wider variety in ITD tuning, resulting in the asymmetric ITD coding [143]. Pharmacological blockade of the forebrain pathway disrupts memory formation [144] but not the auditory targeting behavior [135]. Inactivation of the midbrain pathway, however, leads to degraded head

orientation [135,145]. Outputs of broadly-tuned forebrain neurons may thus serve as a teaching signal to coarsely adjust the auditory spatial maps in the midbrain in a context dependent manner. And skewed ITD representations in the owl's forebrain may be used for controlling attention and binaural unmasking [146].

7. CONCLUDING REMARKS

7.1. Implications and Applications

Spatial hearing is a fundamental auditory function not only for the owl's hunting but also for our daily life. Precise sound localization is essential, for example, to avoid danger (such as incoming traffic), or to separate sound sources in a noisy environment (i.e., the cocktail party problem). Because of its functional clarity and specializations, the barn owl's auditory system has long served as an excellent model system of the study on sound localization and neural adaptation.

People with assistive listening devices often have difficulty in sound localization, because binaural cues necessary for sound localization is not always maintained. For improving bionic devices such as bilateral cochlear implants [147], understanding the neural mechanisms of binaural information processing is particularly important. In addition, the well-studied owls' auditory system may also be a good starting point for modeling the auditory brainstem response, which is a collective electrical activity from the periphery to the midbrain and is used as a non-invasive diagnostic tool for auditory dysfunctions [148]. Moreover, the avian auditory periphery is attracting increasing attention because its sensory hair cells can regenerate after damage [149]. Studies of the avian ear would provide good insights on possible genetic treatments of lost human hair cells in damaged or aged cochleae.

7.2. Further Reading

For interested readers, we here suggest reviews that discuss relevant topics in more detail. For a comparison between mammalian and avian brains, see [137]; for mammalian sound localization, see [17,54]; for a comparison of ITD coding along the auditory pathways, see [146]; for a more comprehensive review focusing on the owl's inferior colliculus, see [150]; for leaning and adaptation in the barn owl's midbrain, see [3,151]; for the prey capture behavior of the barn owl, see [152]; and for a historical account authored by *the* pioneer of the field, see [153].

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REFERENCES

- [1] R. S. Payne, "Acoustic location of prey by barn owls (*Tyto alba*)," *J. Exp. Biol.*, **56**, 535–573 (1971).
- [2] M. Konishi, "How the owl tracks its prey," *Am. Sci.*, **61**, 414–424 (1973).
- [3] J. L. Peña and W. M. DeBello, "Auditory processing, plasticity and learning in the barn owl," *ILAR J.*, **51**, 338–352 (2010).
- [4] C. König and F. Weick, *Owls of the World*, 2nd ed. (Yale University Press, New Haven, CT, 2008).
- [5] M. L. Dyson, G. M. Klump and B. Gauger, "Absolute hearing thresholds and critical masking ratios in the European barn owl: A comparison with other owls," *J. Comp. Physiol. A*, **182**, 695–702 (1998).
- [6] S. du Lac and E. I. Knudsen, "Neural maps of head movement vector and speed in the optic tectum of the barn owl," *J. Neurophysiol.*, **63**, 131–146 (1990).
- [7] E. A. Whitchurch and T. T. Takahashi, "Combined auditory and visual stimuli facilitate head saccades in the barn owl (*Tyto alba*)," *J. Neurophysiol.*, **96**, 730–745 (2006).
- [8] T. Masino and E. I. Knudsen, "Horizontal and vertical components of head movement are controlled by distinct neural circuits in the barn owl," *Nature*, **345**, 434–437 (1990).
- [9] M. Krings, J. A. Nyakatura, M. S. Fischer and H. Wagner, "The cervical spine of the American barn owl (*Tyto furcata pratincola*): I. anatomy of the vertebrae and regionalization in their S-shaped arrangement," *PLoS ONE*, **9**(3), e91653 (2013).
- [10] H. E. Heffner and R. S. Heffner, "Auditory perception," in *Farm Animals and the Environment*, C. Phillips and D. Piggins, Eds. (C. A. B. International, Wallingford, UK, 1992), pp. 159–184.
- [11] R. S. Heffner, G. Koey and H. E. Heffner, "Hearing in alpacas (*Vicugna pacos*): Audiogram, localization acuity, and use of binaural locus cues," *J. Acoust. Soc. Am.*, **135**, 778–788 (2014).
- [12] E. I. Knudsen and M. Konishi, "Mechanisms of Sound Localization in the barn owl (*Tyto alba*)," *J. Comp. Physiol.*, **133**, 13–21 (1979).
- [13] H. Wagner, "A temporal window for lateralization of interaural time difference by barn owls," *J. Comp. Physiol.*, **169**, 281–289 (1991).
- [14] R. Å. Norberg, "Occurrence and independent evolution of bilateral ear asymmetry in owls and implications on owl taxonomy," *Philos. Trans. R. Soc. Lond.*, **280**, 375–408 (1977).
- [15] R. B. Coles and A. Guppy, "Directional hearing in the barn owl (*Tyto alba*)," *J. Comp. Physiol. A*, **163**, 117–133 (1988).
- [16] A. Moiseff, "Binaural disparity cues available to the barn owl for sound localization," *J. Comp. Physiol. A*, **164**, 629–636 (1989).
- [17] B. Grothe, M. Pecka and D. McAlpine, "Mechanisms of sound localization in mammals," *Physiol. Rev.*, **90**, 983–1012 (2010).
- [18] M. Konishi, "Listening with two ears," *Sci. Am.*, **268**, 66–73 (1993).
- [19] C. H. Keller, K. Hartung and T. T. Takahashi, "Head-related transfer functions of the barn owl: Measurement and neural responses," *Hear. Res.*, **118**, 13–34 (1998).
- [20] L. Hausmann, M. von Campenhausen and H. Wagner, "Properties of low-frequency head-related transfer functions in the barn owl (*Tyto alba*)," *J. Comp. Physiol. A*, **196**, 601–612 (2010).
- [21] M. von Campenhausen and H. Wagner, "Influence of the facial ruff on the sound receiving characteristics of the barn owl's ears," *J. Comp. Physiol. A*, **192**, 1073–1082 (2006).
- [22] L. Hausmann, M. von Campenhausen, F. Endler, M. Singheiser and H. Wagner, "Improvements of sound localization abilities by the facial ruff of the barn owl (*Tyto alba*) as demonstrated by virtual ruff removal," *PLoS ONE*, **4**(11), e7721 (2009).
- [23] J. Christensen-Dalsgaard, "Vertebrate pressure-gradient receivers," *Hear. Res.*, **273**, 37–45 (2011).
- [24] A. Moiseff and M. Konishi, "The owl's interaural pathway is not involved in sound localization," *J. Comp. Physiol.*, **144**, 299–304 (1981).
- [25] M. B. Calford and R. W. Piddington, "Avian interaural canal enhances interaural delay," *J. Comp. Physiol. A*, **162**, 503–510 (1988).
- [26] S. A. Walsh, P. M. Barrett, A. C. Milner, G. Manley and L. M. Witmer, "Inner ear anatomy is a proxy for deducing auditory capability and behaviour in reptiles and birds," *Proc. R. Soc. B*, **276**, 1355–1360 (2009).
- [27] G. A. Manley, "Cochlear mechanisms from a phylogenetic viewpoint," *Proc. Natl. Acad. Sci. USA*, **97**, 11736–11743 (2000).
- [28] C. A. Smith, M. Konishi and N. Schuff, "Structure of the barn owl's (*Tyto alba*) inner ear," *Hear. Res.*, **17**, 237–247 (1985).
- [29] F. P. Fischer, C. Köppl and G. A. Manley, "The basilar papilla of the barn owl *Tyto alba*: A quantitative morphological SEM analysis," *Hear. Res.*, **34**, 87–102 (1988).
- [30] O. Gleich and G. A. Manley, "Quantitative morphological analysis of the sensory epithelium of the starling and pigeon basilar papilla," *Hear. Res.*, **34**, 69–85 (1988).
- [31] C. Köppl, O. Gleich and G. A. Manley, "An auditory fovea in the barn owl cochlea," *J. Comp. Physiol. A*, **171**, 695–704 (1993).
- [32] F. P. Fischer, "Quantitative TEM analysis of the barn owl basilar papilla," *Hear. Res.*, **73**, 1–15 (1994).
- [33] C. Köppl, "Number and axon calibres of cochlear afferents in the barn owl," *Aud. Neurosci.*, **3**, 313–334 (1997).
- [34] C. Köppl, "Frequency tuning and spontaneous activity in the auditory nerve and cochlear nucleus magnocellularis of the barn owl *Tyto alba*," *J. Neurophysiol.*, **77**, 364–377 (1997).
- [35] H. Neubauer, C. Köppl and P. Heil, "Spontaneous activity of auditory nerve fibers in the barn owl (*Tyto alba*): Analyses of interspike interval distributions," *J. Neurophysiol.*, **101**, 3169–3191 (2009).
- [36] C. Köppl and G. Yates, "Coding sound pressure level in the barn owl's auditory nerve," *J. Neurosci.*, **19**, 9674–9686 (1999).
- [37] C. Köppl, "Phase locking to high frequencies in the auditory nerve and cochlear nucleus magnocellularis of the barn owl, *Tyto alba*," *J. Neurosci.*, **17**, 3312–3321 (1997).
- [38] C. E. Carr and R. E. Boudreau, "Central projections of auditory nerve fibers in the barn owl," *J. Comp. Neurol.*, **314**, 306–318 (1991).
- [39] T. Takahashi, A. Moiseff and M. Konishi, "Time and intensity cues are processed independently in the auditory system of the owl," *J. Neurosci.*, **4**, 1781–1786 (1984).
- [40] K. M. MacLeod and C. E. Carr, "Beyond timing in the auditory brainstem: Intensity coding in the avian cochlear nucleus angularis," *Prog. Brain Res.*, **165**, 125–135 (2007).
- [41] M. F. Kubke, D. Massoglia and C. E. Carr, "Bigger brains or bigger nuclei? Regulating the size of auditory structures in birds," *Brain Behav. Evol.*, **63**, 169–180 (2004).
- [42] C. Gutiérrez-Ibáñez, A. N. Iwaniuk and D. R. Wylie, "Relative size of auditory pathways in symmetrically and asymmetrically eared owls," *Brain Behav. Evol.*, **78**, 286–301

- (2011).
- [43] H. Held, "Die centrale Gehörleitung," *Arch. Anat. Physiol., Anat. Abteil.*, 201–248 (1893).
- [44] D. K. Ryugo and T. N. Parks, "Primary innervation of the avian and mammalian cochlear nucleus," *Brain Res. Bull.*, **60**, 435–456 (2003).
- [45] R. Schneggenburger and I. D. Forsythe, "The calyx of Held," *Cell Tissue Res.*, **326**, 311–337 (2006).
- [46] S. Brenowitz and L. O. Trussell, "Maturation of synaptic transmission at end-bulb synapses of the cochlear nucleus," *J. Neurosci.*, **21**, 9487–9498 (2001).
- [47] C. E. Carr and R. E. Boudreau, "Organization of the nucleus magnocellularis and the nucleus laminaris in the barn owl: Encoding and measuring interaural time differences," *J. Comp. Neurol.*, **334**, 337–355 (1993).
- [48] C. E. Carr and M. Konishi, "Axonal delay lines for time measurement in the owl's brainstem," *Proc. Natl. Acad. Sci. USA*, **85**, 8311–8315 (1988).
- [49] C. E. Carr and M. Konishi, "A circuit for detection of interaural time differences in the brain stem of the barn owl," *J. Neurosci.*, **10**, 3227–3246 (1990).
- [50] W. E. Sullivan and M. Konishi, "Neural map of interaural phase difference in the owl's brainstem," *Proc. Natl. Acad. Sci. USA*, **83**, 8400–8404 (1986).
- [51] A. H. Seidl, "Regulation of conduction time along axons," *Neuroscience*, **276**, 126–134 (2014).
- [52] W. Gerstner, R. Kempter, J. L. van Hemmen and H. Wagner, "A neuronal learning rule for sub-millisecond temporal coding," *Nature*, **383**, 76–78 (1996).
- [53] S. A. Shamma, "Stereoausis: Binaural processing without neural delays," *J. Acoust. Soc. Am.*, **86**, 989–1006 (1989).
- [54] P. Joris and T. C. T. Yin, "A matter of time: Internal delays in binaural processing," *Trends Neurosci.*, **30**, 70–78 (2007).
- [55] J. L. Peña, S. Viete, K. Funabiki, K. Saberi and M. Konishi, "Cochlear and neural delays for coincidence detection in owls," *J. Neurosci.*, **21**, 9455–9459 (2001).
- [56] M. Singheiser, B. J. Fischer and H. Wagner, "Estimated cochlear delays in low best-frequency neurons in the barn owl cannot explain coding of interaural time difference," *J. Neurophysiol.*, **104**, 1946–1954 (2010).
- [57] L. A. Jeffress, "A place theory of sound localization," *J. Comp. Physiol. Psychol.*, **41**, 35–39 (1948).
- [58] K. M. MacLeod, D. Soares and C. E. Carr, "Interaural timing difference circuits in the auditory brainstem of the emu (*Dromaius novaehollandiae*)," *J. Comp. Neurol.*, **495**, 185–201 (2006).
- [59] E. M. Overholt, E. W. Rubel and R. L. Hyson, "A circuit for coding interaural time differences in the chick brainstem," *J. Neurosci.*, **12**, 1698–1708 (1992).
- [60] C. Köppl and C. E. Carr, "Maps of interaural time difference in the chicken's brainstem nucleus laminaris," *Biol. Cybern.*, **98**, 541–559 (2008).
- [61] C. E. Carr, D. Soares, J. Smolders and J. Z. Simon, "Detection of interaural time differences in the alligator," *J. Neurosci.*, **29**, 7978–7990 (2009).
- [62] G. Ashida and C. E. Carr, "Sound localization: Jeffress and beyond," *Curr. Opin. Neurobiol.*, **21**, 745–751 (2011).
- [63] J. L. Peña, S. Viete, Y. Albeck and M. Konishi, "Tolerance to sound intensity of binaural coincidence detection in the nucleus laminaris of the owl," *J. Neurosci.*, **16**, 7046–7054 (1996).
- [64] P. T. Kuokkanen, H. Wagner, G. Ashida, C. E. Carr and R. Kempter, "On the origin of the extracellular field potential in the nucleus laminaris of the barn owl (*Tyto alba*)," *J. Neurophysiol.*, **104**, 2274–2290 (2010).
- [65] K. Funabiki, G. Ashida and M. Konishi, "Computation of interaural time difference in the owl's coincidence detector neurons," *J. Neurosci.*, **31**, 15245–15256 (2011).
- [66] G. Ashida, K. Abe, K. Funabiki and M. Konishi, "Passive soma facilitates submillisecond coincidence detection in the owl's auditory system," *J. Neurophysiol.*, **97**, 2267–2282 (2007).
- [67] G. Ashida, K. Funabiki and C. E. Carr, "Theoretical foundations of the sound analogue membrane potential that underlies coincidence detection in the barn owl," *Front. Comput. Neurosci.*, **7**, 151 (2013).
- [68] G. Ashida, K. Funabiki and C. E. Carr, "Biophysical basis of the sound analogue membrane potential that underlies coincidence detection in the barn owl," *Front. Comput. Neurosci.*, **7**, 102 (2013).
- [69] C. E. Carr and D. Soares, "Evolutionary convergence and shared computational principles in the auditory system," *Brain Behav. Evol.*, **59**, 294–311 (2002).
- [70] H. Agmon-Snir, C. E. Carr and J. Rinzel, "The role of dendrites in auditory coincidence detection," *Nature*, **393**, 268–272 (1998).
- [71] C. E. Carr and R. E. Boudreau, "An axon with a myelinated initial segment in the bird auditory system," *Brain Res.*, **628**, 330–334 (1993).
- [72] L. L. Scott, P. J. Mathews and N. L. Golding NL, "Posthearing developmental refinement of temporal processing in principal neurons of the medial superior olive," *J. Neurosci.*, **25**, 7887–7895 (2005).
- [73] C. E. Carr, I. Fujita and M. Konishi, "Distribution of GABAergic neurons and terminals in the auditory system of the barn owl," *J. Comp. Neurol.*, **286**, 190–207 (1989).
- [74] T. T. Takahashi and M. Konishi, "Projections of nucleus angularis and nucleus laminaris to the lateral lemniscal nuclear complex of the barn owl," *J. Comp. Neurol.*, **274**, 212–238 (1988).
- [75] T. T. Takahashi and M. Konishi, "Projections of the cochlear nuclei and nucleus laminaris to the inferior colliculus of the barn owl," *J. Comp. Neurol.*, **274**, 190–211 (1988).
- [76] N. O. E. Krützfeldt, P. Logerot, M. F. Kubke and J. M. Wild, "Connections of the auditory brainstem in a songbird, *Taeniopygia guttata*. II. Projections of nucleus angularis and nucleus laminaris to the superior olive and lateral lemniscal nuclei," *J. Comp. Neurol.*, **518**, 2135–2148 (2010).
- [77] B. J. Fischer and M. Konishi, "Variability reduction in interaural time difference tuning in the barn owl," *J. Neurophysiol.*, **100**, 708–715 (2008).
- [78] J. M. Wild, N. O. E. Krützfeldt and M. F. Kubke, "Connections of the auditory brainstem in a songbird, *Taeniopygia guttata*. III. Projections of the superior olive and lateral lemniscal nuclei," *J. Comp. Neurol.*, **518**, 2149–2167 (2010).
- [79] G. B. Christianson and J. L. Peña, "Noise reduction of coincidence detector output by the inferior colliculus of the barn owl," *J. Neurosci.*, **26**, 5948–5954 (2006).
- [80] M. Pecka, I. Siveke, B. Grothe and N. A. Lesica, "Enhancement of ITD coding within the initial stages of the auditory pathway," *J. Neurophysiol.*, **103**, 38–46 (2010).
- [81] J. L. Peña and M. Konishi, "Cellular mechanisms for resolving phase ambiguity in the owl's inferior colliculus," *Proc. Natl. Acad. Sci. USA*, **97**, 11787–11792 (2000).
- [82] H. Wagner, J. A. Mazer and M. von Campenhausen, "Response properties of neurons in the core of the central nucleus of the inferior colliculus of the barn owl," *Eur. J. Neurosci.*, **15**, 1343–1352 (2002).
- [83] C. Köppl, "Tonotopic projections of the auditory nerve to the

- cochlear nucleus angularis in the barn owl," *J. Assoc. Res. Otolaryngol.*, **2**, 41–53 (2001).
- [84] L. J. Steinberg, B. J. Fischer and J. L. Peña, "Binaural gain modulation of spectrotemporal tuning in the interaural level difference-coding pathway," *J. Neurosci.*, **33**, 11089–11099 (2013).
- [85] D. Soares and C. E. Carr, "The cytoarchitecture of the nucleus angularis of the barn owl (*Tyto alba*)," *J. Comp. Neurol.*, **429**, 192–205 (2001).
- [86] C. Köppl and C. E. Carr, "Computational diversity in the cochlear nucleus angularis of the barn owl," *J. Neurophysiol.*, **89**, 2313–2329 (2003).
- [87] N. B. Cant and C. G. Benson, "Parallel auditory pathways: Projection patterns of the different neuronal populations in the dorsal and ventral cochlear nuclei," *Brain Res. Bull.*, **60**, 457–474 (2003).
- [88] R. M. Burger, K. S. Cramer, J. D. Pfeiffer and E. W. Rubel, "Avian superior olivary nucleus provides divergent inhibitory input to parallel auditory pathways," *J. Comp. Neurol.*, **481**, 6–18 (2005).
- [89] S. Viète, J. L. Peña and M. Konishi, "Effects of interaural intensity difference on the processing of interaural time difference in the owl's nucleus laminaris," *J. Neurosci.*, **17**, 1815–1824 (1997).
- [90] I. Fujita and M. Konishi, "The role of GABAergic inhibition in processing of interaural time difference in the owl's auditory system," *J. Neurosci.*, **11**, 722–739 (1991).
- [91] K. Funabiki, K. Koyano and H. Ohmori, "The role of GABAergic inputs for coincidence detection in the neurons of nucleus laminaris of the chick," *J. Physiol.*, **508**, 851–869 (1998).
- [92] S. P. Kuo, L. A. Bradley and L. O. Trussell, "Heterogeneous kinetics and pharmacology of synaptic inhibition in the chick auditory brainstem," *J. Neurosci.*, **29**, 9625–9634 (2009).
- [93] T. T. Takahashi, C. L. Barberini and C. H. Keller, "An anatomical substrate for the inhibitory gradient in the VLVp of the owl," *J. Comp. Neurol.*, **358**, 294–304 (1995).
- [94] G. A. Manley, C. Köppl and M. Konishi, "A neural map of interaural intensity differences in the brain stem of the barn owl," *J. Neurosci.*, **8**, 2665–2676 (1988).
- [95] R. Adolphs, "Bilateral inhibition generates neuronal responses tuned to interaural level differences in the auditory brainstem of the barn owl," *J. Neurosci.*, **13**, 3647–3668 (1993).
- [96] J. Mogdans and E. I. Knudsen, "Representation of interaural level difference in the VLVp, the first site of binaural comparison in the barn owl's auditory system," *Hear. Res.*, **74**, 148–164 (1994).
- [97] L. J. Steinberg and J. L. Peña, "Difference in response reliability predicted by spectrotemporal tuning in the cochlear nuclei of barn owls," *J. Neurosci.*, **31**, 3234–3242 (2011).
- [98] A. Moiseff and M. Konishi, "Binaural characteristics of units in the owl's brainstem auditory pathway: Precursors of restricted spatial receptive fields," *J. Neurosci.*, **3**, 2553–2562 (1983).
- [99] J. M. Wild, M. F. Kubke and C. E. Carr, "Tonotopic and somatotopic representation in the nucleus basalis of the Barn Owl, *Tyto alba*," *Brain Behav. Evol.*, **57**, 39–62 (2001).
- [100] A. N. Iwaniuk, D. H. Clayton and D. R. W. Wylie, "Echolocation, vocal learning, auditory localization and the relative size of the avian auditory midbrain nucleus (MLd)," *Behav. Brain Res.*, **167**, 305–317 (2006).
- [101] T. T. Takahashi, H. Wagner and M. Konishi, "Role of commissural projections in the representation of bilateral auditory space in the barn owl's inferior colliculus," *J. Comp. Neurol.*, **281**, 545–554 (1989).
- [102] B. J. Fischer, J. L. Peña and M. Konishi, "Emergence of multiplicative auditory responses in the midbrain of the barn owl," *J. Neurophysiol.*, **98**, 1181–1193 (2007).
- [103] B. J. Fischer, C. H. Anderson and J. L. Peña, "Multiplicative auditory spatial receptive fields created by a hierarchy of population codes," *PLoS ONE*, **4**, e8015 (2009).
- [104] J. L. Peña and M. Konishi, "Auditory spatial receptive fields created by multiplication," *Science*, **292**, 249–252 (2001).
- [105] Y. Albeck and M. Konishi, "Responses of neurons in the auditory pathway of the barn owl to partially correlated binaural signals," *J. Neurophysiol.*, **74**, 1689–1700 (1995).
- [106] J. A. Mazer, "How the owl resolves auditory coding ambiguity," *Proc. Natl. Acad. Sci. USA*, **95**, 10932–10937 (1998).
- [107] K. Saberi, Y. Takahashi, H. Farahbod and M. Konishi, "Neural bases of an auditory illusion and its elimination in owls," *Nat. Neurosci.*, **2**, 656–659 (1999).
- [108] D. E. Feldman and E. I. Knudsen, "An anatomical basis for visual calibration of the auditory space map in the barn owl's midbrain," *J. Neurosci.*, **17**, 6820–6837 (1997).
- [109] E. I. Knudsen and M. Konishi, "A neural map of auditory space in the owl," *Science*, **200**, 795–797 (1978).
- [110] A. D. S. Bala, M. W. Spitzer and T. T. Takahashi, "Prediction of auditory spatial acuity from neural images on the owl's auditory space map," *Nature*, **424**, 771–774 (2003).
- [111] Y. Wang and J. L. Peña, "Direction selectivity mediated by adaptation in the owl's inferior colliculus," *J. Neurosci.*, **33**, 19167–19175 (2013).
- [112] S. F. Volman and M. Konishi, "Comparative physiology of sound localization in four species of owls," *Brain Behav. Evol.*, **36**, 196–215 (1990).
- [113] M. B. Calford, L. Z. Wise and J. D. Pettigrew, "Coding of sound location and frequency in the auditory midbrain of diurnal birds of prey, families Accipitridae and Falconidae," *J. Comp. Physiol. A*, **157**, 149–160 (1985).
- [114] E. I. Knudsen and P. F. Knudsen, "Space-mapped auditory projections from the inferior colliculus to the optic tectum in the barn owl (*Tyto alba*)," *J. Comp. Neurol.*, **218**, 187–196 (1983).
- [115] J. F. Olsen, E. I. Knudsen and S. D. Esterly, "Neural maps of interaural time and intensity differences in the optic tectum of the barn owl," *J. Neurosci.*, **9**, 2591–2605 (1989).
- [116] H. Bravo and J. D. Pettigrew, "The distribution of neurons projecting from the retina and visual cortex to the thalamus and tectum opticum of the barn owl, *Tyto alba*, and the burrowing owl, *Speotyto cunicularia*," *J. Comp. Neurol.*, **199**, 419–441 (1981).
- [117] E. I. Knudsen, "Auditory and visual maps of space in the optic tectum of the owl," *J. Neurosci.*, **2**, 1177–1194 (1982).
- [118] Y. Zahar, A. Reches and Y. Gutfreund, "Multisensory enhancement in the optic tectum of the barn owl: Spike count and spike timing," *J. Neurophysiol.*, **101**, 2380–2394 (2009).
- [119] W. M. Harmening, M. A. Vobig, P. Walter and H. Wagner, "Ocular aberrations in barn owl eyes," *Vis. Res.*, **47**, 2934–2942 (2007).
- [120] E. I. Knudsen and P. F. Knudsen, "Vision calibrates sound localization in developing barn owls," *J. Neurosci.*, **9**, 3306–3313 (1989).
- [121] E. I. Knudsen and M. S. Brainard, "Visual instruction of the neural map of auditory space in the developing optic tectum," *Science*, **253**, 85–87 (1991).
- [122] T. Masino and E. I. Knudsen, "Anatomical pathways from the optic tectum to the spinal cord subserving orienting move-

- ments in the barn owl," *Exp. Brain Res.*, **92**, 194–208 (1992).
- [123] T. Masino and E. I. Knudsen, "Orienting head movements resulting from electrical microstimulation of the brainstem tegmentum in the barn owl," *J. Neurosci.*, **13**, 351–370 (1993).
- [124] E. I. Knudsen and P. F. Knudsen, "The sensitive period for auditory localization in barn owl is limited by age, not by experience," *J. Neurosci.*, **6**, 1918–1924 (1986).
- [125] J. Mogdans and E. I. Knudsen, "Adaptive adjustment of unit tuning to sound localization cues in response to monaural occlusion in developing owl optic tectum," *J. Neurosci.*, **92**, 3473–3484 (1992).
- [126] J. I. Gold and E. I. Knudsen, "Hearing impairment induces frequency-specific adjustments in auditory spatial tuning in the optic tectum of young owls," *J. Neurophysiol.*, **82**, 2197–2209 (1999).
- [127] J. F. Bergan, P. Ro, D. Ro and E. I. Knudsen, "Hunting increases adaptive auditory map plasticity in adult barn owls," *J. Neurosci.*, **25**, 9816–9820 (2005).
- [128] P. S. Hyde and E. I. Knudsen, "The optic tectum controls visually guided adaptive plasticity in the owl's auditory space map," *Nature*, **415**, 73–76 (2002).
- [129] W. M. DeBello, D. E. Feldman and E. I. Knudsen, "Adaptive axonal remodeling in the midbrain auditory space map," *J. Neurosci.*, **21**, 3161–3174 (2001).
- [130] T. Tzounopoulos and N. Kraus, "Learning to encode timing: Mechanisms of plasticity in the auditory brainstem," *Neuron*, **62**, 463–469 (2009).
- [131] B. J. Arthur, "Distribution within the barn owl's inferior colliculus of neurons projecting to the optic tectum and thalamus," *J. Comp. Neurol.*, **492**, 110–121 (2005).
- [132] L. Proctor and M. Konishi, "Representation of sound localization cues in the auditory thalamus of the barn owl," *Proc. Natl. Acad. Sci. USA*, **94**, 10421–10425 (1997).
- [133] M. L. Pérez and J. L. Peña, "Comparison of midbrain and thalamic space-specific neurons in barn owls," *J. Neurophysiol.*, **95**, 783–790 (2006).
- [134] M. L. Pérez, S. J. Shanbhag and J. L. Peña, "Auditory spatial tuning at the crossroads of the midbrain and forebrain," *J. Neurophysiol.*, **102**, 1472–1482 (2009).
- [135] E. I. Knudsen, P. F. Knudsen and T. Masino, "Parallel pathways mediating both sound localization and gaze control in the forebrain and midbrain of the barn owl," *J. Neurosci.*, **13**, 2837–2852 (1993).
- [136] Y. E. Cohen and E. I. Knudsen, "Forebrain pathway for auditory space processing in the barn owl," *J. Neurophysiol.*, **79**, 891–902 (1998).
- [137] Avian Brain Nomenclature Consortium, "Avian brains and a new understanding of vertebrate brain evolution," *Nat. Rev. Neurosci.*, **6**, 151–159 (2005).
- [138] Y. E. Cohen and E. I. Knudsen, "Representation of frequency in the primary auditory field of the barn owl forebrain," *J. Neurophysiol.*, **76**, 3682–3692 (1996).
- [139] E. I. Knudsen, M. Konishi and J. D. Pettigrew, "Receptive fields of auditory neurons in the owl," *Science*, **198**, 1278–1280 (1977).
- [140] X. Wang, "Neural coding strategies in auditory cortex," *Hear. Res.*, **229**, 81–93 (2007).
- [141] K. Vonderschen and H. Wagner, "Tuning to interaural time difference and frequency differs between the auditory arcopallium and the external nucleus of the inferior colliculus," *J. Neurophysiol.*, **101**, 2348–2361 (2009).
- [142] Y. E. Cohen and E. I. Knudsen, "Maps versus clusters: Different representations of auditory space in the midbrain and forebrain," *Trends Neurosci.*, **22**, 128–135 (1999).
- [143] K. Vonderschen and H. Wagner, "Transformation from a pure time delay to a mixed time and phase delay representation in the auditory forebrain pathway," *J. Neurosci.*, **32**, 5911–5923 (2012).
- [144] E. I. Knudsen and P. F. Knudsen, "Disruption of auditory spatial working memory by inactivation of the forebrain archistriatum in barn owls," *Nature*, **383**, 428–431 (1996).
- [145] H. Wagner, "Sound-localization deficits induced by lesions in the barn owl's auditory space map," *J. Neurosci.*, **13**, 371–386 (1993).
- [146] K. Vonderschen and H. Wagner, "Detecting interaural time differences and remodeling their representation," *Trends Neurosci.*, **37**, 289–300 (2014).
- [147] R. van Hoesel, "Bilateral cochlear implants," in *Auditory Prostheses: New Horizons*, Zeng *et al.*, Eds. (Springer, New York, 2011), pp. 13–57.
- [148] F. A. Boettcher, "Presbycusis and the auditory brainstem response," *J. Speech Lang. Hear. Res.*, **45**, 1249–1261 (2002).
- [149] E. W. Rubel, S. A. Furrer and J. S. Stone, "A brief history of hair cell regeneration research and speculations on the future," *Hear. Res.*, **297**, 42–51 (2013).
- [150] M. Singheiser, Y. Gutfreund and H. Wagner, "The representation of sound localization cues in the barn owl's inferior colliculus," *Front. Neural Circuits*, **6**, 45 (2012).
- [151] E. I. Knudsen, "Instructed learning in the auditory localization pathway of the barn owl," *Nature*, **417**, 322–328 (2002).
- [152] H. Wagner, L. Kettler, J. Orłowski and P. Tellers, "Neuroethology of prey capture in the barn owl (*Tyto alba* L.)," *J. Physiol. (Paris)*, **107**, 51–61 (2013).
- [153] M. Konishi, "Masakazu Konishi," in *The History of Neuroscience in Autobiography*, Vol. 6, Squire, Ed. (Oxford University Press, Oxford, 2008), pp. 226–262.
- [154] E. M. Hill, G. Koey, R. S. Heffner and H. E. Heffner, "Audiogram of the chicken (*Gallus gallus domesticus*) from 2 Hz to 9 kHz," *J. Comp. Physiol. A*, **200**, 863–870 (2014).