A EUROPEAN JOURNAL

CHEMPHYSCHEM

OF CHEMICAL PHYSICS AND PHYSICAL CHEMISTRY

REPRINT

Silent but deadly is the owl's swooping attack but how does it find mice while in mid-flight at night? A neurophysical map of auditory signals allows the owl to focus on its prey's position to a remarkable 2°—but this is not as remarkable as the internal neural processing that occurs simultaneously. Drawing on this and other examples, the mapping problem on the border of biology, behaviorial psychology, theoretical biophysics, and neuroscience is lucidly clarified.

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The Map in Your Head: How Does the Brain Represent the Outside World?

J. Leo van Hemmen*[a]

In neurophysics, a "map" is a neuronal representation of the outside world. It originates from spatiotemporal activity of a sensory organ. For example, touch provides a one-to-one representation of our skin in the cortex, a somatosensory map. In a similar way, visual and auditory maps are representations of the retina and the cochlea and provide us with spatial, temporal, and, more generally, spatiotemporal maps of sensory activity. In this introduction we concentrate on temporal aspects and show how temporal maps arise in the brain. Through prey localization the sand scorpion, the barn owl, and the paddle fish provide fascinating examples of neuronal maps, which are analyzed in detail.

KEYWORDS:

biophysics · neurons · sensors

Introduction

In neural science, one of the presumably most often asked, and also by its content most fascinating, question reads: *How does the brain represent the world surrounding it?* To frame an answer, one of the presumably most often used experimental techniques poses another question: *How does neuronal activity change if we modify the surroundings?* Practically everything we know about the brain's functioning is due to this paradigm. Consequently it is not too surprising that the major portion of knowledge and understanding of neural activity has been gathered on those parts of the brain that are just "behind" the sensory organs.

In both the retina and the cochlea and in subsequent areas, that is, the collections of neurons that are defined by common anatomical and/or functional properties, many neurons operate together while handling an external object and, through their collective dynamics, generate a signal that influences other areas. In many cases there is also feedback, which is one of the main unsolved problems, since we barely understand what it is good for.

Both as separate entities and as an ensemble, neurons are described and analyzed by means of coupled nonlinear differential equations and their analytic simplifications, so as to understand neuronal *information processing*. Finding efficient descriptions through merging mathematics and neurobiology into a unified theory is a challenge in particular to theoretical biophysicists. It is fair to say that many of them work successfully in the new domains of systems neuroscience and neurophysics.

In the process of developing techniques of experimental analysis and evaluation, devising stimulus protocols, and building models of neural functioning, theoretical biophysics plays a key role in that it meanwhile provides predictions that can be verified experimentally, often even to a high precision. This is new to many biologists, who seem to think that proposing an experiment to check theory is an insult, as theory comes before experiment. I expect that in a decade from now things will look more or less "as in physics". Before long, biology will be confronting physics with deep questions but at the same time mathematical analysis will be accepted as an indispensable tool. The rich history, and success, of physics clearly shows that true progress can only come from an *interaction*, an intensive discussion as an exchange of ideas, between experiment and theory once the latter has a mathematical formalism to cope with the problems of the former.

To illustrate these points, I will present the mapping problem from the point of view of systems neurophysics and, thus, systems neuroscience. In so doing we will meet three animals, the sand scorpion, the barn owl (Figure 1), and the paddlefish, that give us some insight into the underlying biophysics.

How Does a Brain Represent its Sensory Surroundings?

As early as 1943, Roger W. Sperry[1] realized that areas in the frog brain that are the first in receiving optic-nerve signals have a retinotopic organization. That is to say, the topology of the nerve cells in the retina and, thus, of the visual image is mapped to a large extent one-to-one onto corresponding nerve cells in primary visual areas. Phrased differently, neighboring points in the retina are mapped onto neighboring points in primary visual areas. (Throughout this Section we consider a vertebrate visual system.) Hence the optics of the eye leads to a neuronal representation of spatiotemporal surroundings in the primary visual cortex, a *map*. Similar maps are found in the auditory and

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Figure 1. *Barn owls hunt for mice during the night. All they need are acoustic signals generated by their prey; the direction towards the prey is "computed" through determining the time difference between the owl's two ears. In so doing, the barn owl reaches an accuracy of 2°, as described further later. Photograph courtesy of Prof. Hermann Wagner (RWTH, Aachen).*

somatosensory cortex. Here too one finds an *ordered* representation of the surroundings or, if you like, of sensory cells.[2]

In spite of an overwhelming multitude of experiments showing the neuronal organization of how sensory stimuli are processed, they nevertheless did not answer the question: *Why do neuronal maps exist and what are they good for?*

Before we can start answering the above question, it seems appropriate to first turn to neuronal coding. A neuron consists of three parts: input (a dendritic tree), central processor (a soma collecting and evaluating the input potentials from the dendritic tree), and output (an axon hillock, where action potentials or "spikes", typically of amplitude and duration 0.1 V and 1 ms, are generated and propagate, soliton-like, through the axon, an kind of active cable). In vertebrates and also in insects and arachnids such as scorpions and spiders, a neuron is a threshold element that "compares" the membrane potential at the axon hillock with a threshold value ϑ. A spike is generated if the potential passes ϑ from below and in turn leaves the neuron via its axon. An axon may, and often does, bifurcate several times. Nevertheless the amplitude remains constant. At the ends of an axon one finds synapses. A synapse is on a dendritic tree of another neuron, a postsynaptic neuron, and they are separated by a synaptic cleft; see the box Synaptic Transmission.

More or less by definition, the *synaptic strength* determines how much (or little) ionic current is induced on the other side of a synaptic cleft by an action potential arriving at the adjoining synapse. If the input current is positive, one calls the synapse excitatory; if negative, inhibitory. "Learning" in a neuronal system means in the present biological context that a synaptic strength changes—no more, no less. "Learned" information, then, is in general stored in synapses and *not* in neurons. Please note, however, there are exceptions "proving" the rule—as everywhere else in biology—but these exceptions are quite rare.

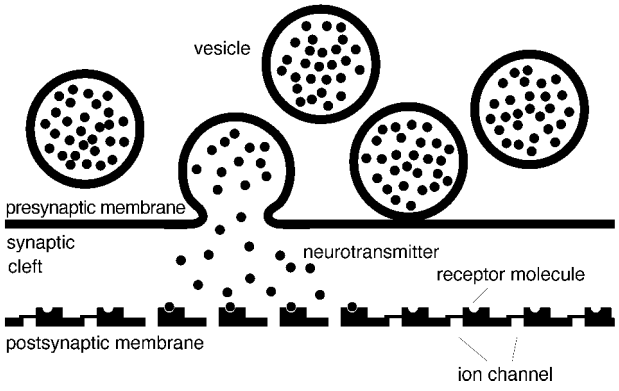
Map Formation and Hebbian Learning

Since the theory of spatiotemporal learning was conceived quite a while ago,[3] a detailed theoretical description[4] of synaptic dynamics, the temporal evolution of synaptic strengths, has arisen. Here we can just skim over it. More empirically inclined readers can directly proceed to the next Section on *place maps*.

A synapse with strength J_{ij} transfers the spiking activity of a presynaptic neuron j to a connected postsynaptic neuron i. In the present context, learning means a modification of the synaptic strength J_{ij}; see Figure 2 for the proper spatial context. According to a brilliant idea of Donald Hebb,[5] which was questioned for a long time but has meanwhile been confirmed extensively, the temporal evolution of J_{ij} is determined by

Synaptic Transmission

A chemical synapse looks like a knob at the end of an axon, represented by a black dot in Figure 2. There one finds numerous 20 – 30 nm diameter small spheres or *vesicles* filled with neurotransmitter that originates from the cell's soma. Arrival of an action potential at the synapse leads to an influx of Ca^{2+} ions and, consequently, to a fusion of one or several vesicles with the presynaptic membrane at specific sites, as shown in the Figure here.



Neurotransmitter diffuses rapidly (1 ms) across the 20 nm wide *synaptic cleft* and binds to specific receptors on the postsynaptic membrane. They typically open ionic channels and, as a consequence, there is current influx. The *synaptic strength* is a measure of how much (or little) ionic current is admitted postsynaptically (bottom of the Figure), if a spike arrives presynaptically (top of the Figure). An excitatory synapse admits positive ions and is associated, for example, with Na^+; an inhibitory one could admit Cl^- ions.

The synaptic strength, which depends on an ensemble of membrane conductances,[6] may be determined by different factors, for example a) the density of receptors on the postsynaptic membrane, b) the number of fusion sites in the presynaptic membrane, c) the probability of presynaptic release, d) the vesicle size, and e) the time during which postsynaptic ionic channels are open. For an extensive discussion of these possibilities, see Koch.[6]

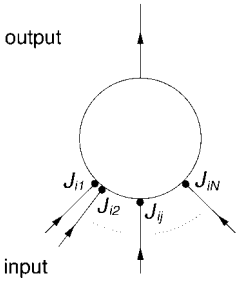


Figure 2. *Presynaptic action potentials arrive at* N *synapses (black dots) on a postsynaptic neuron* i *(large circle). They originate from* $1 \leq j \leq N$ *presynaptic neurons and travel via axons (straight solid lines with arrow). The amplitude of the postsynaptic membrane potential at neuron* i *and originating from the synapse at the end of axon* j *is the synaptic strength indicated by* J_{ij}.

pre- and postsynaptic activity. The prefix "pre" is clear as it refers to the neuron innervating the synapse. On the other hand, "post" refers to the receiving neuron beyond the synaptic cleft; see the box Synaptic Transmission. A fast response signaling to the synapse that the neuron it is on has fired comes from, for instance, a backpropagating Ca^{2+} action potential.[6]

To what extent does a synapse change under the influence of both pre- and postsynaptic activity? To devlop some feeling, let us consider an excitatory synapse and imagine that the postsynaptic neuron fires at time $s = 0$. If the presynaptic spike arrives "slightly" earlier ($s < 0$), then the synapse is operating normally in that it stimulates the postsynaptic neuron in time, as behooves an excitatory synapse. Hence the synapse should be strengthened. If, however, the spike comes "too late" ($s > 0$), namely after the postsynaptic neuron has fired at $s = 0$, then this makes no sense and the synapse is to be weakened.

It could indeed be shown, first theoretically,[7] then confirmed experimentally, that the time difference s between presynaptic arrival and postsynaptic spiking determines whether and to what extent the synaptic strength in- or decreases; see Equation (1) below. The key notion is that of a learning window W that quantifies synaptic growth and weakening. Let $s < 0$ indicate that the presynaptic spike arrives "in time" and $s > 0$ that it is "too late". A typical learning window describing the above example is shown in Figure 3.

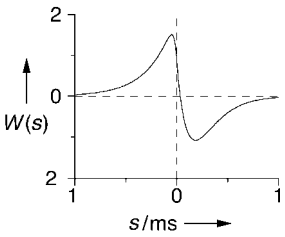


Figure 3. *Learning window* W *as a function of the time difference* s *between presynaptic arrival and postsynaptic spiking.[7, 8] If a spike arrives at the synapse shortly before the postsynaptic neuron fires ($s < 0$), then the synapse is strengthened ($W(s) > 0$), otherwise $s > 0$ and the synapse is weakened ($W(s) < 0$). Clearly* W *governs the synaptic learning process through the activity of both pre- and postsynaptic neurons.*

- $W(s) > 0$ for $s < 0$, namely when the postsynaptic neuron fires as an immediate consequence of presynaptic activation, whereas
- $W(s) < 0$ for $s > 0$; life punishes those who come too late.

Of course the learning window has a finite width depending on the system. For instance, in the hippocampus it is of the order of 10 – 100 ms whereas in the auditory system it is bound to be about two orders of magnitude narrower.[8]

In a brain, learning can happen in many ways and at many levels. Spatiotemporal patterns which, for instance, occur during finger and arm movements while playing a piano can be learnt either by synaptic plasticity in a *given* topology of synaptic connections or by changing the topology itself by adding new and/or removing old connections. Novel sensory experiences or motor tasks can in this way be mastered through a modification of a neuronal map.[2]

How, then, do maps arise? A simple solution is by genetic coding. It not very plausible, though, since coding a—nearly always—extremely detailed map would require too much genetic storage space. An alternative, bottom-up approach that is advocated here explain maps as a learning process on the basis of a global, genetically determined substrate. The process evolves during the youth (ontogeny) of an individual. It is a collective one where many neurons and very many synapses determine a neuronal and, hence, the synaptic dynamics.

Furthermore, nearly everything in sight is nonlinear. If both neuronal and synaptic dynamics were evolving at the same rate then the problem would be insoluble. They are not, however, since synaptic dynamics are very slow compared to the neuronal ones, and we end up with two different timescales. Exploiting this fact one can derive[4, 9] a set of local equations for the synaptic coupling strength J_{ij} between the i-th and j-th neuron, Equation (1).

$$\frac{\mathrm{d}}{\mathrm{d}t} J_{ij} = a_0 + a_1 \nu_j(t) + a_2 \nu_i(t) + \int W(s)\, C_{ij}(t,\, t+s)\, \mathrm{d}s \qquad (1)$$

We meet the neuronal activity of i and j as time-averaged rates ν_i and ν_j whereas C_{ij} is the time-averaged correlation between spike times at i and j. Since the latter contain the J_{ij} terms implicitly, the system of equations arising from Equation (1) is in general nonlinear.

Learning rules based on a *correlation* matrix, such as C_{ij}, of pre- and postsynaptic activities are called Hebbian,[5] since correlation is the essence of Hebb's idea. He did not specify anything though, neither quantitatively nor temporally. The "synaptic" interaction between two neurons i and j has been made specific by the learning window W.[7] Taking advantage of Equation (1), one can explain the way in which retinotopic, cochleotopic,[4, 8–10] and somatotopic maps arise and what a neuronal map of the retina, the cochlea, or the body surface looks like.

Place Maps

We now turn to three examples, three animals that are going to show how an individual's position in space is represented in a neuronal map through activation of its sensory organs. The sand scorpion provides presumably one of the simplest examples of how such a map works. A neuronal model will be shown to reproduce psychophysical experiments. The barn owl's azimuthal sound localization, formally a map into $[-\pi, \pi]$, has been explained more than half a century ago by Jeffress,[16] and we will now see how such a map can come about by means of Hebbian learning or, in more practical terms, by training of a juvenile.

Finally, the paddlefish, still fairly abundant in the Mississippi river and its larger tributaries, exemplifies a somatotopic map originating from electroreception.

Sand Scorpions

The sand scorpion (*Paruroctonus mesaensis*, Figure 4) lives in the Mojave Desert of Southern California. It is a predator that is active during night and feeds on insects. Its physiology is quite amazing, in that a single succulent moth suffices for a whole year. When a moth appears, the key issue for the scorpion is how to capture it. While moving, the moth produces surface waves, the so-called Rayleigh waves, which are detected by mechanoreceptors in the sand scorpion's feet;[11] a deviation of only a few Ångström units (10^{-10} m) is enough.

How can the scorpion determine the direction of its prey from the signals (spikes) that are generated by receptors in a circular array with a diameter of about 5 cm? To answer this question, a neuronal model has been devised[12] that predicts the scorpion's turning angle for a given stimulus angle. In sand, the effectively transverse Rayleigh waves move slowly, about 50 m s^{-1}. As is evident from Figure 5, the time difference between the receptors is at most 1 ms. This is in the range of conventional neuronal "hardware".

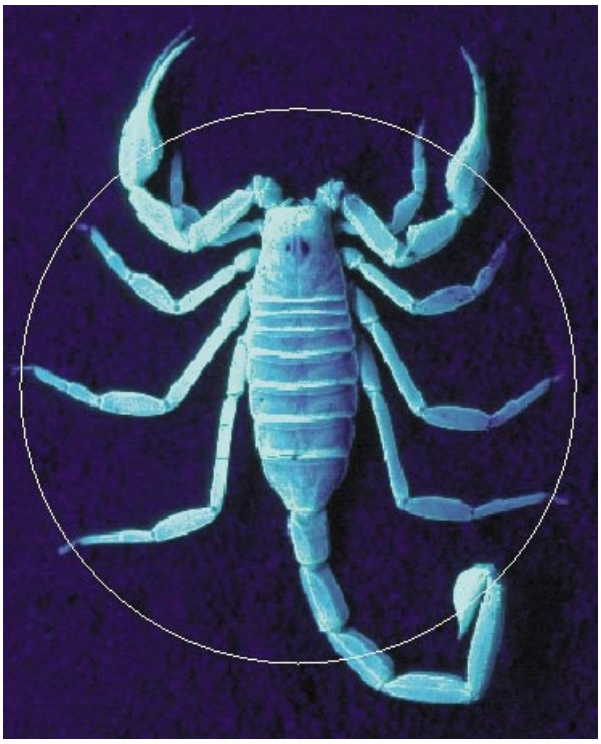


Figure 4. *A sand scorpion's eight feet lie, to a good approximation, on a circle of diameter 5 cm. The two big pedipalps will catch prey once the scorpion has reached it. The mechanoreceptors on the scorpion's eight feet sense surface (Rayleigh) waves generated by moving prey. Biophysics now faces the problem:* How does the animal determine the prey's direction? *Sand scorpions fluoresce in the dark under ultraviolet light. Photograph courtesy of Prof. Philip H. Brownell (Oregon State University at Corvallis).*

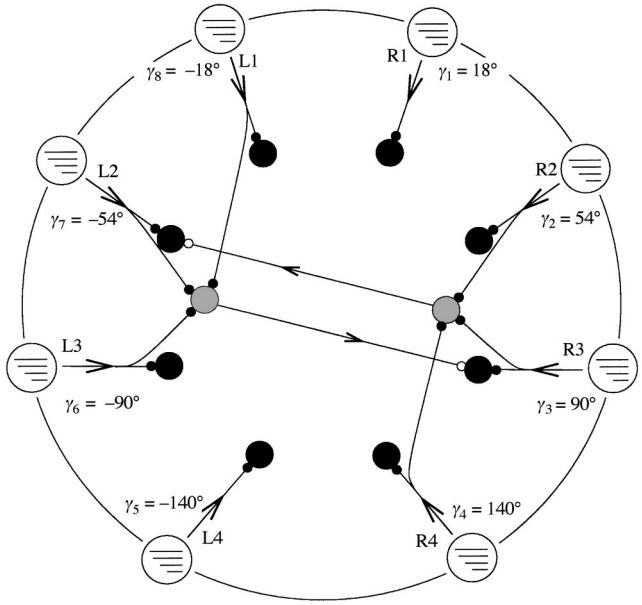


Figure 5. *As shown by Figure 4, mechanoreceptors at the feet (one of the eight outer circles) are in a circular array. In a sand scorpion's brain, there belongs a command neuron (black disk on inner circle) to each leg which receives spikes from detector neurons at the foot. If the prey direction is that of leg R3 (approximately perpendicular to the scorpion's principal axis), then the command neuron corresponding to R3 will react first. The triad L1 – L3 opposite to R3 will inhibit this neuron as they activate their inhibitory partner neuron (gray; only two of the eight such triads are shown) but when the detector neurons of L1 – L3 receive their input, about 1 ms later because of the delay due to the sand wave propagating at a finite (50 m s^{-1}) speed, R3's firing is done. On the other hand, for the command neuron belonging to L2 the inhibition due to the triad R2 – R4 arrives before it receives input from its mechanoreceptors and, hence, it cannot react. The period of Rayleigh waves in sand is on the average 3 ms.*

In the sand scorpion's brain there is a ring of eight (or a multiple thereof) *command neurons* that encode the directions γ_n, $1 \le n \le 8$, of the eight legs from which they receive input. They constitute a kind of committee that operates in the setup given by Figure 5. Depending on the stimulus angle φ_S, each command neuron fires spikes at a rate of $\nu_n(\varphi_S)$ Hz. Together they give rise to a rate vector $\boldsymbol{\nu} = \{\nu_n(\varphi_S),\ 1 \le n \le 8\}$. The transformation $\varphi_S \mapsto \boldsymbol{\nu}$ is the "map", a neuronal representation of the direction φ_S in a two-dimensional world. It leads from the stimulus angle φ_S to the scorpion's turning angle ϕ by means of a vector or population code,[13] Equation (2), which is nothing but a vector sum where each direction $\exp(i\gamma_n)$, a two-dimensional vector, is weighted with the firing rate ν_n of the command neuron n encoding it.

$$r\exp(i\phi) := \sum_{n=1}^{8} \nu_n \exp(i\gamma_n) \qquad (2)$$

As is shown by Figure 5, ν_n depends on the stimulus angle φ_S and, counting the votes, the committee then decides by Equation (2) which direction is to be taken. The vector code is Newton's law for motor neurons, which are here direct neighbors of the command neurons.

So "all" that is to be done is computation of the map $\varphi_S \mapsto \boldsymbol{\nu}$. The animal then either turns or does nothing when a general blocking mechanism decides that the recent food supply

sufficed. In the model,[12] the command neurons and their inhibitory triads are simulated numerically. Action potentials originating from the mechanoreceptors give rise to synaptic activation or inhibition, as specified by Figure 5. The number of spikes in a certain time window determines the rate vector $\boldsymbol{\nu}$. Whereas spike generation at the command neurons is deterministic, it is intrinsically stochastic at the mechanoreceptors, so that there it is modeled as an inhomogeneous Poisson process driven by the Rayleigh waves. All theory can, and does, predict is a probability distribution.

In this way, the sand scorpion provides one of the simplest examples of a neuronal map where the spatiotemporal character of the stimulus as recorded by sensory organs, here mechanoreceptors, leads to *collective* behavior of neurons and, hence, to a place code, here in the form of Equation (2). Theory agrees nicely with Brownell's behavioral experiments,[11, 14] in which a scorpion's response has been determined in relation to the number of *ablated* sensory organs; see Figure 6.

The theory[12] is quite general. While it was devised to explain orientation to vibrational information in substrates, it applies equally well to aquatic insects orienting to ripples in the surface film, such as backswimmers (*Notonecta* sp.). Instead of eight legs with sensors for vibration they have only four in front plus two sites at the end, altogether six detection sites. The combined action of excitation and well-timed, stimulus-dependent inhibition is also a widely used mechanism in horizontal sound localization of mammals. Hence, we suggest it is one of the *universals* of azimuthal localization.

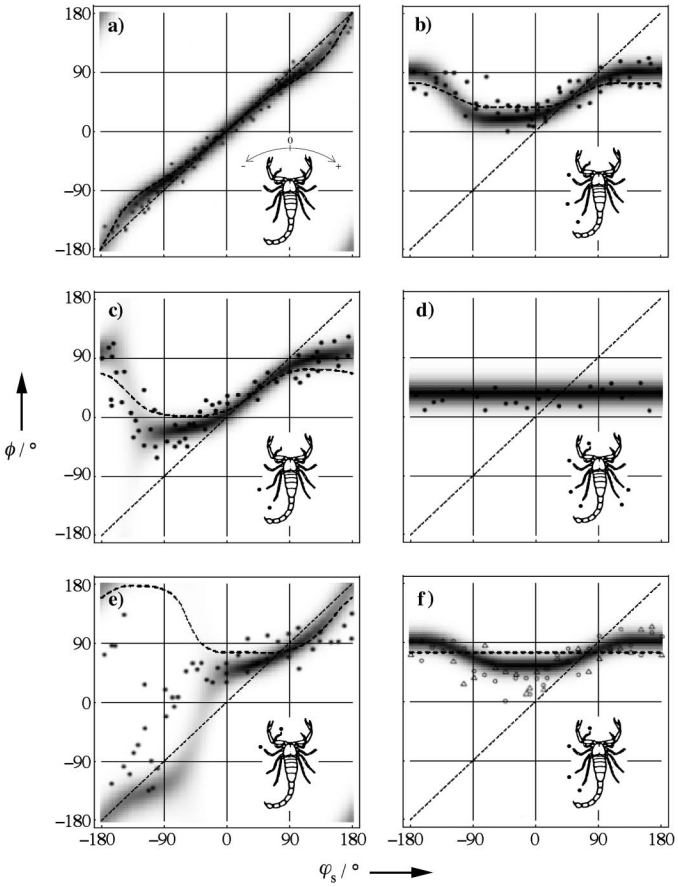


Figure 6. *Sand scorpion psychophysics. Except for (a), the mechanoreceptors of certain feet (tarsi) have been ablated, as indicated by black dots at the legs's ends. The scorpion turning angles ϕ (dots and triangles) after a stimulus from azimuthal direction φ_S are nearly always in the darkly shaded region corresponding to the theoretical probability density. Both experiment and theory show that the scorpion's angular resolution is between 10° and 15°. If for each inhibitory neuron the three inputs due to three feet, namely the triad, are replaced by a single input, say the middle one (L2 and R3 in Figure 5), then the agreement with experiment is in general less good, as is shown by the* mean *response given by the dashed line. The experimental data are due to Brownell;[11] the Figure has been modified after Stürzl et al.[12]*

Barn Owls

The barn owl (*Tyto alba*, Figure 1) is another nocturnal predator. An adult animal needs about five mice per night but, after five to seven youngsters have hatched, the adult owl has to catch a mouse roughly every ten minutes. Though the visual system is excellent, in the dark only acoustic signals are relevant and, consequently, the barn owl's auditory system is exceptionally good. In azimuthal sound localization, frequencies up to 9 kHz are used; for vertebrates this is a huge range. Humans, for instance, do not exploit more than 1 – 2 kHz.[15]

The barn owl determines the prey's direction φ_S by means of the time difference between the two ears, which are at a distance of about 5 cm. It does so with an astounding accuracy of at least 2°—of the same order as in humans, who locate low-frequency sources but with a much larger inter-ear distance. Meanwhile, the fundamental problem of how azimuthal sound localization in the barn owl functions and how a map arises has been solved in terms of a biophysical model.[7, 8] We turn to its essentials.

A key idea dates from a paper by Lloyd Jeffress[16] published more than half a century ago. He proposed a network architecture (Figure 7) that transforms time differences between the two ears into firing rate differences and in this way generates a place code. The simplicity of the Jeffress idea is that acoustic delays are to be compensated by neuronal delays so that by coincidence detection in an ordered array of neurons only a

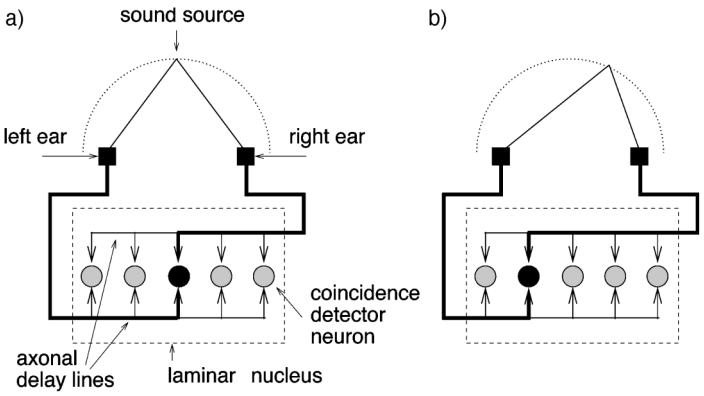


Figure 7. *The Jeffress model.[16] The time difference between the two ears, which depends on the azimuthal position of the sound source (here, directly ahead or slightly to the right), gives rise to a characteristic time difference in the laminar nucleus, the first station in the barn owl's brain with inputs from* both *ears. According to Jeffress, neurons are ordered in a linear array, which is correct.[17]*

specific position is allowed to fire at a *maximal* rate. A coincidence detector[6] fires at a maximal rate whenever input spikes from two (or more) different sources arrive *at the same time*, a most useful property.

In the laminar nucleus, the first station in the barn owl's brainstem that receives signals from both ears, anatomical conditions following Figure 7 with axonal delay lines and coincidence detector cells could be verified.[17] The cochlea provides the input. It is a kind of "inverse piano" that decomposes a signal into its frequency components, a *tonotopic* arrangement. In a sense, the cochlea does for the auditory system what the retina does for the visual system, that is, producing a *retinotopic* arrangement.

Tonotopy is present everywhere in the auditory system, so that we can, and often will, concentrate on a small frequency domain, a frequency channel. The laminar nucleus can be thought of as consisting of many layers, each receiving input from a specific cochlear frequency channel. Despite striking similarities between Figure 7 and reality, there is a cardinal difference in that the laminar nucleus has hundreds of inputs instead of a single pair of delay lines as shown in Figure 7. Theory has to take this complication into account.

- If the source is directly in front of the head ($\varphi_S = 0^\circ$, Figure 7 a), then the spikes that come from the left and from the right meet at the neuron in the middle (black disk). As a coincidence detector, it fires most often; that is, at a maximal rate. Its neighbors (gray disks) fire less.
- For a source that is located further to the right (Figure 7 b), the signals meet further to the left (black disk). Through the spatially regular arrangement of the neurons, a map of the stimulus direction φ_S arises out of the spatial distribution of the firing rates; effectively, the positions of the "black" neurons. The problem of how the map, as a specific arrangement of neuronal "hardware", arises has been solved recently.[8]

In view of hundreds of inputs to the laminar nucleus and, associated with them, a temporal scatter of about 1 ms for the delays with respect to the arrival at the ears, mere anatomy cannot explain how coincidence detectors reach a temporal precision of 20 μs. This precision is needed[7] for the barn owl's spatial resolution of 2° in azimuthal prey localization. Furthermore, a map is a rather special arrangement, so that synapses would need some kind of interaction. At a first sight, however, there is practically none in the laminar nucleus.

Both problems have meanwhile been solved[7, 8] by means of a self-organizing process based on a Hebbian learning rule, Equation (1). First,[7] for synapses on the same neuron, such as in Figure 2, the ones with the correct delay are strengthened and the others are weakened. Here we arrive at an effective "interaction" between the synapses, since they determine *together* whether and when the neuron fires. Once it does so, a learning window W such as the one in Figure 3 decides which are to be strengthened and which are to be weakened.

For synapses located at different neurons, a new idea[8] is needed, namely, that of axon-mediated spike-based learning (AMSL): If a specific synapse changes by $\frac{dJ_{ij}}{dt}$, then all the other synapses connected to it by the *same* axon change by $\rho\frac{dJ_{ij}}{dt}$, where the interaction parameter ρ is quite small, of the order of 0.05. In this way we get a generalized Hebbian learning rule that leads to a map, not only for a bunch of axons in an "isofrequency" layer associated with some frequency channel and coming from the left and the right ear but also for the whole laminar nucleus. Its effect for an isofrequency layer is shown in Figure 8.

From this position, both a numerically exact evaluation of neuronal processes, such as in Figure 8, and also an analytic solution to a linearized learning equation, in the form of Equation (1) but now with $\rho \neq 0$, is possible.[10] Thanks to tonotopy, we can start by restricting ourselves to a single frequency channel and analyze synaptic growth both in space, along an axon, and in time, in terms of the learning equation's dominant eigenvector, specifically with the largest eigenvalue $\lambda_{dom} > 0$. The latter is proportional to the Fourier transform of the learning window W in Equation (1) and, in agreement with experiment, leads to restrictions in W so as to guarantee map formation.

One may wonder, though, why the barn owl's brain takes that much effort in converting a very precise time code representing the stimulus into a spatially distributed rate code. To wit, a) *all* laminar axons have a spike-conduction velocity of about 4 m s^{-1}, b) the coincidence-detecting neurons have an exceptionally short membrane time constant of about 0.1 ms, c) input from the auditory nerve up to 9 kHz (!) is processed, and d) in comparison to the homologous structure in mammals, the laminar nucleus is large and contains many more neurons (12 000). I will suggest an

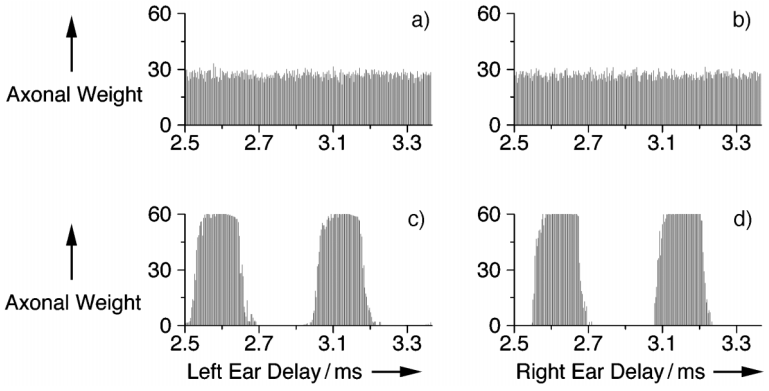


Figure 8. *Selection of delay lines during map formation in a 3 kHz frequency channel. Let us call axonal weight the sum of all synaptic strengths J_{ij} connected to one and the same axon, which functions as a delay line passing and contacting the neurons; see also Figure 7. From both from the left (a, c) and the right ear (b, d), and in contrast to what Figure 7 might suggest, not two but hundreds of axons reach the laminar nucleus (LN). In a young barn owl, the axonal time difference between the respective ear and LN has originally (a, b) a broad, 1 ms wide distribution. When the owl chick has aged a few weeks, the "interaction" (AMSL) between synapses at* different *neurons but at the* same *axon selects synapses and, hence, axons, with the right LN delay (c, d). Consequently the temporal precision of arriving spikes increases. Of course axonal selection is always modulo the period, here* $T = 1/3$ *ms.*

answer in the next Section, where we are facing the question of what precisely a map may be good for.

It may be well to realize that when a barn owl flies almost no noise is produced, so that, trivially, the mouse cannot hear the incoming owl until it is too late but, at least equally important, the owl can adapt its flight while the mouse changes its position, as mice are wont to do. It is not possible for the owl to halt in mid-flight, whereas a sand scorpion can just stop walking, and hence the barn owl must, and does, adapt its flight. To this end an acoustic map of its surroundings seems extremely useful.

Paddlefish

For locating its prey, the sand scorpion's sensory organs need sand, the barn owl ears need air, and a natural alternative to sand and air is water. Though there is a rich choice of predators exploiting water as their medium and time as their agent, we will focus here on the paddlefish to provide an illustrative example of a somatosensory map.

Figure 9 shows a juvenile paddlefish.[19] In the muddy water of the Mississippi river and its larger tributaries, a visual system is not a great help. Moreover, paddlefish feed on zooplankton,

Figure 9. *Juvenile paddlefish snapping at an artificial dipole at the end of the white-coated wires (center). The huge rostrum in front of its mouth is covered by electroreceptors, which are similar to the ampullae of Lorenzini of sharks and rays. The adult animal simply opens its mouth to filter the water but apparently no longer employs the electroreceptors. Photograph courtesy of Prof. Lon A. Wilkens (University of Missouri at St. Louis).*

especially water fleas (*Daphnia*), which through their small but permanent dipole moment stimulate passive electroreceptors on the "rostrum" in front of the fishes' mouths provided the distance is less than 1.5 – 2.0 cm. Water fleas are caught individually. The two sides of the rostrum detect prey independently of each other. Since the fish tend to swim into the oncoming stream, the average speed with respect to river water surrounding it is about 20 cm s^{-1} and hence the time of stimulation is at most 0.2 s.

How, then, does a fish locate its prey? Though the final proof has not been given yet, I expect that a somatosensory map, here a neuronal representation of electroreception at the surface of the rostrum, does the job. The fish "follows" the signal on its rostrum and behaves accordingly in that it simply opens its mouth if a water flea is directly below the rostrum or else turns around first. No precise timing is needed and all that is required is a straightforward map from the two sides of the rostrum into, presumably, the dorsal octavolateral nucleus (DON), as it is called here.

What is a Neuronal Map Good For?

Maps have been found in the brains of many species. As a neuronal representation of the world surrounding an individual, they depend on, and are quite frequently induced by, the topology of sensory organs. As such they are bound to respect neighborhood relations. If we ask *What is a neuronal map good for?* a trivial answer would be *Representing the animal's position in its sensory surroundings*. It makes sense to ask a more specific question: *Why is the neuronal representation as it is, and what does the brain do with it?* Let us see what the above examples suggest.

- For the sand scorpion, the command neurons provide a representation that is directly transferred to the adjacent motor neurons in its legs. This arrangement looks very natural and self-evident, as behooves a standard example.
- For the barn owl, our question a far subtler. As we have seen, there is a one-dimensional representation of the azimuthal stimulus angle φ_S. In terms of orthogonal spherical coordinates $\{\theta, \phi\}$ with $-\pi/2 < \phi < \pi/2$, the sound source's location $\{\vartheta_S, \varphi_S\}$ is represented in the brain by means of two different and separate techniques handling interaural intensity and time differences[17] and giving rise to two different one-dimensional representations.

  The two parallel pathways merge later on, in the *inferior colliculus*, and both representations are combined by multiplication instead of addition.[18] Why combine them? The answer might be that in the *tectum opticum*, the auditory and visual representation are superimposed *and compared* through synaptic connections, the visual one being dominant.[20] Since the retina can be described in terms of spherical coordinates too, there would be a good reason for the auditory system to encode similarly and allow comparison. Note, however, that at the moment this is nothing but a well-educated guess.
- The paddlefish again seems quite simple. It spends its time with a somatosensory map of the rostrum and locating prey is straightforward. As for map formation, all that is known to apply to the retina[21] should hold, with the necessary changes, for the rostral surface.

In summary, neuronal maps are widespread in the animal kingdom. As a rule, they represent both the topology and the temporal character of sensory input. We have isolated and analyzed two principles, coincidence detection and an interplay of excitation and inhibition. It is not known yet whether these are the only two universals, although I would speculate so. The functional role of maps in neuronal information processing is not clear either. It is a fact, though, that motor control, the ultimate goal of brain activity, is based on rate and not on time coding. Time coding needs the precise timing of spikes, while rate coding requires only counting spikes in a relatively narrow time window, whose width depends on the context at hand. At a high

enough level in the brain, rate coding is the rule: Exactly this is what a map gives rise to.

I am most indebted to Christian Leibold for his invaluable help in preparing the manuscript and to Philip Brownell for constructive criticism. Furthermore, I thank Armin Bartsch for the box Figure and Wolfgang Stürzl for Figure 5.

[1] R. W. Sperry, *J. Exp. Zool.* **1943**, *92*, 236 – 279.
[2] D. V. Buonomano, M. M. Merzenich, *Annu. Rev. Neurosci.* **1998**, *21*, 149 – 186.
[3] A. V. M. Herz, B. Sulzer, R. Kühn, J. L. van Hemmen, *Europhys. Lett.* **1988**, *7*, 663 – 669.
[4] "Theory of Synaptic Plasticity": J. L. van Hemmen in *Handbook of Biological Physics, Vol. 4* (Eds.: F. Moss, S. Gielen), Elsevier, Amsterdam, **2001**, pp. 771 – 823, and references therein.
[5] D. O. Hebb, *The Organization of Behavior*, Wiley, New York, NY, **1949**.
[6] C. Koch, *Biophysics of Computation: Information Processing in Single Neurons*, Oxford University Press, New York, NY, **1999**.
[7] W. Gerstner, R. Kempter, J. L. van Hemmen, H. Wagner, *Nature* **1996**, *383*, 76 – 78.
[8] R. Kempter, C. Leibold, H. Wagner, J. L. van Hemmen, *Proc. Natl. Acad. Sci. USA* **2001**, *98*, 4166 – 4171, and references therein.
[9] R. Kempter, W. Gerstner, J. L. van Hemmen, *Phys. Rev. E* **1999**, *59*, 4498 – 4514.
[10] C. Leibold, R. Kempter, J. L. van Hemmen, *Phys. Rev. Lett.* **2001**, *87*, 248 101.
[11] P. H. Brownell, *Science* **1977**, *197*, 479 – 81; P. H. Brownell, *Sci. Am.* **1984**, *251*(6), 94 – 105; P. H. Brownell, R. D. Farley, *J. Comp. Physiol.* **1979**, *131*, 23 – 30; P. H. Brownell, R. D. Farley, *J. Comp. Physiol.* **1979**, *131*, 31 – 38.
[12] W. Stürzl, R. Kempter, J. L. van Hemmen, *Phys. Rev. Lett.* **2000**, *84*, 5668 – 5671.
[13] A. Georgopoulos, A. B. Schwartz, R. E. Kettner, *Science* **1986**, *233*, 1416 – 1419; E. Salinas, L. F. Abbott, *J. Comp. Neurosci.* **1994**, *1*, 89 – 107; J. E. Lewis, *J. Comp. Physiol. A* **1999**, *185*, 373 – 378.
[14] P. H. Brownell, J. L. van Hemmen, *Am. Zool.* **2001**, *41*, 177 – 188.
[15] W. M. Hartmann, *Phys. Today* **1999**, *52*(11), 23 – 29.
[16] L. A. Jeffress, *J. Comp. Physiol. Psychol.* **1948**, *41*, 35 – 39; see also P. X. Joris, P. H. Smith, T. C. T. Yin, *Neuron* **1998**, *21*, 1235 – 1238.
[17] M. Konishi, *Sci. Am.* **1993**, *268*(4), 34 – 41.
[18] J. L. Pena, M. Konishi, *Science* **2001**, *292*, 249 – 252.
[19] L. A. Wilkens, D. F. Russell, X. Pei, C. Gurgens, *Proc. R. Soc. London Sect. B* **1997**, *264*, 1723 – 1729.
[20] E. I. Knudsen, P. F. Knudsen, *Science* **1985**, *230*, 545 – 548.
[21] A. Bartsch, J. L. van Hemmen, *Biol. Cybern.* **2001**, *84*, 41 – 55.

Received: September 18, 2001 [C 310]