

CLASSICS

Cracking an improbable sensory map



Catherine E. Carr and Jose L. Peña discuss the impact of a series of classic papers presenting the discovery of the owl auditory map published by Mark Konishi and Eric Knudsen in the 1970s.

We use our two ears to construct auditory objects, pull sounds out of the background and localize sound sources. These ‘binaural’ computations depend largely upon detecting small differences in the timing and loudness of the sounds at each ear, and are all the more remarkable because of how hard the brain must work to create a perception of auditory space from binaural cues. By comparison, the world of images conveyed by vision and touch are effortless: inputs from our two eyes form retinotopic maps of the visual world, and skin receptors form maps of our body surface in the brain just by direct point-to-point projections. The ears, however, do not directly represent spatial information but are instead organized by frequency. Thus, to form a map of auditory space, spatial binaural cues must be extracted and integrated in the ascending auditory stream. An unexpected map of auditory space was discovered by Masakazu (Mark) Konishi and his postdoc, Eric Knudsen, in the 1970s (Knudsen and Konishi, 1978).

Knudsen and Konishi’s discovery that barn owls had a brain map of auditory space had an immediate impact. The

paper won the best paper of the year from *Science* (AAAS) in 1978, and diagrams of the owl’s auditory space are still found in neuroscience textbooks. Less immediate, but potentially more important, was the impact of these studies on how we view the brain’s neural coding strategies. First, the demonstration that a map of auditory space existed was proof that the brain could and would synthesize a data structure to represent information. This gave strong support to the idea that the brain finds it useful to create ordered representations of relevant stimulus variables. Konishi later pointed out that once a brain map is generated, the same rules of projection and interactions among the constituent neurons apply, whether the map is peripherally or centrally generated. We could, for example, generate maps of complex visual stimuli, such as faces.

To some extent, Knudsen and Konishi were in the right place at the right time to perform these experiments. Konishi had become interested in barn owls after he heard Roger Payne present his thesis work on prey capture by barn owls in the 1963 International Congress of Ethology (Hausmann et al., 2010). After Konishi moved to Princeton University in 1966, a local birder brought in three orphaned baby barn owls and someone else arranged for free mice to be provided by a big pharmaceutical company. The original birds were bred in an old house on campus, and their hand-reared progeny became so tame that students could use behavioral approaches to study their discrimination of sound signals, leading to two landmark papers in the *American Naturalist* and *American Scientist* (Konishi, 1973a,b).

Konishi then moved to Caltech in the 1970s and took the owls from Princeton with him. At that time, the legendary Jack Pettigrew was also there and was working on binocular vision in cats, so they began studying barn owl vision together while Konishi waited for his sound-proof room to be built (Pettigrew and Konishi, 1976) – most academics will be familiar with these delays. Eventually, the large

acoustic chamber was completed after Pettigrew and Konishi had been working together for about a year, and Konishi describes what happened next in his autobiography: ‘Jack asked me what I was going to do. My original intent was to continue to analyze sound localization behavior by owls in a more acoustically better-defined environment... Well, this idea ceased to occupy me after Jack and I had studied the visual Wulst cells. I naively thought that central auditory neurons might have spatial receptive fields like the visual cells. I also thought that these auditory cells might form a map of auditory space. There had been some reports of auditory neurons with spatial receptive fields, but systematic approaches to this question seemed lacking.’ Pettigrew asked the renowned Caltech machinist Herb Adams – better known for his work on the Viking lander in the first Mars mission – to design and build devices and instruments necessary for this project. Picking up the challenge, Adams constructed a light semicircular rail along which a small remotely controlled loudspeaker could travel around an owl’s head at a constant distance in the horizontal and vertical directions. Konishi later recalled, ‘I do not know to this day who paid the bill, because I did not have any seed money or grant for this project’ (<https://www.sfn.org/About/History-of-Neuroscience/Autobiographical-Videos-of-Prominent-Neuroscientists/Masakazu-Konishi>).

Using the new equipment, Konishi and Knudsen easily found auditory neurons in the owl’s forebrain that responded only when the speaker was in a particular location in space; that is, the neurons had individual auditory receptive fields, but they did not find a map (Knudsen et al., 1977). They then shifted their attention to the midbrain auditory area, which Knudsen knew well from his PhD work on catfish with Ted Bullock (Knudsen, 1976), and found auditory neurons with well-defined receptive fields that were organized topographically by spatial coordinates, i.e. forming a map of auditory space (Knudsen and Konishi, 1978).

Subsequent work by postdoc Andrew Moiseff and Konishi showed that the spatial selectivity of neurons in the map was owed to their selectivity to binaural cues (Moiseff and Konishi, 1983). The work was an instructive example of the relationship between neuronal stimulus selectivity and coding. They showed that the owl uses interaural time and loudness differences to localize sound in the azimuth and elevation projections, respectively, indicating that the bird's auditory space consists of a matrix of binaural time and intensity disparities (Fig. 1). The neural substrate for this matrix is the midbrain map of auditory space, where neurons tuned to different combinations of binaural cues are arranged systematically. This tuning is responsible for the spatial selectivity of these neurons; they respond maximally to noise stimuli located in a small, restricted area, termed the receptive field (Fig. 1). Experiments showed that a neuron's tuning to binaural time and intensity disparities determines, respectively, the azimuthal and elevational positions and dimensions of its receptive field. Later work demonstrated that time and intensity disparities were processed independently by the brain (Takahashi et al., 1984).

After his time with Konishi, Knudsen went on to study the experience-dependent calibration of sound localization, making the barn owl a model for understanding how experience modifies neural circuits. He and his group at Stanford University showed that the auditory map can be altered by sensory experience during a sensitive period of development and, germane to the discussion of maps, found that when visual and auditory maps conflict, even barn owls rely on vision. Barn owls raised blind have abnormal auditory space maps, and it turned out that visual input guides the development of the auditory space map. In a key experiment, Michael Brainard and Knudsen raised young barn owls with displacing prisms mounted in spectacle frames in front of the eyes. The prisms provided erroneous visual signals that caused the auditory map to shift. Thus, vision exerts an overriding 'instructive' influence on auditory map organization (Knudsen and Brainard, 1991) and ultimately, the Knudsen lab went on to identify axonal remodeling, and NMDA and GABA

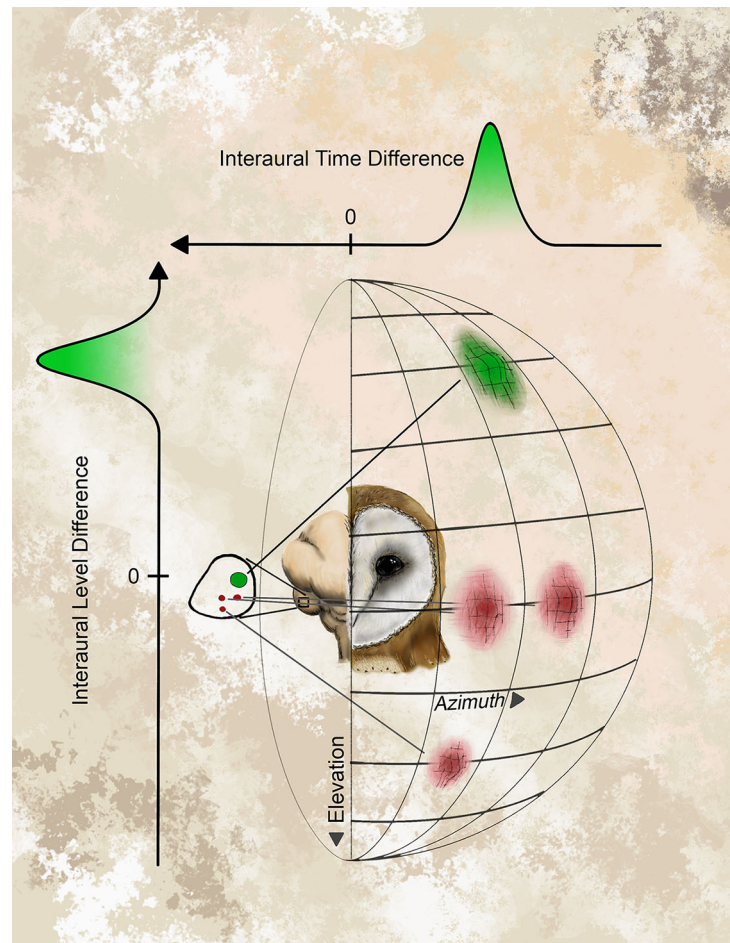


Fig. 1. The owl's map of auditory space. The optic lobe (inset) contains a topographic representation of auditory space. Neurons in the map respond to sounds at different locations in auditory space (green and red blobs). The tuning to interaural time and level differences (ITD and ILD, respectively) confer, respectively, the selectivity in azimuth (horizontal) and elevation (vertical) of each cell. Tuning to ITD and ILD is shown for an example cell (green blob). Illustration by Michael V. Beckert.

receptor changes, as agents for instructed learning.

In Konishi's lab, the discovery of the map of auditory space was followed by a series of germinal experiments that explained how the first 'computational' sensory map in the brain was synthesized. The brain processing underlying the emergence of the map is elegant and efficient. Two independent processing pathways compute the binaural cues of interaural time and level differences (ITD and ILD, respectively) (Takahashi et al., 1984), and these converge downstream on space-specific neurons (Takahashi and Konishi, 1986). Interaural time and level differences are topographically represented in the brainstem (Carr and Konishi, 1990; Manley et al., 1988; Wagner et al., 1987), supporting the emergence of the downstream map. Later studies tracked the owl's behavioral

performance back to response properties of neurons in the map (Bala et al., 2003; Saberi et al., 1998).

An emerging question was whether the brain needs maps, to which the answer was only a qualified yes: maps are useful, but not necessary. They can provide speed and accuracy in a nocturnal predator such as the barn owl, which aligns its auditory map with the visual map in the overlying optic tectum, and can use both sound and vision to orient to prey. However, barn owls are sound localization specialists – they are even able to catch mice in total darkness (Payne, 1971). Most other animals simply align their binaural auditory responses with a precise visual map in the tectum (Palmer and King, 1982). However, our understanding of how populations of neurons encode sound source location is still incomplete. A focus on ITDs has

emerged as a powerful means to investigate coding strategies across species. In a small mammal such as the gerbil, evidence suggests that ITD is coded by population activity in two broad, hemispheric spatial channels (Grothe et al., 2010). In barn owls and other birds, in contrast, data reveal a topographic representation of ITD (Carr and Konishi, 1990; Carr et al., 2015; Köppl and Carr, 2008). Therefore, barn owls and small mammals are believed to use different strategies for coding ITD (Schnupp and Carr, 2009). However, even barn owls don't absolutely require an auditory space map for sound localization; their ascending auditory pathways from midbrain to forebrain do not map auditory space, but can still guide sound localization because owls recover this ability after lesions of the midbrain map (Knudsen et al., 1993; Wagner, 1993). Localization is only irretrievably compromised when both forebrain and midbrain pathways are lesioned.

Work on barn owls continues to yield core biological principles, including providing answers to the question of whether mathematical formulations can explain brain processing. Observations of the owl's brain and behavior suggest that the answer is 'very much'. For example, the sound localization system of the barn owl implements various mathematical operations, such as multiplication (Pena and Konishi, 2001), averaging (Christianson and Peña, 2006), cross-correlation (Saber et al., 1998; Fischer et al., 2008) and Bayesian inference (Cazettes et al., 2016; Fischer and Peña, 2011). These operations had been predicted by models of human psychophysics (Jeffress et al., 1962; Licklider, 1959; Sayers and Cherry, 1957; Stern and Steven Colburn, 1978; Stern et al., 1988), but never demonstrated in neural responses. Thus, as supernatural as it may appear, the owl's specialized auditory maps have allowed us to validate theoretical principles of how our brain

represents and computes information and guides behavior.

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