III From the Ear to the Cortex

1) Anatomy

2) Neurophysiology: Transport from the Cochlea to the Cortex

3) Cochlear Mechanics and Neural Signals

4) The Problem of Pitch Recognition





Notation in anatomy



Brain mass	1508 g
Total number of neurons in brain	86 billion
Total number of non-neurons in brain	85 billion
Mass, cerebral cortex	1233 g
Neurons, cerebral cortex	16 billion
Relative size of the cerebral cortex	82% of brain mass
Relative number of neurons in cerebral cortex	19% of brain neurons
Mass, cerebellum	154 g
Neurons, cerebellum	69 billion
Relative size of the cerebellum	10% of brain mass

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Brain consists of neurons and glial cells (glue).

1 billion = 10^9

The stations communicate by neurons. Soma, axion, dendrits. Communicate by synapses with about 10³ synapses per neuron



Drawing by Ramon y Cajal

Photograph



Information on neurophysiology from

*Anatomy (Lesions, zytoarchitecture (post mortem) with high resolution MRI perhaps also non-invasive)

*Direct measurement Patch clamps, mostly from animals, from huamns only if medically indicated. ``Gold Standard"

*Noninvasive methods:

Direct: Measurement of evoked fields: EEG, MEG

Indirect: Through change in metabolism: FMRI, PET

Encoding of information transported and processed by neurons.

Labeled line code. A special nerve fiber conveys specific information from its origin. Johannes Mueller, early XIXth: different nerve fibers elicit different sensations according to their ``specific nerve energy. If someone hits your eyeball, you see a flash



Rate code. Information is transmitted by the firing rate. Very apt for quantitative information (e.g. sound volume)

Temporal code. The firing rate is phase locked with the signal. The neurons fire in volley.

Ensemble code. Only an ensemble of neurons can transmit specific information.

At higher stages codes tend to be transformed into rate codes (digitalized)

Schematic auditory pathway

Each station seves as a relais, but it does not only transmit, but also integrates them, it can be considered as a neural computer.

As can be seen the connection is complicated and goes in both directions, up and down and between both sides, right and left.







The auditory pathway and its stations from the cochlear nucleus to the auditory cortex.





FIGURE 1.1. Schematic diagram of the innervation of the human cochlea based on the data of Nadol and his colleagues (Nadol, 1990; Nadol, Burgess, and Reisser 1990). The three rows of outer hair cells (OHCs) and one row of inner hair cells [IHCs) are shown for a short segment of one cochlear turn. Solid fibers are of afferent neurons and dashed fibers are of efferent neurons. Three Type I spiral panglion neurons (I) and one Type II spiral ganglion neuron (II) are shown. Type I cells comprise 88% and type II 12% of the afferent neurons. A single medial plivocochlear bundle (OCB) fiber to outer hair cells and a single lateral olivocochlear bundle fiber to type I spiral ganglion fibers are shown. SG, spiral ganglion.



FIGURE 2.1. Afferent nerve endings (A) near the base of an IHC in a squirrel monkey. One afferent ending receives a synapse (arrow) characterized by a marked thickening of the postsynaptic membrane and a presynaptic body surrounded by a halo of round vesicles. An efferent ending (E), filled with synaptic vesicles, forms a synapse (arrowhead) on the afferent ending. Efferent endings do not usually make synaptic contact directly with the IHC. Scale bar equals 1 μ m. (This micrograph is courtesy of Dr. R.S. Kimura.)



FIGURE 2.2. Nerve endings at the base of an OHC of a rhesus monkey. The afferent nerve ending (A) is relatively small and the synaptic contact with the hair cell (arrow) is characterized by a membrane thickening, a presynaptic body, and a few synaptic vesicles. The efferent ending (E) is typically large, filled with synaptic vesicles, and makes direct contact with the outer hair cell. In addition to the synaptic vesicles, the efferent ending opposes a long subsynaptic cystern (arrowheads) inside the hair cell. Scale bar equals 1 μ m. (This micrograph is courtesy of Dr. R.S. Kimura.)



Prof. Jonathan Ashmore - Lab Page Rock around the clock Hair Cell.

The movie shows a short video of an outer hair cell being stimulated electrically by a patch pipette which enters from the lower left. It was recorded one cold Saturday morning for a BBC programme called ``Ear We Go'' and originally broadcast on 13th August 1987. I still have the holes in my equipment where they put the camera.

This is an outer hair cell microdissected from the low frequency (apical) end of the cochlea and placed on the stage of a microscope. Cells such as this survive for a couple of hours if kept in the right culture conditions. To change the cell's potential and then make the cell change length I just played Rock-Around-the-Clock (Bill Haley's 1954 classic) from my (then) Walkman into the input socket of the electrophysiology amplifer. The BBC producer was delighted because even then RAtC was so ancient that they did not have to pay copyright charges.

For the scientifically minded: This outer hair cell gets thinner when it gets longer and fatter when it gets shorter. Measuring up these changes indicates that the cell volume stays constant. This supports the idea that the ``motor'' is a molecule whose job it is to change membrane area. The molecule, discovered in 2000 by Peter Dallos' lab in the US, is called "prestin".

videos_rockaroundtheclock.mpg





The tonotopic organization is preserved through the whole auditory pathway until the auditory cortex

auditory cortex of a cat. Tonotopically organized areas are shown in yellow

> **RE** 5.2. (A) Lateral view of the cerebral cortex of cat showing the parcellation ditory cortex. Auditory cortex contains four tonotopically organized fields: mary field (AI), an anterior field (Field A; alternatively termed AAF, after ht 1977), a posterior field (Field P or PAF), and a ventroposterior field (Field r VPAF). (B) Further details of the frequency represented (high or low) at orders of these fields, and extensions of them into the sulci, are shown in ustration of auditory cortex in which the sulci have been unfolded (sulcal hs shaded) and adjacent points on cortex have been split (thin dashed lines). unding the tonotopic fields is a belt of acoustically responsive cortex divided four regions that lack precise tonotopic arrangement: a second auditory area , a dorsoposterior (DP) and ventral (V) field, and a temporal (T) area. Abntions: aes, anterior ectosylvian sulcus; pes, posterior ectosylvian sulcus; pss, losylvian sulcus; sss, suprasylvian sulcus. (From Imig and Reale, *Journal of parative Neurology*, 1980: Reprinted by permission of John Wiley and Sons,

Tonotopic organization of the auditory cortex of a macaque



Rate coding. Normally there is a spontaneous firing rate and the signal is transmitted by a change of this spontaneous rate, either by increasing or diminishing it.



Neural tuning curve of a chinchilla. The threshold of spl at which the firing rate starts to deviate from the sponatneous one is displayed for different single neurons.



FREQUENCY (kHz)

bm human (dead) (linear y-axis!!)

bm movement, primate



Neural and mechanical (bm) tuning curve for chinchilla

For animals in pristine conditions the tuning curves are much narrower than for dead subjects.



Neural response of a squirrel monkey to a tone of 6200 Hz at different spl











301praat:sin30, sin720, sin720+360



Loss of outer hair cells near the stapes increases the threshold and broadens the frequency sensitivity in that region of the cochlea. This is very well in line with the outer hair cells as a device to ``dedamp" the motion of the bm.



The nu-dependence of Abs v_y is plotted at x=2.5 (CF=480Hz) for de=0.05 (black) and at x=1 (CF= 4940 Hz) for de=0.5

black: percentage of normal hair cell population. Im the gray areas no counting was possible

praat: bip.collection

Temporal code



firing rate of a neuron with CF 9450 to a tone with 9450 Hz (left) and 500 Hz (right)

Back to hair cells

Hair cells fire only, if bm moves downward

b m movement

measured at chinchilla

calculated with Greenwood parameters for humans

0.015

0.015

0.015

0.02

0.02

0.02

In a linear model the answer of the BM to a signal p(t) is

$$Y(x,\tau) = \int dt \, p(t) \, B(x,\tau-t)$$

 $B(x,\tau)$ is the answer to a click:

 $Y(x,\tau)_{\text{click}} = \int dt \,\delta(t) B(x,\tau-t) = B(x,\tau)$

we now form the integral (convolution)

$$c(\tau) = \int dt' p(t') Y(x, \tau - t')$$

= $\int \int dt' dt p(t') p(t) B(x, \tau + t' - t)$

with new variable $t_1 = t' - t$

$$c(\tau) = \int dt_1 dt \, p(t) \, p(t_1 + t) B(x, \tau + t_1)$$

for stochastic noise: $\int dt \, p(t) \, p(t+t_1) = \delta(t_1)$

$$c(\tau) = \int dt_1 \delta(t_1) B(x, \tau - t_1) = B(x, \tau)$$

Measure answer to a noise, convolute with that noise, the resulting quantity is the answer to a click (note that compressions and depressions vary stochstically in noise).

Firing rates of different nerves with deconvoluted noise.

optimal up-chirp: A signal with increasing frequency such that the bm is excited at the same time

optimal up chirp

down-chirp

301praat up-chirp, down_chirp

The problem of pitch sensation

After Ohm-Helmholtz-Bekesy the problem of pitch sensation seemed solved by the place theory : The pitch of a (complex) tone is determined by the position of its (lowest) spectral component

The information of the pitch is transmitted by labled line coding to the cortex.

New fact: Tracking of the fundamental. The pitch is perceived, even if the characteristic part of the bm is not excited.

This, together with the observed neural temporal encoding speaks for pitch recognition as a temporal effect (Telephone theory of Rutherford)
Pro and contra temporal theory:

Pro: Fundamental tracking easily explained by temporal tracking: Period is always that of fundamental, even if it is missing.

Contra: Phase independence of the sensation, e.g. Schroeder phase

Example (a bit unfair with loudspeaker): chopped noise



realized as $p(t) \sin^8(2\pi \nu t)$.



Goldstein's pitch extractor:

Find harmonic series which approximates shifted series.



If the frequencies of the presented tone are $\nu_{n_1}, \nu_{n_1+1}, \ldots, \nu_{n_1+k_1}$, then look for an harmonic tone with fundamental frequency ν_g such that the difference

$$\Delta_g = \sum_{k=n_1}^{n_1+k_1} \left(\nu_{n_1} - (m_1 + k_1 - 1)\nu_g \right)^2 \tag{5.8}$$

is minimal

In the simple case of a shifted harmonic tone the minimum of Δ can be determined analytically:

$$\Delta_g(\nu_0) = -\frac{3\,\delta\,k_1 - 6\,\delta\,m_1 - k - 1\,\nu_0 - 2\,k_1^2\,\nu_0 - 3\,k_1\,m_1\,\nu_0 - 3\,k_1\,n_1\,\nu_0 - 6\,m_1\,n_1\,\nu_0}{k_1 + 2\,k_1^2 + 6\,k_1\,m_1 + 6\,m_1^2} \tag{5.9}$$



Extreme high pass filtering.

One cuts off so many lower harmonics, that the remaining ones can certainly not be resolved on the bm.

Example: Extremely high pass filtered melody

301praat: melodie-cut-200, melodie-1-20, melodie-fundamentals



Abbildung 5.16: Spectrogram and pitch (PRAAT ac) the high passed beginning of the theme of the *Kunst der Fuge*.



signal and response



signal and response







signal and response+ noise





signal p(t), r(t)

$$c(\tau) = \int dt' p(t') r(t' + \tau)$$

Closely related to convolution:

$$c(\tau) = \int \int dt' dt'' \, p(t') \, r(t'') \, \delta(t'' - t' - \tau)$$

$$p * r(\tau) = \int \int dt'' \, dt' p(t') \, r(t'') \, \delta(t'' + t' - \tau)$$

For noise n(t)

$$\frac{1}{2T} \int_{-T}^{T} dt' p(t') n(t' + \tau) \to 0$$

for any signal p(t) (except for p(t) = n(t), the same noise).

Therefore

$$\int dt' p(t') r(t' + \tau) + n(t + \tau) \rightarrow \int dt' p(t') r(t' + \tau)$$

For p(t) = n(t) we have: $\int dt' n(t') n(t' + \tau) = \delta(\tau)$

This brings us to autocorrelation:

Autocorrelation:

$$p_{ac}(\tau) = \frac{1}{2T} \int_{-T}^{T} dt' p(t') p(t' + \tau)$$

In a coded world, the autocorrelation is easy to handle:

Be $\{p_1, p_2, \dots, p_k \dots\}$ the digitalized version of a function, i.e. $p_n = p(\frac{n}{\Delta t})$ e.g. then the autocorrelation is just the sum $p_{ac}(k) = \sum_n p_n \cdot p_{n+k}.$

This is fast on a computer, and presumably also in a neural processor.





Autocorrelation of the Schroeder-phase signal.

$$p_{ac}(\tau) = \frac{1}{2T} \int_{-T}^{T} dt' p(t') p(t' + \tau)$$

Schröder phase:

 $p(t) = \sum_{n=1}^{10} \sin(2\pi (n \, 220 \, t + \frac{n^2}{10}))$



Zero phase

 $p(t) = \sum_{n=1}^{10} \sin(2\pi n \, 220 \, t)$

$$\tau = 1/\nu$$



The period $\tau = 1/\nu$ is the distance to the first maximum of the autocorrelation function

No accident: The Wiener theorem states: The autocorrelation function is the Fourier-transform of the power spectrum

$$p_{ac}(t) = \frac{1}{T} \int d\nu' e^{-2i\pi\nu' t} |\tilde{p}(2\pi\nu')|^2$$

For a physicist, using the magic formula

$$\int \frac{d\omega}{2\pi} e^{i\omega\alpha} e^{-i\omega t} = \delta(t - \alpha)$$

and beeing a bit cavalier about the ``infinite T" the proof is very simple:

 $p_{ac}(t) = \frac{1}{T} \int_{-T}^{T} dt' \, p(t') \, p(t'+t)$ where T is big enough to apply the magic formula

$$p(t) = \int d\nu \, e^{-i2\pi\nu t} \, \tilde{p}(2\pi\nu) = \int d\nu \, e^{i2\pi\nu t} \, \tilde{p}^*(2\pi\nu)$$

$$T p_{ac}(t) := \int dt' \int d\nu \, e^{i2\pi\nu t'} \tilde{p}^*(2\pi\nu) \int d\nu' \, e^{-i2\pi\nu'(t+t')} \tilde{p}(2\pi\nu')$$

$$= \int dt' \int d\nu \int d\nu' e^{i2\pi\nu t' - 2i\pi\nu'(t+t')} \tilde{p}^*(2\pi\nu) \, \tilde{p}(2\pi\nu')$$

$$= \int d\nu \int d\nu' \,\delta(\nu' - \nu) \delta(e^{-2i\pi\nu' t} \,\tilde{p}^*(2\pi\nu) \,\tilde{p}(2\pi\nu'))$$

$$= \int dt' \int d\nu \int d\nu' e^{i2\pi\nu t' - 2i\pi\nu'(t+t')} \tilde{p}^*(2\pi\nu) \tilde{p}(2\pi\nu')$$

$$= \int d\nu \int d\nu' \,\delta(\nu' - \nu) \,\delta(e^{-2i\pi\nu' t} \tilde{p}^*(2\pi\nu)) \tilde{p}(2\pi\nu')$$

$$= \int d\nu' e^{-2i\pi\nu' t} \tilde{p}^*(2\pi\nu') \tilde{p}(2\pi\nu') = \int d\nu' e^{-2i\pi\nu' t} |\tilde{p}(2\pi\nu')|^2$$

$$q e d$$

Hence no wonder that the autocorrelation function for the zero and Schroeder phase are identical, since the power spectra are the same.

Hence all positive points for the spectra concerning phase independence can be also applied for temporal coding, if the latter makes use of the autocorrelation (J C R Licklider).

Though the direct definition of the autocorrelation is very convenient in a digitalized world, it is for analytic calculations normally easier to start with the power spectrum and Fourier transform it.

Consider the shifted harmonics under this aspect.

$$p(t) = \sum_k \cos[(\nu - (m+k)\nu_0 - \delta)t]$$

$$\tilde{p}(2\pi\nu) = \frac{1}{2} \sum_{k} [\delta(\nu - (m+k)\nu_0 - \delta) + \delta(\nu + (m+k)\nu_0 + \delta)]^2$$

The autocorrelation is given by:

$$p_{ac}(t) = \frac{1}{4} \int d\nu \, e^{-i2\pi \, \nu \, t} \sum_{k} [\delta(\nu - (m+k)\nu_0 - \delta) + \delta(\nu + (m+k)\nu_0 + \delta)]$$

= $1/2 \sum_{k} \cos[2\pi((m+k)\nu_0 + \delta))t]$

Autocorrelation of the unshifted and shifted harmonic series. The period of the shifted harmonic is a bit shorter than that of the unshifted To the relief of the mathematical consience the following remark: The Fourier transform of chopped noise contains delta-functions, how can you square them. Answer:

We define $\delta_T(t) = \int_{-T} T e^{i\omega t} d\omega$

The magic formula is $\lim_{T\to\infty} \delta_T(t) = \delta(t)$

One can in this sense show: $\lim_{T\to\infty} \frac{1}{2T} (\delta_T(t))^2 = \delta(t)$

Optimal frequency for a shifted harmonic series as function of the shift delta



from autocorrelation

from spectral optimization

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The magic formula is $\lim_{T\to\infty} \delta_T(t) = \delta(t)$

One can in this sense show:

$$\lim_{T \to \infty} \frac{1}{2T} (\delta_T(t))^2 = \delta(t)$$



If there is an ambiguity, one tends to hear the smaller interval. e.g. if there is an ambiguity between 4th and 5th one chooses the 4th

Deutsch's Tritonus paradox: There is no smaller interval for the tritonus, which is half way between the octave.





In case of pitch ambiguity one has the tendency to choose the smaller interval.



Huyghens noise (Iterated rippled noise, IRN)



Christian Huygens 1693 im Park von Chantilly

sound reflected from the first step

+ sound reflected from the second step etc

INR with ℓ iterations and the gain factor g is defined as

$$p^{H\ell}(t) = \sum_{k=0}^{\ell} g^k \, p(t+k\,\Delta) \tag{5.31}$$

The autocorrelation is given by

$$p_{ac}^{H\,\ell}(t) = \frac{1}{T} \int_{-\infty}^{\infty} dt' \sum_{k=0}^{\ell} g^{k} p(t'+k\,\Delta) \sum_{k'=0}^{\ell} g^{k'} p(t+t'+k'\,\Delta)$$
$$= \sum_{k,k'=0}^{\ell} g^{k+k'} \delta(t+(k'-k)\Delta)$$
(5.32)

There is a finite set of correlation times $T_{k',k} = (k'-k)\Delta$, that is times, where the autocorrelation function has a maximum:

$$p_{ac}^{H\,\ell}(t) = (\ell+1)\delta(t) + g\,\ell\delta(t \dashv \Delta) + g^2\,(\ell-2)\delta(t-2\Delta) + \dots$$
(5.33)

The nearest correlation time $|\Delta|$ determines the pitch $|\nu| = 1/|\Delta|$



Sp curves for noise and Huygens noise with 1 and 5 iterations.



Abbildung 5.19: Spectra and autocorrelation functions of huygens noise with $\ell = 1$ and with $\ell = 5$ repetitions

Huygens noise with positive gain (g=+1) and negative gain (g=-1) and 5 iterations





Huygens noise with positive gain (g=+1) and negative gain (g=-1) and 1 iteration cochleogram of unfiltered and high-pass filtered g=+1 and g=-1 noise, 1 iteration





We come back to this question in the treatment of electrophysiology

Last item in this section: Pitch test of Smorenburg

302praat: 440_3_5, 366_4_6




Systematische Untersuchung der Psychoakustik, Neurophysiologie und Anatomie

Structural and functional asymmetry of lateral Hesch's gyrus reflects pitch perception preference P.Schneider, V. Sluming, N. Roberts, M. Scherg, R. Goebel, H.J. Specht, H.G. Dosch, S. Bleeck, C. Stippich, A. Rupp *nature-neuroscience*, **8** (2005) 1241-1247

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