

Applications of Information Theory.

Information capacity in the nervous system.

A. Gradual response versus all or none action potentials.

1. Capacity of receptors.

a) *Visual receptors.*

(1) Composition.

120×10^6 cones.

6.5×10^6 rods.

1×10^6 afferent neurons.

(2) Distinguishable intensity levels.

Fovea centralis $m = 250$ distinguishable light intensity levels: coding requires 8 bit.

(3) Number of distinguishable images per unit of time.

At low intensity 10 images/s.

At high intensity 60 images/s.

TV 25 images/s: results in flickering at settings with too high intensity (some newer TV sets present images at a rate of 100 Hz (via data processing), and thereby show less flickering).

(4) Information capacity.

Range: $C \cong 100 \times 10^6$ bit/s (little influenced by added color information).

b) *Auditive system.*

(1) Distinguishable intensity levels: $m = 80$.

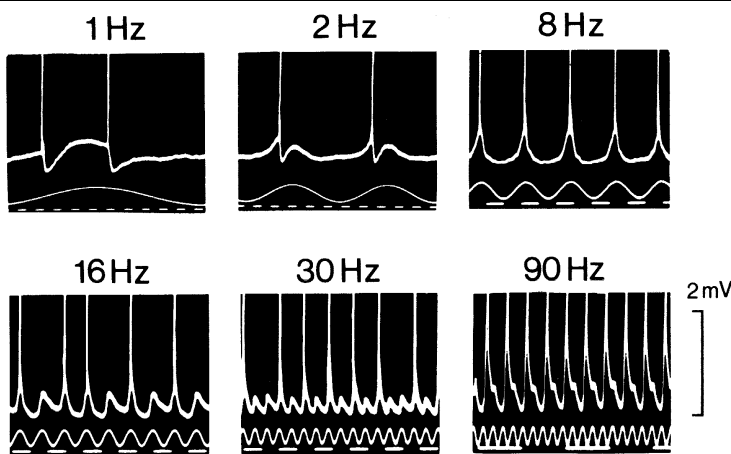
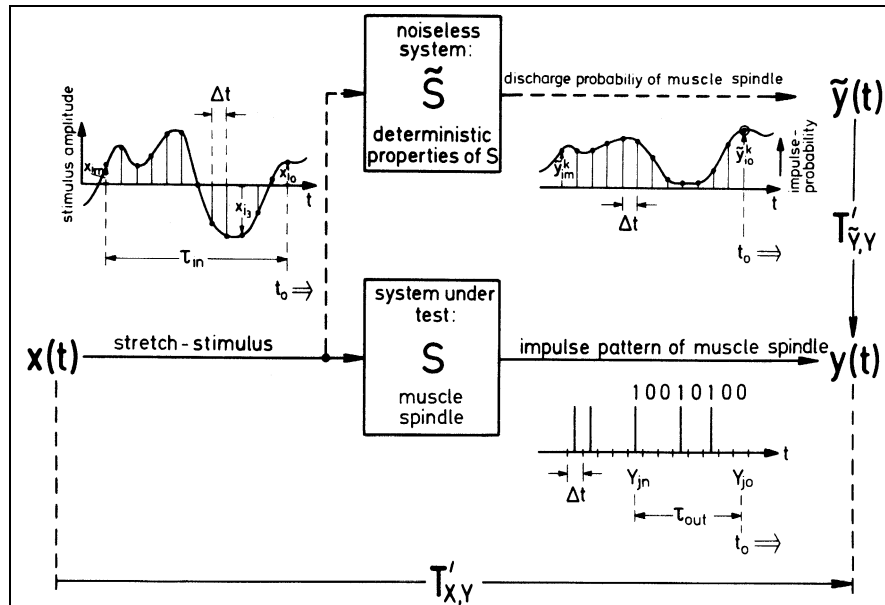
(2) Frequency range: $W = 20$ kHz.

(3) Number of distinguishable tones: 850.

(4) Information capacity: $C = 20 \times 10^3$ tot 50×10^3 bit/s.

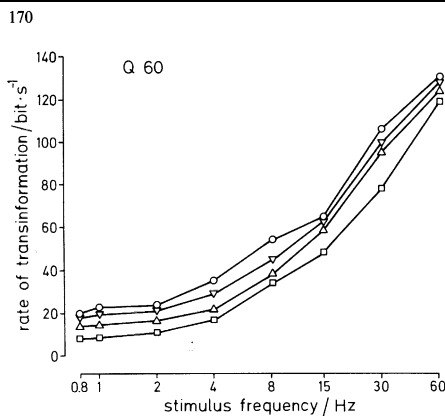
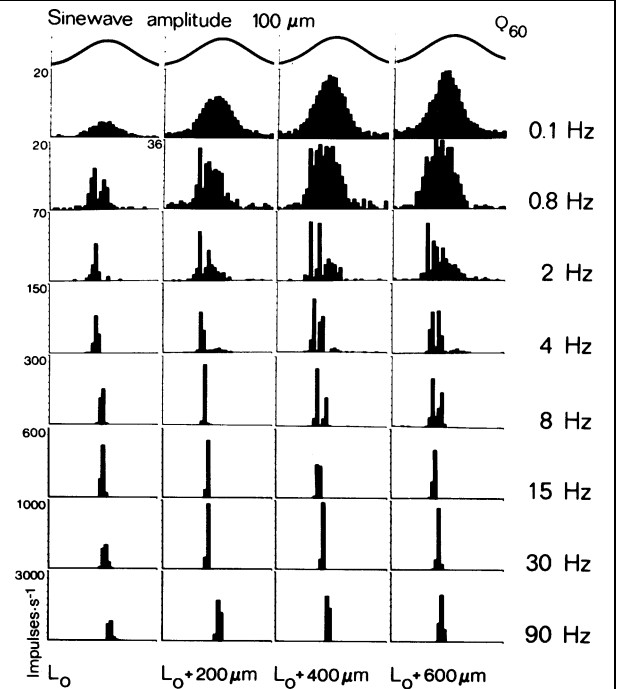
c) *Muscle spindle.*

The electrical activity of the first node of Ranvier of the afferent fiber of the musculus extensor digitorum longus IV of the frog was measured in response to mechanical stretch of the muscle, with different types mechanical stimuli (sinus, Gaussian noise and combination of the two). Each stimulus pattern was repeated several times, and the response was measured. An idealized response impulse pattern was constructed by assigning the value of one to a time interval Δt in which an action potential was recorded, while a value of zero was assigned to time intervals without action potentials. From data of repeated application of the stimulus also the probability was determined for each time interval that in this particular interval an action potential can be observed (ensemble average). The information that is present in the idealized response as well as in the ensemble average is obviously transmitted from stimulus to response. From the relation between the individual idealized responses and the ensemble average, the channel matrix can be determined. From these data, the rate of information transmission can be calculated.



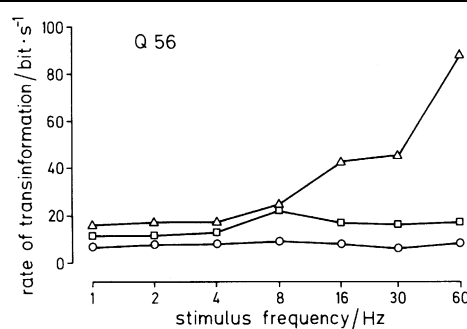
Upper panel: Response of the muscle spindle at different frequencies

Right: Cycle histograms of the average response at different frequencies and different base stretch



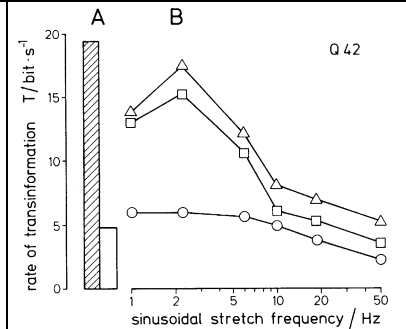
Information transmission rate as a function of stretch frequency at large stretch and different base stretch.

Squares at normal base length, other symbols at increasing base lengths.



Information transmission rate as a function of stretch frequency at small stretch and different base stretches.

Circles at rest length, squares and triangles at larger base length.



A: Total transmission rate (crosshatched bar) compared to the linear component.

B: Noise (triangles and squares) increases transmission rate in comparison to pure sinusoidal stimulation.

Sinusoidal stretches of the spindle at frequencies below 2 Hz result in sinusoidally varying action potential frequencies that are linearly related to the stimulus. The transinformation rate is low (between 5 and 15 bit/s), and independent of the amplitude of the stimulus. When the experiment is repeated on a stretched spindle (thus sinusoidal length changes around another base length) the modulation depth of the response is enhanced, but the rate of information transmission is increased by less than 10 bit/s.

Sinusoidal stimulations at frequencies larger than 2 Hz result in a non-linear response: it can be seen from the cycle histogram that the action potentials are centered only in a small part of the cycle. The transinformation rate increases with larger frequencies up to 130 bit/s at 60 Hz (left panel). However at small amplitudes of the sinusoidal stimulation, the transinformation is only high when the spindle is prestretched to a large base length (middle panel).

For stretches with random signals (Gaussian noise), the transinformation rate varies between 5 and 30 bit/s, dependent on the amplitude and on the base stretch. In this case the response contains a linear as well as a non-linear component. The information rate is mainly carried by the non-linear component of the response: the linear component of the response carries only up to a maximum of 25% of the rate of information transmission (right panel).

From experiments with combination of sinusoidal stretch with Gaussian noise it appears that the rate of information transmission of the sinusoidal signals is enhanced by the presence of the noise. While this appears paradoxical, this is a natural consequence of the non-linear properties of the system: the noise can bring the spindle at some times into a range of stretch and frequencies where the spindle shows a higher transmission capacity (see also stochastic resonance).

2. Capacity of neurons.

a) *Non-spiking neurons.*

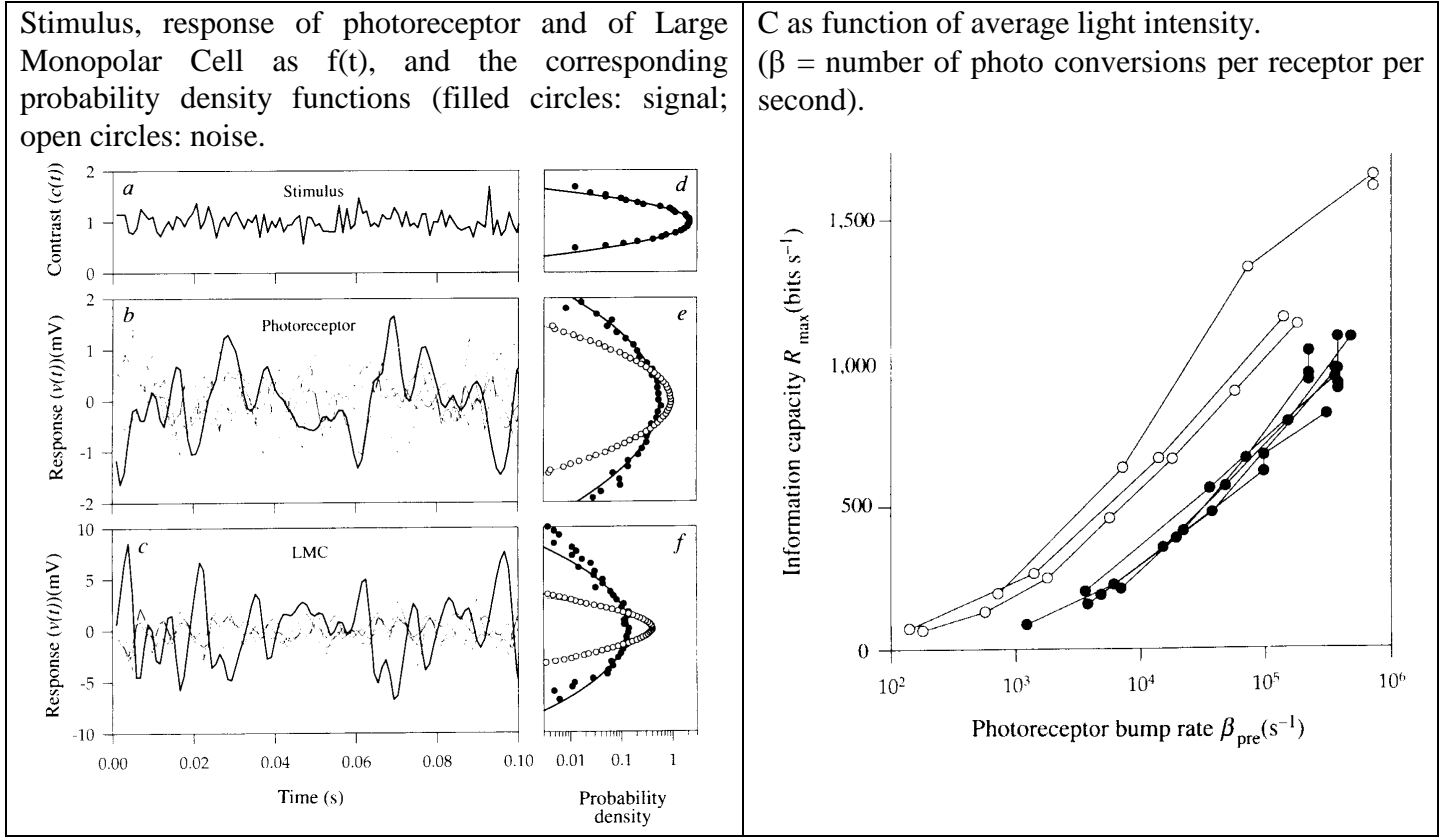
The rate of information transmission from photoreceptors (of the fly) via chemical synapses to LMC (Large Monopolar Cells) was measured. These LMC are second order neurons that obtain redundant convergent information from six photoreceptors. These cells do not show action potentials, but graded potentials.

The light intensity was modulated in a repetitive pattern with a pseudo-random sequence. The resulting potential changes were measured in the photoreceptor and in the LMC. Frequency spectra were constructed of the stimulus, as well as of the responses of both cell types. The difference between the output and input spectra is the Bode diagram of the systems (stimulus - photoreceptor, photoreceptor - LMC, or stimulus - LMC). Each response shows random deviations from the average of the responses obtained from repeated presentation of the stimulus. Also the spectrum (noise spectrum) was constructed from deviations of individual responses from the average. With these data the maximal rate of information transmission can be calculated using following equation:

$$C = \int_0^{\infty} \log [1 + S(f) / N(f)] df$$

in which $S(f)$ and $N(f)$ respectively represent the signal and noise power spectrum, f the frequency and C the information capacity (The expression gives the information capacity for a continuous channel with noise).

These LMC reach a capacity of 1650 bit/s. The synaptic information capacity amounted to 2110 bit/s at the highest light intensity. Since there is convergence via six synapses with photoreceptors, and each synapse contains about 200 active zones from which the output is averaged, the capacity is estimated at 1.8 bit/s per active zone. This value is the consequence of the redundancy and is much less than the value of about 55 bit/s per active synaptic zone that can be calculated in the absence of redundancy.



b) Spiking neurons.

(1) Estimation of channel capacity.

Coding in nerves is a frequency coding: the number of impulses per second (or in other words, the code element) is the average time difference between 2 impulses (τ) during a short period.

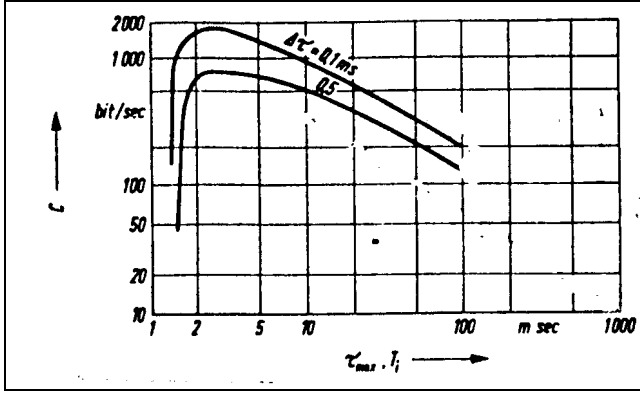
As a consequence of the refractory period following activation and inactivation of the Na current, the time difference between 2 action potentials cannot be smaller than some minimum value τ_{\min} . The time difference also has a maximal value (τ_{\max}) as a consequence of disturbances and of the requirement of a short response time, so that the delay of decoding cannot be too long. The question can then be asked how many different signal levels can be coded by a nerve. It is evident that a certain spread ($\pm \Delta\tau$) can exist in the determination of the time between impulses frequency spectra (uncertainty). The different levels must therefore at least differ by a time $2\Delta\tau$ in order to be able to uniquely determine the time interval (level).

The number of distinguishable levels is then: $n = (\tau_{\max} - \tau_{\min})/2\Delta\tau + 1$

When all levels are equally probable the average impulse distance is $\tau_m = (\tau_{\max} + \tau_{\min})/2$. The average number of elementary signals that can be transmitted per unit of time is then $L = 1/\tau_m$. At n equally probable levels, the entropy of the elementary signal is $\log n$. The channel capacity can then be calculated:

$$C = L \log n = \frac{\log n}{\tau_m} = \frac{2 \log \{(\tau_{\max} - \tau_{\min})/2\Delta\tau + 1\}}{\tau_{\max} + \tau_{\min}}$$

At a $\tau_{\min} = 1$ ms, $\tau_{\max} = 10$ ms and $\Delta\tau = 0.1$ ms, we obtain $n = 46$ and $C = 1000$ bit/s



The curve gives the value of C as function of the maximum allowable time interval between 2 impulses. These curve shows a maximum for $\tau_{\max} = 2$ ms. At small τ_{\max} the number of levels is small and C will thus be small. While at large τ_{\max} the number of levels is large, the average impulse distance is also large, so that the average rate per elementary signal is small.

(2) Experimental determination of channel capacity.

The best experimental estimations of the capacity of spiking neurons was obtained by measurement in third class neurons of the lobular plate of the fly. This was reached by applying to measured trains of action potentials, a model that can provide an accurate estimation (s_{est}) of the presented continuous input stimuli (s) that caused these trains of action potentials. It was first demonstrated that the decoding of the train can be approximated as a non-linear filter, and that only the first linear term in $(t - t_i)$ dominates the response (t_i is the time of the i^{th} action potential). The model thus is of the form $s_{\text{est}} \cong \sum K_1(t - t_i)$, where K_1 is a filter factor. (When K_1 is very slow, the output is an estimation of the average action potential frequency, and contains little or no information about the individual intervals between the action potentials).

The relation between the spectrum of the estimated stimulus $s_{\text{est}}(f)$ and of the real stimulus $s(f)$ contains an amplification factor $g(f)$ and a noise term $n(f)$:

$$s_{\text{est}}(f) = g(f) [s(f) + n(f)]$$

From the correlation between $s_{\text{est}}(f)$ and $s(f)$, one can calculate $n(f)$. With $s(f)$ and $n(f)$ known, the information transmission capacity can then be calculated (using the equation for C of a continuous channel with noise).

The measurements derived from these experiments gave a value of 300 bit/s (with a average action potential frequency of 100 /s, this means that each interval between two consecutive action potentials contains on the average 3 bit of information). The measured capacity in spiking neurons is thus about five times lower than the value of 1650 bit/s obtained for non-spiking neurons.

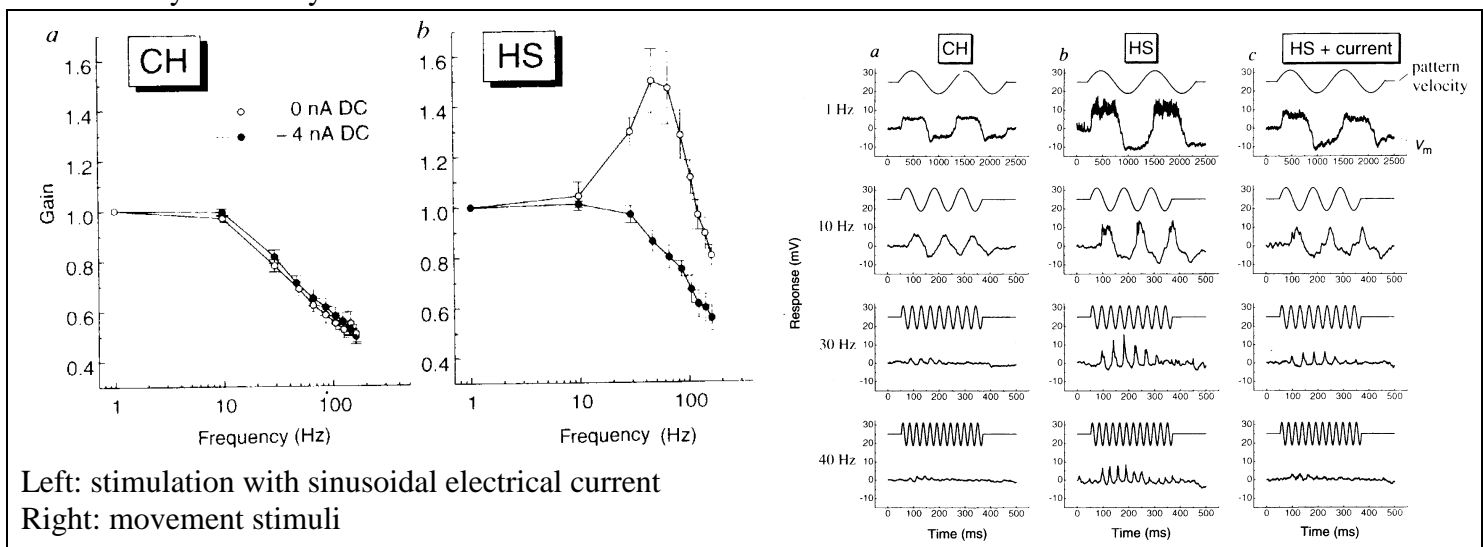
c) Activity in dendrites.

During synaptic transmission between neurons, the action potential in the postsynaptic cell is not initiated in the dendrites, but in the intermediate segment (axon hillock) between the axon and the soma (this is caused by the much higher density of Na channels in the intermediate segment than in dendrites). However, retrograde (backward) electrotonic conduction causes the action potential in the intermediate segment to produce an additional component of depolarization in the dendrite. During the last years it has become clear that, as a consequence of these additional dendritic depolarizations, in many cases also an action potential is then triggered in the dendrites. Until recently the role of this process was not understood. Measurements of the frequency spectrum of two types of non-spiking neurons in the lobular plate of the fly, nl. in HS cells, which have dendrites with fast Na currents, and in CH cells, which have dendrites without fast Na currents, allowed to investigate the role of these Na currents and action potentials in dendrites. Both types of neurons are movement sensitive visual interneurons (tangential cells). They receive input from several hundreds of retinotopically organized elements on their dendrite

tree. The CH cells react only to synaptic input with changes in their steady state membrane potential. The HS cells respond with irregular action potential-like changes, superimposed on graded shifts of the membrane potential.

The membrane potentials in axon and dendrites were measured in both types of neurons during injection in the axon of sinusoidal currents of different frequencies, and the Bode diagrams of the input resistance were constructed. While in CH cells attenuation occurs at frequencies larger than 10 Hz, the spectrum of the HS cells show an important peak between 10 and 100 Hz. When the membrane is hyperpolarized during the experiment using a constant current, so that fast Na currents cannot occur (because of inactivation), no changes are seen in the spectrum of the CH cell, but the peak in the HS cell disappears, so that the Bode diagram of the HS cell becomes similar to the one of the CH cell. This demonstrates that the peak in the HS cell is caused by the Na current.

Similar results were obtained when the sinusoidal current were replaced by sinusoidal movement stimuli for the eye of the fly: the HS cells follow better the faster movements than the CH cells.



These experiments demonstrate that neurons with Na current in the dendrite can react much better to fast (high frequent) changes in their synaptic input. Thus fast Na currents lead to frequency dependent amplification of synaptic signals. This causes amplification of the cellular responses to transient inputs, that otherwise would be attenuated by the passive electrical properties of the dendrite tree.

3. Conclusions: physiological significance of spiking.

Receptors and non-spiking neurons can transmit information in analog form in a frequency range which is limited only by the maximal rate and the uncertainty of the membrane potential changes (charging of the membrane capacity). Receptors receive an enormous amount of information that they have to transmit rather accurately. It thus appears logical that in the receptors (which form the most peripheral part of the transmission channel) mechanisms are used that maximize information transmission capacity: channels with large capacity, eventually using local networks for noise reduction and redundancy reduction (data compression).

The relatively low capacity of spiking neurons is the consequence of the fact that in neurons the information is coded by the time intervals between action potentials. These time intervals are typical of the order of about ten ms: the variation in duration of the individual action potentials does not allow a lower average value of inter spike intervals, since this would reduce the number of distinguishable

intervals, and thus the channel capacity. The high average time interval (duration of a signal) implies that the average number of signals per second, and thus also the channel capacity is relatively small.

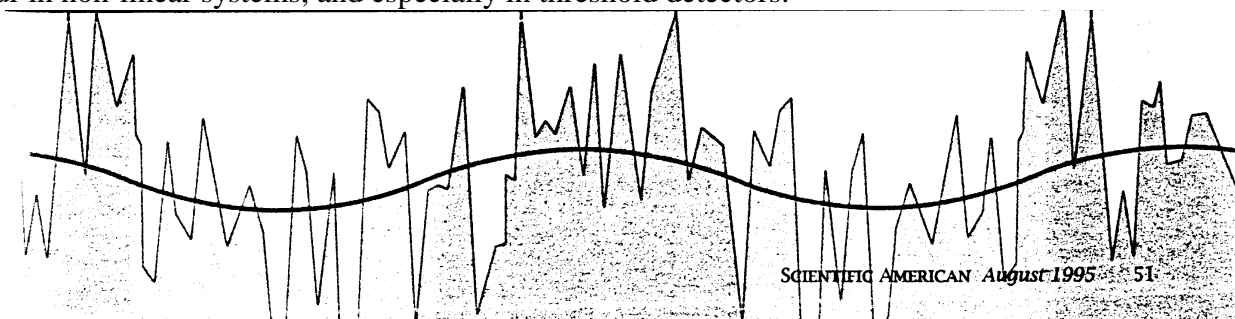
Higher centers such as the visual cortex do not function like a TV screen, which (via its HIFI input channels) presents complete and accurate images, which have to be interpreted by an observer, but these neuronal circuits function themselves as interpreters. Information from the photoreceptors is processed in different stages using parallel processing, in a way that enables to use the smallest possible number of active neurons to yield a representation of the stimuli that is as complete as possible as required for ensuring an adequate response (in general an adequate response does not require all the information in the source). This has the advantage to reduce the volume of information that has to be transmitted per unit of time by individual neurons. The individual neurons can thus have a relatively low information capacity. They however have to transmit the information over relatively large distances. Passive graded electrical signals show important attenuation as function of distance, as a consequence of the electrical cable properties of the cell, and large distances can not be reached without intermediate stages of amplification (e.g. action potentials in nodes of Ranvier). Spiking neurons give the possibility to bridge larger distances, but this occurs at the expense of a decreased capacity. Therefore spiking neurons are most useful for transmission of processed and reduced information over long distances.

Also the occurrence of fast Na currents and action potential-like phenomena in dendrites of some neurons helps to compensate for the effect of electrotonic attenuation of transient inputs. An additional and important function of spiking in dendrites is to produce the stronger depolarizations in the dendrites that are needed for long term potentiation (see LTP).

B. Stochastic resonance.

1. Theoretical background.

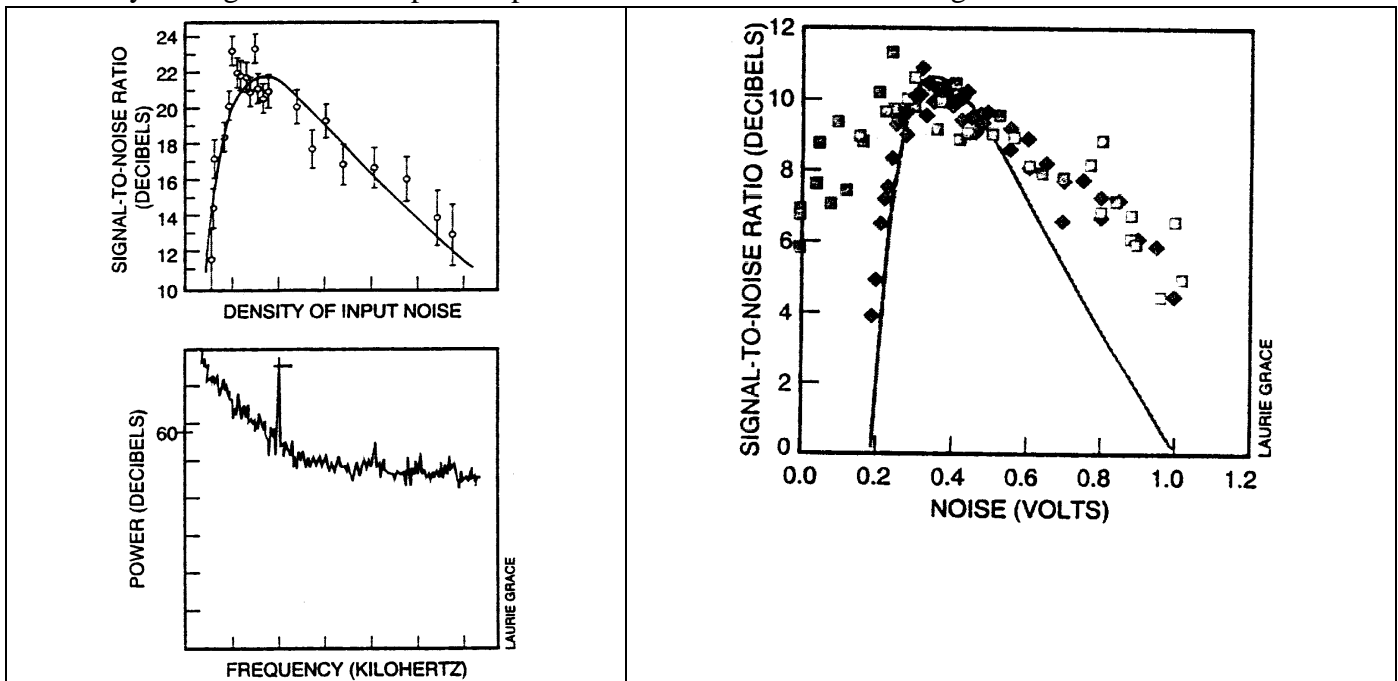
While it was generally accepted that noise reduces the capacity to detect and to distinguish signals, and this way decreases the channel capacity, recent evidence demonstrated that in many cases (from physical systems, such as electronic circuits, ring lasers and SQUIDs (Superconducting Quantum Interference Devices), to biological systems such as neurons in mechano-detection and hearing) the presence of noise improves signal detection. The basis of this effect is the phenomenon of “Stochastic Resonance” that can occur in non-linear systems, and especially in threshold detectors.



When in strongly non-linear systems, such as threshold detectors, the input signal has an amplitude below a certain value (threshold), the amplitude of the output signal is zero. Random noise on top of these small input signals can ensure that once in a while the threshold is reached, and thus that an output signal is triggered. This output signal is however not totally unpredictable: the probability that the threshold is crossed is largest when the input signal (which fluctuates with an amplitude below the threshold!) reaches

its largest value. The crossing of the threshold as a consequence of the combination of signal and noise thus contains information about the signal. Since at very small input signals in absence of noise the threshold will never be crossed, addition of noise thus increases the sensitivity of the system. Since obviously the amplitude of the noise may not be too high, it is clear that there is an optimal noise amplitude at which the system will optimally function.

The information capacity (at a given bandwidth) is determined by the signal to noise ratio. In non-linear systems such as threshold detectors, the signal to noise ratio in function of noise amplitude does not reach its maximum when the noise amplitude goes toward zero, but it is maximal for a certain finite value of the noise. The left figure shows experimental data and the theoretical value of signal to noise ratio in function of the noise amplitude, as well as the power spectrum (obtained in a ring laser experiment). The figure indeed demonstrates that the signal to noise ratio reaches a maximum, and that a narrow signal peak can be clearly distinguished in the power spectrum from a wide band of background noise.



2. Stochastic resonance in biological systems.

a) *Measurement in the mechanoreceptor system of the crayfish.*

The tail of the crayfish contains cells ending on fine hairs (length between 25 and 100 μm) that are specialized in detecting weak (probably periodical) water movements, such as can be produced by movements of the tail of predators in the vicinity. Slight bending of the hair cells triggers action potentials in the afferent neurons. These action potentials are conducted to a ganglion, consisting of a few hundreds of neurons, that integrates the information from different hair cells. The sensorial neurons act as threshold detectors.

To investigate this system, a section of the tail of the crayfish that contains hair cells, the sensorial nerve and the ganglion was isolated. This preparation was mounted on a movable holder in a tissue bath containing physiological solution. The electrical activity of a single neuron was registered using an electrode in the nerve bundle, and the hair cell connected to it was identified. An irregular pattern of nerve discharges was observed during small regular periodical movements of the holder. These discharges were converted (idealized) to standard rectangular pulses, and the power spectrum was measured. The spectra

show a wide background noise in addition to a narrow peak at the frequency of the movement of the holder. From the power spectrum the signal to noise ratio was determined. It could be demonstrated that this sensorial system of the crayfish can detect periodical movements of the holder with a minimal amplitude of the order of about ten nanometer. Subsequently the amplitude of the movement of the holder was made so small that it was merely detectable or undetectable. Then random noise (simulation of the random water movements) was superimposed on top of these very small periodical movements of the holder, and the power spectrum was measured and the signal to noise ratio was determined. The experiment was repeated for different values of the noise amplitude.

The experiments demonstrated that the signal to noise ratio is maximal for a finite non-zero value of the amplitude of the noise (see symbols figure right panel), and thus that introducing a certain amount of noise enhances the sensitivity of the system. The sensitivity of the system is however larger than the theoretically calculated value (continuous line), in the frequency range of the positive slope as well as in the negative slope region of the curve.

The unexpected high values of the signal to noise ratio at high noise intensities are the consequence of the refractory period. At high noise levels the action potential frequency is larger, but since each action potential is followed by a refractory period, the effect of the noise is blocked in the refractory period; this results in a higher signal to noise ratio.

The unexpected high values of the signal to noise ratio at low noise levels is caused by the inevitable internal noise (e.g. electrical noise produced by spontaneous channel openings) in the sensorial system itself, that contributes to the total noise level. Evidence for such an explanation was obtained by testing many different neurons of different crayfishes. A number of them did not show stochastic resonance, and in these cases it could be demonstrated that the internal noise levels were very high. When the internal noise is already so large that the optimal point is reached or passed, addition of external noise cannot cause further improvement of the signal to noise ratio.

b) Measurement of sensitivity and discrimination power of human hearing.

The remarkable possibility of the human auditory system to discriminate the signals of a conversation from the noise in a noisy environment is well known. Experiments were described to determine the perception threshold of audio signals of a particular frequency in presence of different noise levels. Also these experiments demonstrated that the detection threshold is minimal in presence of a certain amount of noise. The exact shape of the curve can differ from person to person, and is dependent on age and individual sensitivity of hearing.

c) Stochastic resonance in the human muscle spindle.

Electrical activity of individual muscle spindle afferents of the extensors of hand muscles in the radial nerve of human subjects was registered during passive rotation of the fist with sinusoidal signals of small amplitude. At the same time, small muscle stretches were imposed by means of a tendon stimulator, using random noise signals as input. The experiment was repeated for different values of the average noise amplitude. The signal to noise ratio was measured from the power spectrum, as the ratio of the area of the signal peak to the average amplitude of the background noise at the frequency of the input signal.

For six of the eight afferents measured, the signal to noise ratio increased with increasing noise amplitude, till a maximal value was reached; a further increase of noise amplitude then resulted in a decrease of the

signal to noise ratio. The phenomenon remained present when fusimotor activity was eliminated. The receptor - afferent nervous system of the spindle thus shows stochastic resonance.

There is also evidence of fully tuneable stochastic resonance in the response of afferents from Golgi tendon organs and the primary and secondary endings of muscle spindles in the soleus muscle of the cat to imposed muscle length changes.

d) Stochastic resonance in tactile sensitivity.

The skin of human subjects was stimulated using a stimulus protocol with random alternation of absence of stimulation and of a stimulus with amplitude of about the normal sensitivity threshold. By asking each time whether the subjects felt a stimulus, the stimulus threshold was determined. The experiment was repeated with stimuli with amplitude below the sensitivity threshold, which were superimposed with random noise of different amplitudes. It was demonstrated that the addition of small amounts of noise enhanced the sensitivity of the system.

Elderly people often begin to lose their balance and grow wobbly, in part because their nervous system becomes less sensitive to changes in foot pressure whenever they lean one way or another. Collins investigated the possibility that stochastic resonance could help people with balance problems. He built a platform with hundreds of randomly vibrating small nylon rods on which volunteers stood barefoot with eyes closed. The rod movement was first tuned so that the participants did no longer feel their vibrations. He found that in this conditions the 16 volunteer seniors swayed much less. When the vibrations were perceptible no benefits were seen. These experiments indicate that stochastic resonance can improve stability of posture in elderly people. Following up on this finding, Collins developed vibrating gel insoles for shoes. When subjects stood on these prototypes they swayed even less than they did on the platform. It was also shown that mechanical noise stimulation improves vibration and tactile perception in diabetic patients with moderate to severe neuropathy.

e) Stochastic resonance in potential dependent ion channels.

The power spectrum of the ionic current flowing through alamethicine channels was measured at constant potential. A small sinusoidal potential component was imposed, together with random noise, and power spectrum of the channel current was measured, from which the signal to noise ratio was obtained. The experiment was repeated for different values of the average noise amplitude. The signal to noise ratio was plotted in function of the noise amplitude. The curve shows a maximum: adding a small amount of noise thus improves the information capacity of the channel.

f) Stochastic resonance in a hippocampal CA3-CA1 model for memory recall.

The CA1 cells in the hippocampus are involved in memory. They receive input through Schaffer Collaterals (SC) from CA3 cells and by Perforant Path fibers (PP) from layer III of the Entorhinal Cortex (EC). The CA3 network spontaneously generates rhythmic activity that is quite irregular, and which causes membrane fluctuations in CA1. The input to CA1 from the PP is too weak to discharge CA1. Using a hippocampal network model, it was demonstrated that CA1 cells can be fired by subthreshold PP signals when they are accompanied by signals from CA3 (serving as noise), demonstrating stochastic resonance in the model. The authors propose a memory recall model based on stochastic resonance, and

discuss the possibility that memory recall in the hippocampus is based on such a process of stochastic resonance.

3. Significance of stochastic resonance in biological systems.

The response of sensory receptors is almost always non-linear (see e.g. the law of Weber - Fechner). In addition, the conversion of generator or receptor potential to action potentials is accompanied by a threshold phenomenon. In principle, all these systems are thus susceptible to stochastic resonance. Since the receptors operate in an environment with noise, and their own activity also introduces some noise, the phenomenon of stochastic resonance can eventually contribute to a considerable extent to enhancement of the sensitivity and information capacity.

Different diseases are due to an increase of the thresholds in receptors or neurons. Elderly persons often have equilibrium problems as a consequence of decreased sensitivity of proprioceptors or pressure receptors, or show a decreased auditive or tactile sensitivity. In these cases, addition of a small amount of noise could eventually improve the sense of equilibrium, hearing or tactile sensitivity via the phenomenon of stochastic resonance.

References.

- Bialek W, Rieke F, De Ruyter van Steveninck RR, Warland D. (1991). Reading the neural code. *Science* 252: 1854 -1857.
- Bialek W, Rieke F. (1992). Reliability and information transmission in spiking neurons. *TINS* 15: 428 - 434.
- Boring EG. Gustav Theodore Fechner. In "The world of mathematics" Newman JR(ed). p1123. Tempus Books. (1988).
- Berzakov SM, Vodyanoy J. (1995). Noise-induced enhancement of signal transduction across voltage-dependent ion channels. *Nature* 378: 362 - 364.
- Collins JJ, Imhoff TT, Grigg P. (1996). Noise-enhances tactile sensors. *Nature* 383: 770.
- Cordo P, Inglis JT, Verschueren S, Collins JJ, Merfeld DM, Rosenblum S, Buchley S, Moss F. (1996). Noise in human muscle spindles. *Nature* 383: 769 - 770.
- De Ruyter van Steveninck RR, Bialek W. (1988). Real-time performance of a movement-sensitive neuron in the blowfly visual system: coding and information transfer in short spike sequences. *Proc Roy Soc London B*234: 379 -414.
- De Ruyter van Steveninck RR, Laughlin SB. (1996). The rate of information transfer at graded - potential synapses. *Nature* 379: 642 - 645.
- Douglas JK, Wilkens L, Pantazelou E, Moss F. (1993). Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance. *Nature* 365: 337 - 340.
- Douglas RJ, Martin KAC. (1996). The information superflyway. *Nature* 379: 684 - 585.
- Eckhorn and Querfurth (1985). Information transmission by isolated frog muscle spindle. *Biol. Cybern.* 52: 165-176.
- Garver W, Moss F. (1995). Detecting signals with noise. *Sc Am* 273 (aug): 84 - 87.
- Haag J, Borst A. (1996). Amplification of high - frequency synaptic inputs by active dendritic membrane processes. *Nature* 379: 639 - 641.
- Maddox J. (1994). Bringing more order out of noisiness. *Nature* 369: 271.
- Moss F, Wiesenfeld K. (1995). The benefits of background noise. *Sc Am* 173 (aug): 50 - 53.
- Priplata A, Niemi J, Salen M, Harry J, Lipsitz LA, Collins JJ (2002). Noise-enhanced human balance control. *Phys Rev Lett.* 89(23):238101.
- Wiesenfeld K, Moss F. (1995). Stochastic resonance and the benefits of noise: from ice ages to crayfish and squids. *Nature* 373: 33 - 36.