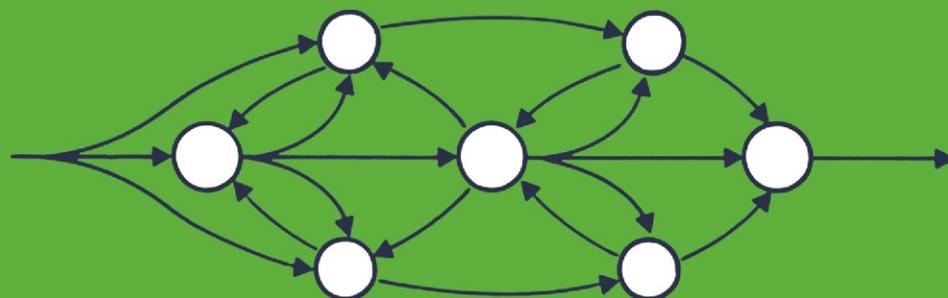
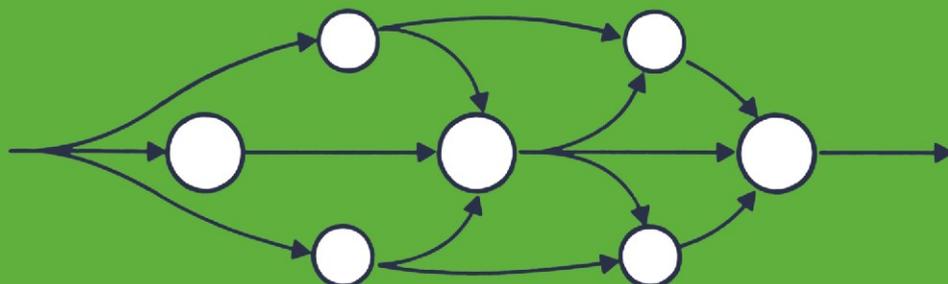


Brain Theory

Edited by
Günther Palm and Ad Aertsen





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Reactive and creative system differing in absence or presence of closed loops. From P. Johannesma, this Volume, page 34, Figure 6.

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From Synchrony to Harmony: Ideas on the Function of Neural Assemblies and on the Interpretation of Neural Synchrony

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1 Introduction

Point of departure are experimental data acquired by simultaneous recording of the activity of a number (2–16) of individual neurons during presentation of a sensory stimulus. The area under investigation is the auditory midbrain (Torus semicircularis) of the immobilized grassfrog (*Rana temporaria L.*). The sensory stimuli are both artificial (noise, tones and clicks) and natural sounds (vocalizations and environmental sounds). The goal of investigation is an insight into the neural representation of the sensory environment.

In a first approach the multi-unit recording is regarded as a set of separate recordings of single neurons. Second order correlation of auditory stimulus and neural events leads to the functional description of each neuron in terms of its spectro-temporal sensitivity (STS) in relation to a given stimulus ensemble. Making use of nonlinear system theory (i.e. Wiener functions and Volterra kernels) it turns out that for a fraction of the neurons the STS can be normalized with respect to the stimulus ensemble (SE). In this case a stimulus-invariant spectro-temporal receptive field (STRF) is defined and measured for the neuron (Aertsen and Johannesma 1981a,b, Eggermont et al. 1983a). If the SE is considered as a distribution of signals in acoustic space then the receptive field forms the subspace of this acoustic space where the neuron is most sensitive; its "focal zone" (Scheich 1977, Johannesma and Aertsen 1982). When, to a good approximation, a stimulus-invariant STRF does exist the focal zone of the neuron in acoustic space forms an inherent property of that neuron independent of sensory context. For many neurons, however, in the frog's auditory midbrain the STS for different stimulus-ensembles cannot be normalized into a unique STRF. This implies that, at least using the known methods of system theory, the concept of single unit receptive field (SURF) loses its well-defined and unique features as a functional characteristic of the sensitivity of a neuron for sensory stimuli (Johannesma and Eggermont 1983).

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In a second approach the multi-unit recording is considered as the observation of dynamic patterns of activity from a set of neurons (Gerstein 1970, Gerstein and Michalski 1981). As such it may be the representation of the activity of a neural assembly (Hebb 1949). The interest now focuses on analysis and interpretation of neural synchrony, synchrony being defined as the spatio-temporal form of the neural activity pattern. To what extent are the events of different neurons correlated? Only as far as can be explained by the structure of the stimulus in combination with the single unit receptive fields or is there an additional correlation caused by neural interaction? This aspect of spatio-temporal correlation (coherence) is thought to be generated by a population of neurons interacting cooperatively (assembly) under the given environmental situation (Braitenberg 1977, Palm 1982). Recently investigations have been made of the characteristics of synchrony of firing in multi-unit recordings from the torus semicircularis of the frog, again under a variety of stimulus conditions. It appeared that neural correlation, i.e. after application of a stimulus normalization procedure, essentially based on an additive model, again may be stimulus-dependent. In a number of cases the neural correlation turns out to be stimulus-variant, possibly context-sensitive (Eggermont et al. 1983b, Epping et al. 1984).

One way to put these results together would be to attach "labels" to the SURF and the neural correlation, the label specifying the particular stimulus context in which the neuron characteristic applies. This "solution", however, from the point of view of modeling the central nervous system is far from attractive. As an alternative we propose the hypothesis that the stimulus-invariance of both the SURF and the neural correlation are intrinsically interconnected. In fact, they both are manifestations of one underlying mechanism: the neurons being elements in an interacting population, possibly giving rise to neural assemblies. From this point of view the activity of the neuron under experimental observation is, apart from the direct influence of stimulus and local connectivity at least partially influenced by the activity pattern in the (non-observed) remainder of the network, this remainder in turn is (at least partially) influenced both reciprocal and by direct stimulus influence. The net effect would be an apparent stimulus control of various neural characteristics like SURF and neural correlation, without, however, the necessity to assign this overall stimulus effect to a specific neuron, connection or local circuit. A strategic consequence of this hypothesis would be that for a fruitful approach of the question of stimulus-variance of the SURF and neural correlation both aspects should be addressed in an integrated manner: stimulus-event correlation on its own, as well as event-event correlation on its own will only lead to a multitude of images, each one with its associated context of "validity". It is in the interrelation of stimulus-event relations and neural interaction that meaningful models, i.e. with a functional meaning associated to them, may hopefully emerge.

The composition of this exposition is as follows. In Sect. 2 experimental data from multi-unit recordings are presented as well as some transformations of these data. General ideas from system theory are given in Sect. 3 and the dif-

ference between reactive and creative systems is introduced. In Sect. 4 equations for neural interaction and synaptic plasticity are summarized. Some concepts and speculations with respect to perception, brain and behaviour are presented in Sect. 5. Finally in Sect. 6 an experimental procedure is proposed for the investigation of neural assemblies in relation to perception.

The main theme of this presentation is a discrimination of two ways of analysis and interpretation of multi-unit recordings. On one hand the “syntactical” approach as introduced by Gerstein and coworkers relating structure and process of the nervous system. On the other hand the “semantical” method as described before by Johannesma (1981) and Johannesma and Aertsen (1982) trying to connect process and function of the nervous system. The contribution of Aertsen et al., in this Vol. and this contribution are intended as integrated complementary views on the treatment of multi-unit recordings.

2 Registration and Representation of Neural Activity Patterns

Experimental data as recorded in the auditory midbrain of the immobilized grassfrog are yet far from a complete observation of activity patterns of a neural population. At this moment we can present the results of simultaneous recordings of up to four neurons under different stimulus conditions. These data are insufficient for investigation of the actual role of neural assemblies but, provided neural assemblies do occur in this region of the brain of the frog, they may well form the base for a delineation of the questions which have to be treated if large scale multi-unit recordings become available. For a description of experimental methods see Eggermont et al. (1983c) and for data analysis and results Epping et al. (1984).

Given the measurement of the simultaneous activity of four neurons during presentation of a sequence of tones with different frequencies, the first goal is the presentation of these data in such a way that the identity of the neurons is preserved. This is realized by using colour as the code for identification of each neuron. The resulting display, the “neurochrome”, gives in an integrated way the activity of the neurons (colour-dots) as function of time (horizontal) and the number of the tonal stimulus (vertical). The results for a quadruple recording are depicted in Fig. 1. In order to prevent sequential effects of the tonal series the frequencies were presented in a pseudo-random order. Rearrangement of the responses of the neuron with respect to increasing/frequency results in the ordered neurochromes shown in Fig. 2. The results show clearly that the time structure of the response to tones depends on the frequency of the tone and that this dependence is different for different neurons. It should be noted that the four neurons were recorded on one micro-electrode, i.e. they were in close proximity.

The neurochrome contains the full information concerning the stimulus-associated neural activity patterns as far as observed through the multi-unit

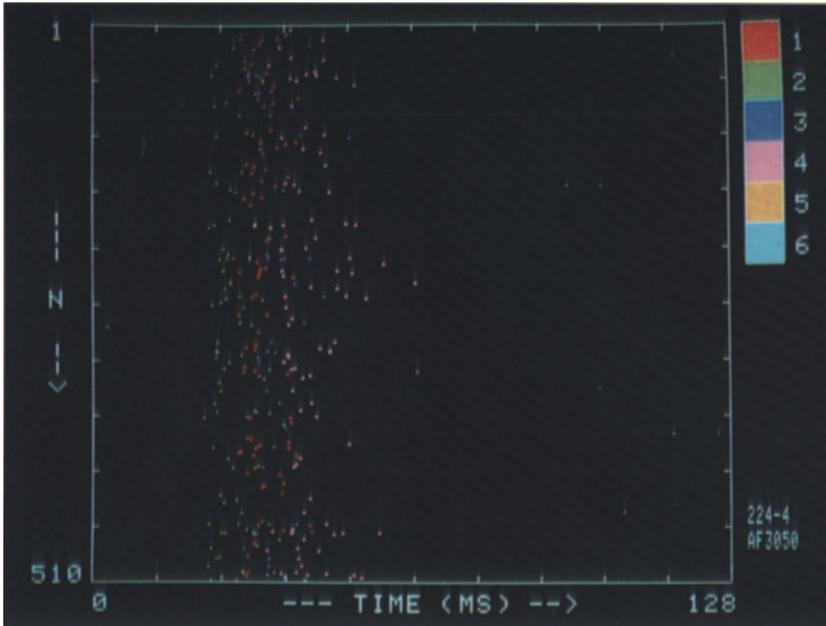


Fig. 1. Chromatic representation of the simultaneous measurement of action potentials of four neurons in the Torus Semicircularis of the grassfrog during tonal stimulation. *Horizontal axis* represents time, *vertical axis* the sequential index of the tones which were presented in random order

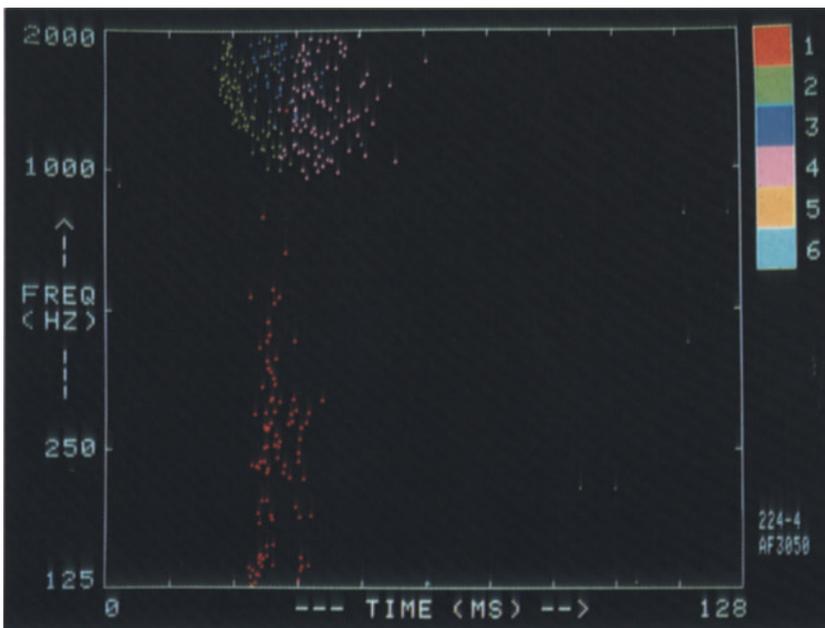


Fig. 2. Chromatic representation of the simultaneous measurement of action potentials of four neurons in the Torus Semicircularis of the grassfrog during tonal stimulation. *Horizontal axis* represents time, *vertical axis* the frequency of the tone. Note different response areas of different neurons

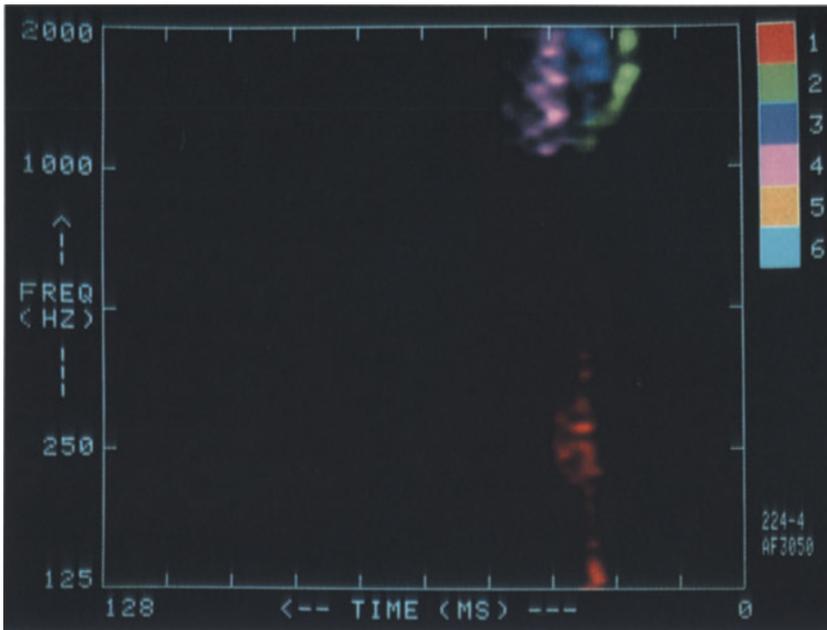


Fig. 3. Chromatic representation of spectro-temporal sensitivity of four neurons in the Torus Semicircularis of the grassfrog recorded simultaneously during tonal stimulation

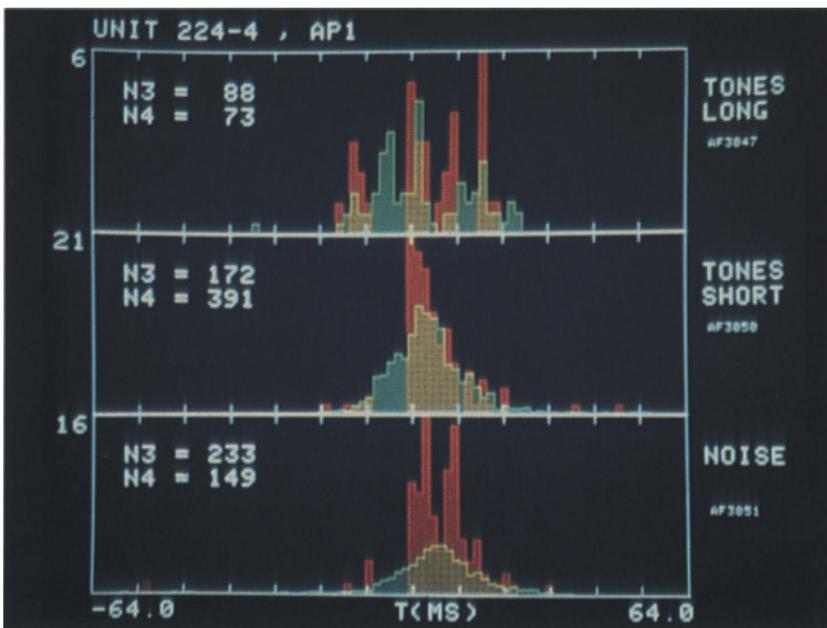


Fig. 4. Simultaneous and nonsimultaneous cross-coincidence histograms of a pair of neurons in the Torus Semicircularis of the grassfrog under different stimular conditions

recording (SAMUR). For the evaluation of the SAMUR two ways are open: a “syntactical” and a “semantical” analysis. The syntactical one concentrates upon the form of the activity patterns by means of analysis of the correlation of activity of different neurons: event-event correlation. The semantical approach is directed toward the meaning of the neural activity through a study of the association of sensory stimulus and neural action potentials: stimulus-event correlation. In both points of view action potentials as generated by a single neuron are considered as events: irreducible elements for representation of sensory stimuli. Form and size of an action potential are irrelevant, only when and where it occurs is significant.

2.1 Semantic Analysis of Neural Activity

For a given neuron the action potentials indicate the selection of a stimulus out of the ensemble of stimuli presented to the animal. This selection can be investigated by constructing the pre-event stimulus ensemble (PESE) which forms a subset of the stimulus ensemble (SE).

The characteristics of the PESE in relation to the SE represent the stimulus-selective function of the neuron (Johannesma 1972, 1980, 1981, Johannesma and Aertsen 1982, Eggermont et al. 1983c). A plausible way to determine these characteristics is to perform a spectro-temporal averaging of the PESE. The result of this procedure is the spectro-temporal sensitivity (STS) of the neuron (Aertsen and Johannesma 1981a). In Fig. 3 the STS is given for different neurons showing clearly that neurons which are spatial neighbours in the auditory midbrain do not have to be spectro-temporal neighbours in acoustic space: topography does not appear to be preserved.

For the definition of a single unit receptive field (SURF) the characteristics of the PESE should be normalized with respect to the SE and then result in a stimulus-invariant spectro-temporal sensitivity. The theoretical aspects and mathematical equations of this procedure are given in Aertsen and Johannesma (1981a) and comparative results for tonal and natural stimuli are presented in Aertsen and Johannesma (1981b) and Johannesma and Eggermont (1983) and Aertsen et al. (this Vol.).

The conclusion from the experimental data is that for a considerable fraction of the neurons in the auditory midbrain of the immobilized grassfrog the normalized spectro-temporal sensitivity does depend on the choice of the stimulus ensemble. A stimulus invariant single unit receptive field does not anymore exist in this central region of the frog’s brain. A plausible explanation for this result is the presence of not only afferent connections to these neurons: the neuron forms part of a system where there is no longer an exclusive forward stream of information, lateral and recurrent interaction between neurons may become influential. We will return to this point in Sect. 4.

2.2 Syntactic Analysis of Neural Activity

In this approach the action potentials are again considered as events: irreducible elements for communication among neurons. A neural activity pattern is considered as a parallel series of point processes or “marked point process” (Snyder 1975). The focus of interest is now the internal structure of this marked point process. In a qualitative way this amounts to a study of coincidences of events of different neurons shown in Fig. 1. For a systematic approach we may search for the structure of each neural spike train (singlet), that of each pair of neurons (doublet), that of three neurons at a time (triplet) etc.

Some examples of pair correlations are given in the coincidence histograms in Fig. 4. In order to get an impression of the interaction giving rise to this correlation we compare simultaneous and non-simultaneous cross coincidence histograms. As can be seen in Fig. 4 the form of the cross-coincidence does depend on the stimulus-ensemble which has been used. For certain classes of models of the neural interaction, essentially limiting this interaction to a non-reciprocal form, it appears possible to compute expressions for the normalization of the simultaneous coincidence by the non-simultaneous one (van den Boogaard et al. 1985). However both experimental data as recorded in frog’s auditory mid-brain (Eggermont et al. 1983c) and the theoretical considerations exposed in Sect. 4 indicate that in general the pair correlation will be stimulus-dependent.

A further problem for the systematic computation of multiple correlation is the fast increase of the number of correlations of multiplets of order k as function of the number N of neurons which have been observed simultaneously. As an illustration Table 1 gives these numbers for $N = 1 - 8$. Even if the computer is able to do all necessary calculations within an acceptable time, the number of resulting graphs or displays will exceed the cognitive and associative capacity of the observer. Moreover coincidences or doublets can be shown in a histogram, triplets in an event-display (snowflake) but for quadruplets and higher multiplets no form of display is known. This further limits the acquisition of insight by a human observer.

An alternative evaluation of the form of multi-unit activity patterns has been proposed by Gerstein and coworkers: “gravitational clustering”. The grav-

Table 1. Number of correlation functions of order k for a group N neurons

$\binom{N}{k}$	$k = 1$	2	3	4	5	6	7	8
$N = 1$	1							
2	2	1						
3	3	3	1					
4	4	6	4	1				
5	5	10	10	5	1			
6	6	15	20	15	6	1		
7	7	21	35	35	21	7	1	
8	8	28	56	70	56	28	8	1

itional clustering method influences location of the neurons in a hypothetical space according to their synchrony of firing. See the contribution of Aertsen et al. in this Vol. for a detailed description of concepts, methods, results and for references. However, also with this approach some problems do exist. Up till now only pair correlations have been taken into account in the clustering algorithm; how to include multiple correlations? The dimensionality of the hypothetical neural space is apriori equal to N ; even if by the clustering the dimensionality reduces, it may well remain larger than three, leading to serious representational difficulties.

2.3 Conclusions

The conclusions from the experimental point of view for central regions in sensory parts of the brain are:

1. Relation of sensory stimulus and neural events depends on choice of stimulus-ensemble: a stimulus-invariant single unit receptive field in many cases does not exist.
2. Correlation of activity of different neurons depends on stimulus ensemble.
3. No general method exists for the analysis and interpretation of stimulus associated multi-unit recording.

3 System Theory

In order to treat the stimulus-associated multi-unit recording (SAMUR) some general ideas on typology of systems are exposed. The brain may be considered as a multi-input/multi-output system composed of nonlinear stochastic elements. Sensory stimuli, e.g. sound, form the input, behavioural activity is the output. Two types of global feedback are present: internal and external. Internal receptors monitor the behavioural activity (proprioception) and behavioural acts change the external environment and/or the position of the animal in this environment both leading to changes in the sensory stimulus. A sketch is given in Fig. 5.

For a more detailed characterization of the brain as a system it is relevant to make a distinction into “*reactive*” and “*creative*” systems. We assume that the system consists of N elements each characterized by a state variable u_n . Neglecting for the moment the stochastic aspects, the system may be represented by a set of N -coupled nonlinear differential equations. Now the relevant point is if by a well-chosen labeling of the elements the system may be drawn in such a way that there exist only forward influences. If this possibility does exist the system is defined as “*reactive*”. The mathematical description then becomes

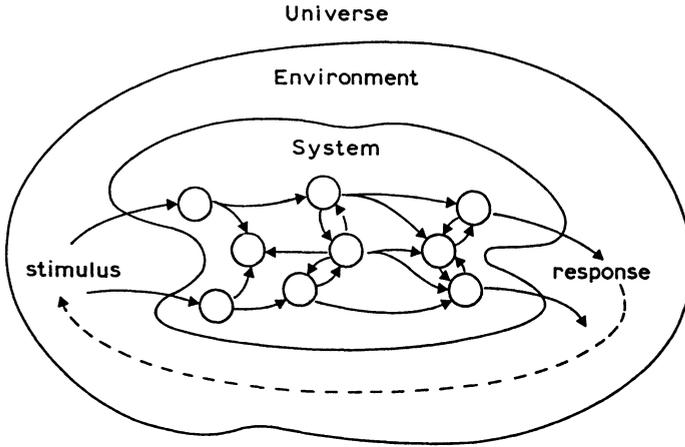


Fig. 5. Sketch of a system as a set of elements and relations in interaction with its environment and embedded in a universe

$$\begin{aligned} \frac{d}{dt}u_n &= f_n(x; u_1, \dots, u_n) \quad n = 1, N \\ y &= g(x; u_1, \dots, u_N) \end{aligned} \quad (3.1)$$

where x = input, y = output, and u_n = state of element n .

If such a unidirectional description does not apply because of the presence of closed loops caused by mutual interaction and/or recurrent connections, then the system is defined as “creative”. The mathematical description cannot be reduced to the form given in Eq. (3.1) but reads instead

$$\begin{aligned} \frac{d}{dt}u_n &= f_n(x; u_1, \dots, u_N) \quad n = 1, N \\ y &= g(x; u_1, \dots, u_N) \end{aligned} \quad (3.2)$$

Illustrations of the structure of a reactive and a creative system are given in Fig. 6. The difference between Eq. (3.1) and Eq. (3.2) is solely in the index n or N for the differential equations; however, this has far reaching consequences. Equation (3.1) can be written in a more explicit form

$$\frac{d}{dt}u_1 = f_1(x; u_1) \quad (3.1a)$$

$$\frac{d}{dt}u_2 = f_2(x; u_1, u_2) \quad (3.1b)$$

$$\frac{d}{dt}u_3 = f_3(x; u_1, u_2, u_3) \quad (3.1c)$$

Equation (3.1a) is a first-order non-homogeneous nonlinear differential equation. Given the forcing function $x(t)$ and the initial value of $u_1(t)$ then under some restrictions for the function f_1 , e.g.

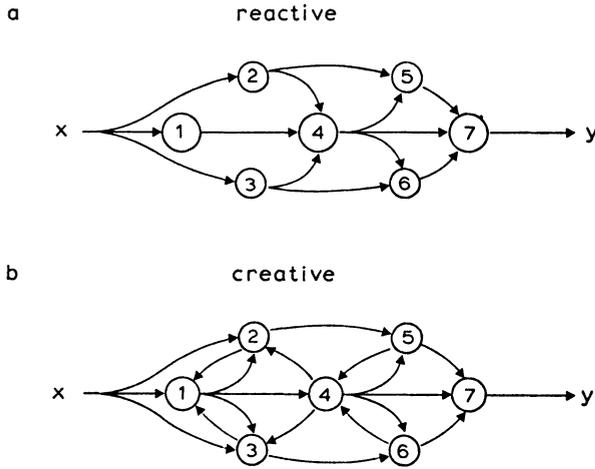


Fig. 6. Reactive and creative system differing in absence or presence of closed loops

$$f_1(x; u_1) = a(x) + b(u_1)$$

$$f_1/x; u_1 = c(x) \times d(u_1)$$

or

with again some restrictions on $b(u_1)$ and $d(u_1)$ Eq. (3.1a) can be solved in the form

$$u_1(t) = F_1[x(s), s < t] := F_1[x] . \tag{3.3a}$$

Substitution of Eq. (3.3a) into Eq. (3.1b) leads to

$$\frac{d}{dt}u_2 = f_2(x; F_1[x], u_2) := g_2(H_2[x]; u_2) .$$

In an analogue way and under analogue conditions this equation can be solved with the result

$$u_2(t) = F_2[x] . \tag{3.3b}$$

This approach can successively be applied to the complete set of Eqs. (3.1). However, because of its recursive form, such a sequential solution procedure cannot be applied to the set of Eqs. (3.2).

The general solution for the reactive system characterized by Eq. (3.1) has the form

$$u_n(t) = F_n[x(s), s < t; u_m(0), m \leq n] \tag{3.3}$$

indicating that the state of element n depends on the previous input and on the initial state of element n and of the preceding elements. The form of $b(u)$ or $d(u)$ determines if the influence of the initial state decays as time progresses. If this is the case, then Eq. (3.1) can be rewritten in an integral form such that each state variable u_n as well as the output y can be expressed as a sum and approximated by a finite sum of weighted integrals of power functions of the input x : the Volterra expansion.

$$u_n(t) = \sum_{m=0}^{M(n)} V_{nm}[x;t] \quad (3.4)$$

where

$$V_{nm}(t) = \int ds_1 \int \dots \int ds_m v_{nm}(s_1, \dots, s_m) \prod_{l=1}^m x(t - s_l)$$

and an analogous expression applies to the output $y(t)$. Equation (3.4) is the Volterra expansion of the dependence of state variable $u_n(t)$ on the input $x(t)$. The Volterra kernels $v_{nm}(s_1, \dots, s_m)$ represent the m^{th} degree dynamical dependence of $u_n(t)$ on $x(t)$.

If the system is reactive, then Eq. (3.4) applies and the relation of internal variable u_n with stimulus x as represented by v_{nm} can be investigated by means of correlation functions C_{nm} defined by

$$C_{nm}(s_1, \dots, s_m) = \int dt u_n(t) \prod_{l=1}^m x(t - s_l). \quad (3.5)$$

The multivariate function C_{nm} represents the correlation of the state variable $u_n(t)$ with the m^{th} -order product function of the stimulus $x(t)$. An essential requirement, usually not fulfilled by extracellular recordings, is that the state variable can actually be observed. In fact, the application of Eq. (3.5) requires simultaneous, intracellular multi-unit recordings. In the sequel we will proceed as if these recordings were already available.

In case the stimulus is taken as the realization $\underline{x}(t)$ of a Gaussian white process then the expected value of the functional C_{nm} is related simply to the Wiener kernels w_{nm} . For systems of known finite order $M(n)$ the set of Wiener kernels $w_{nm}(m = 1, M(n))$ is related unequivocally to the set of Volterra kernels $v_{nm}(m = 1, M(n))$ (Aertsen and Johannesma 1981a). However, accurate measurement and computation may be difficult if $M(n) \geq 4$. An important property of reactive systems is that each component $u_n(t)$ of the state variable $\mathbf{u}(t)$ can be analyzed separately with respect to its relation to the stimulus. Moreover Eq. (3.3) or more explicitly Eq. (3.4) indicate that the correlation between different components of the state variable is completely determined by the correlation of both components with the stimulus.

As a general conclusion it follows that reactive systems are solvable with respect to their characteristics and predictable with respect to their behaviour. The trajectories of their state variable are always regular and relax toward a single stable point in state space. In general, but not necessarily for each intermediate step, more reliable measurement and more elaborate computation will result in more precise knowledge concerning the system.

For creative systems the situation is quite different. For these systems we assert the following without proof (for reference, however, see Guckenheimer and Holmes 1983). The trajectory of the state variable $u(t)$ may, and probably will, show autonomous dynamics: attracted by one or more quasi-stable points or regions it may behave quasi-periodically or show chaotic behaviour

determined by strange attractors. If parameters of the system change, even slightly, during the observation, catastrophic changes in behaviour may occur. Parameter estimation and trajectory prediction cannot be derived anymore from separate analysis of individual components $u_n(t)$ of state variable $\vec{u}(t)$; correlation between different components u_n and u_m of the state variable is not primarily determined by their correlation with the stimulus. As a consequence the system should be analysed using specific model assumptions, based upon knowledge concerning development, structure and function of the system.

Some general remarks on the description of systems are relevant for the study of information processing in the nervous system. For any system three different aspects or levels are characteristic: *structure*, *process* and *function*. The structure of a system is the time invariant material base for the physico-chemical process associated with its internal dynamics and induced by influences from the environment (input) exerting again effect on this environment (output).

In this description reactive systems may also be named *heteronomous* systems: their behaviour is essentially determined by their input. On the other hand creative systems incorporate considerable *autonomous* aspects: their behaviour is only partly determined by the influences of the environment and the effect of this input depends on the present state of the system. In mathematical terms this follows from the irreducible form of Eq. (3.2). In physiological terms it implies the disappearance of the (stimulus invariant) receptive field.

In order to find a generalization for the receptive field for creative neural populations a fourth aspect only present in certain type of systems has to be considered. *Productive* or *throughput* systems which are evolved or designed primarily for the transformation of input into output, e.g. digestive system, are internally interesting mainly as far as there is relation with the input-output function. However, *cognitive* or *representational* systems, e.g. the visual system, not only have an input-output function, e.g. oculo-motor behaviour, but also create an internal image of the external world. For study of a representational system we should add *interpretation* as a fourth aspect to the system. This aspect is less objective than the other ones. Structure and process can be studied on a system in isolation, function is related to the interaction of system and environment, interpretation depends on the frame of reference of the observer. No interpretation can be given to a system of natural or artificial intelligence where there does not exist a sufficient overlap of (mental) images between subject and object. This does apply to computers, brains and languages.

The different aspects of a cognitive system are shown in Table 2.

Note that the present exposition was fundamentally based on the availability of adequate observations of the state variables u_n . As already stated this condition generally is not fulfilled in the context of electrophysiology. As such this framework should be regarded as an idealized view, important connections with experimental practice still are missing.

Table 2. Aspects of cognitive system

Interpretation	= Internal image of environment	Representation
Function	= Interaction with environment	Transformation
Process	= Physico-chemical activity	Output
Structure	= Material substrate	Input
		Variables
		Parameters
		Relations
		Elements

4 Neural Interaction

In order to relate these general notions on representational systems to the central nervous system and to the analysis and interpretation of multi-unit neural recordings a formal description is given for neural interaction. The neurodynamical equations for a neural population with time-invariant parameters are in a compact form given as follows (Johannesma and van den Boogaard 1985):

$$|U\rangle = |V\rangle + W * |z\rangle \quad (4.1a)$$

$$P(\langle z|\Delta t|U\rangle) = \Lambda^{-1} \exp\langle z|U + R\rangle \quad (4.1b)$$

$$\Lambda = \sum_{\langle z|} \exp\langle z|U + R\rangle \quad (4.1c)$$

where

$\langle \cdot |$ indicates a bra-vector

$|\cdot\rangle$ indicates a ket-vector

$*$ indicates temporal convolution

$V_k(t)$:= sensory input to neuron k at time t

$U_k(t)$:= generating variable of neuron k at time t

$z_k(t)$:= action-variable of neuron k at time t

R_k := spontaneous activity level of neuron k

W_{kl} := synaptic connectivity from neuron l to neuron k

$P_k(z_k|\Delta t|U_k)$:= probability that neuron k generates an action-potential between t and $t + \Delta t$ given that its generator potential assumed the value U_k at time t .

$P(\langle z|\Delta t|U\rangle)$:= probability that activity pattern at $(t, t + \Delta t)$ equals $\langle z|$ given the state of the generator potential equals $|U\rangle$ at time t .

W := connectivity matrix.

A sketch of the signal processing in two neurons according to Eq. (4.1) is given in Fig. 7. Linear spectro-temporal integration of action potentials in-

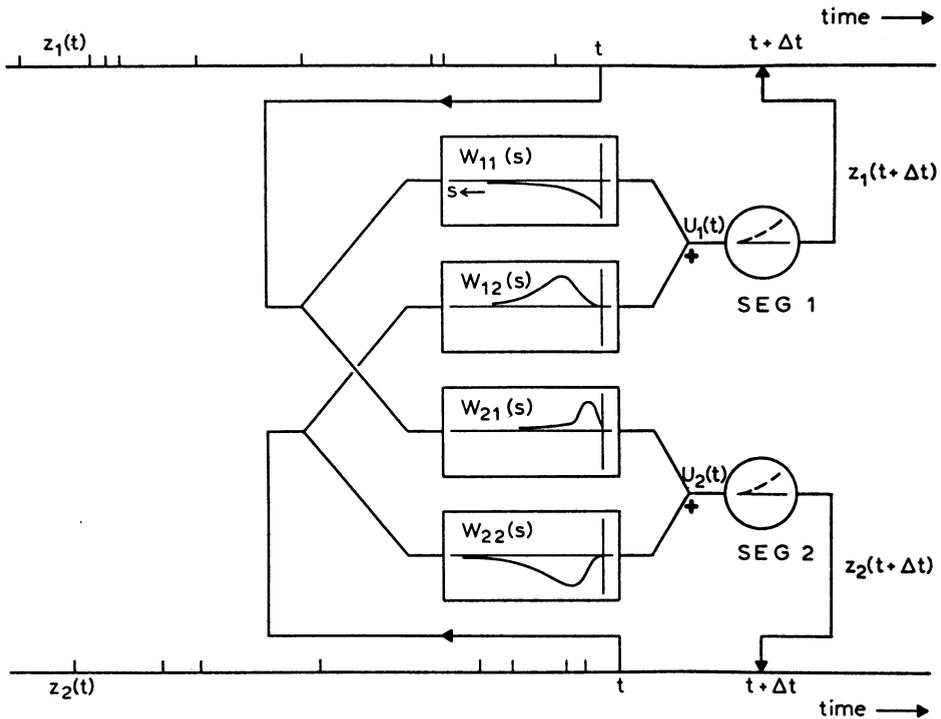


Fig. 7. Signal processing in neural interaction. Incoming sequences $z_l(t)$ of action potentials are temporally integrated and spatially summated into the generator potential $U_k(t)$ which again in a stochastic way creates the action potential $z_k(t + \Delta t)$. *SEG* indicates the stochastic event generator. (From Johannesma and van den Boogaard 1985)

duces the generator-potential, which in a local, nonlinear stochastic way again generates the action potentials.

Since the generator potential in neuron k exerts only an influence on the probability of spike generation in the same neuron it follows that the conditional probability of generation of an activity pattern factorizes in the product of conditional probabilities of the individual action potentials:

$$P(\langle z | \Delta t | U \rangle) = \prod_k P_k(z_k | \Delta t | U_k). \quad (4.2)$$

Under certain conditions for synaptic connectivity W the generator variable $|U\rangle$ may be considered as the state variable of the neural system forming the base of its dynamics. The partition function $\Lambda(|U\rangle)$, given by Eq. (4.1c), is mathematically analogous with the characteristic functional of a stochastic process and does allow the computation of all types of statistical properties of the neural population, including entropy, by proper differentiation. For more detailed mathematical treatment of these equations see Johannesma and van den Boogaard (1985), as well as van den Boogaard and Johannesma (1985).

In an equally compact form equations can be formulated for the development and/or plasticity of a neural population. In this point of view the

connectivity matrix W is not longer a time invariant matrix of functions but as such the subject of a dynamical process, albeit on a longer time scale. The idea behind the equations is given by Hebb-like evolution of structure: temporal association induces structural connectivity. A general form for these equations can be given by

$$\frac{d}{dt}W(t, \tau) = \phi(\tau) \cdot \{|z(t - \tau) - Z(t - \tau|e)\}\{\langle z(t)| - \langle e|Z(t)\rangle\} \quad (4.3)$$

where:

W := matrix of connectivity functions

ϕ := scalar evolution kernel

$\langle z|$:= neural activity pattern

$\langle e|$:= unit vector = $\frac{1}{\sqrt{K}}(1, 1, 1, \dots, 1)$

$$Z := \langle e|z\rangle = \frac{1}{\sqrt{K}} \sum_{k=1}^K z_k$$

Z forms a measure for total or average activity of the population.

In Eq. (4.9) two constraints have been incorporated:

$$\frac{d}{dt} \sum_k W_{kl} = 0 \quad \text{or} \quad \langle e|W \quad \text{is time-invariant}$$

which implies that the sum of output weights is invariant preventing absolute domination of a single neuron on the population.

$$\frac{d}{dt} \sum_l W_{kl} = 0 \quad \text{or} \quad W|e\rangle \quad \text{is time-invariant}$$

which implies that the sum of input weights is invariant, preventing absolute submission of a given neuron to the population.

If $\phi(\tau)$ is positive the plasticity develops in the form of cooperative evolution, for negative $\phi(\tau)$ a competitive evolution takes place. Combined forms can be represented by e.g. a $\phi(\tau)$ which is positive for small τ and negative for large τ . Equation (4.1) for neural interaction and Eq. (4.3) for synaptic evolution have a long history in brain theory (Caianiello 1961). The form of the connectivity matrix W determines the behaviour of the neural population in a fundamental way. In our opinion the following property holds: if W is not in triangular form and cannot be transformed in triangular form by a simple permutation of the neurons, then the neural population has creative features and cannot be analysed purely in terms of receptive and effective fields of its neurons. This implies that an evolution of W , according to Eq. (4.9), from a triangular form to a non-triangular form may transform the neural population from reactive into creative and change its information processing in an essential way.

5 Conceptual Base for Evaluation of Neural Activity Patterns

For a systematic approach to analysis and interpretation of neural activity patterns a fundamental hypothesis is formulated:

Neural activity patterns

- are evoked by sensory stimuli (receptive field)
- transformed by neural populations (assemblies)
- specified by sensitivity and connectivity (structure)
- as evolved in phylogenesis (selection)
- and modified in ontogenesis (plasticity)
- in such a way as to enhance forms of neural synchrony (coherence)
- which induce perceptual integration (harmony)
- and produce behavioural coordination (synergy)

A diagram of the mechanisms and influences expressed in this hypothesis is given in Fig. 8.

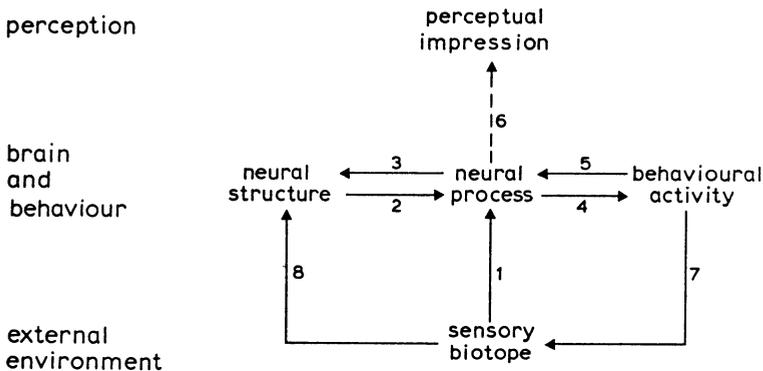


Fig. 8. Mechanisms and interactions influencing the activity patterns in a neural population

The nature of the interconnections, indicated by arrows in Fig. 8 is as follows:

1. Influence of sensory stimulus on neural activity ($10^{-3} - 1$ s.)
2. Influence of neural structure (synaptic connectivity) on neural activity patterns ($10^{-3} - 1$ s.)
3. Influence of neural activity on structure of the population: plasticity, associative memory, "learning" ($1 - 10^3$ s.)
4. Neural production of behavioural activity ($10^{-3} - 1$ s.)
5. Neural sensitivity for behavioural activity: proprioception ($10^{-3} - 1$ s.)

6. Sensory interpretation of neural activity ($10^{-3} - 10^3$ s.)
7. Influence of behaviour on sensory stimuli and sensory biotope ($10^{-3} - 10^3$ s.)
8. Evolutionary selection of neural structures ($10^5 - 10^8$ s.)

A consequence of this hypothesis is the definition of a neural assembly as a population of neurons which generates a coherent neural activity pattern. Coherence of neural activity should then be recognized and understood on the base of its functional interpretation as specified by the relation to internal structure of the sensory biotope (symphony), to perceptual integration (harmony) and behavioural coordination (synergy). An illustrative drawing of this point of view is given in Fig. 9.

In this line of thought a neural assembly is a dynamic structure influenced both by external variables and internal states; however, the time constant of variation of composition of assemblies is assumed to be considerably longer than the time constant involved in elementary aspects of perception and behaviour. The “harmony” in perception can be related to the tendency to favour sensory impressions with natural plausibility and relevance. The “synergy” in behaviour is related to elegance and efficiency of behavioural sequences. “Symphony”, “synergy”, “harmony” and “assembly” are considered as functions on their respective domain of definition. The mappings of these functions are assumed to be simpler than the mappings of their arguments.

The inclusion of the aspect “perception” in Fig. 8 and “mind” in Fig. 9 is an attempt to include the “representational” aspect of the nervous system. It is not intended as a description of experimental data, but as a conceptual interpretation. Mental aspects of neural activity are not operational variables, but formal expressions of these variables derived from meta-physiological consid-

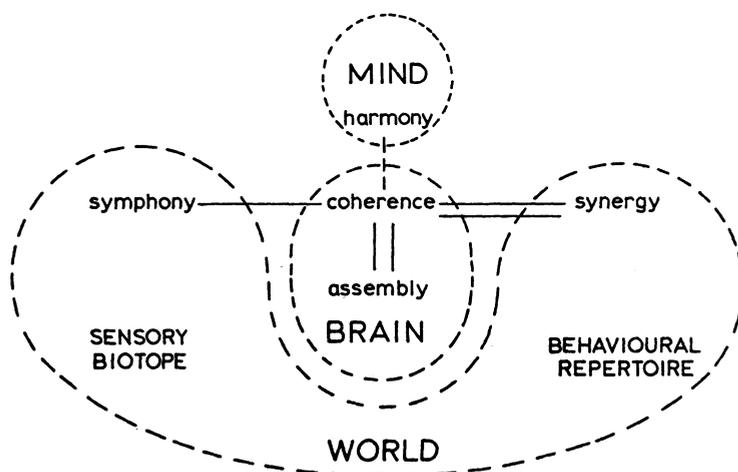


Fig. 9. Sketch of sensory “symphony”, behavioural “synergy” and mental “harmony” in their relation to neural “assembly”

erations e.g. evolution and behaviour. From the point of view of experimental neurophysiology this may appear speculative, on the other hand it may well be that the specific value of stimulus associated multi-unit recording compared to single unit recording is given by the data it supplies with respect to the neural base of perception and behaviour. The multi-unit recording gives a specific possibility to investigate the creative processes of neural populations and as such it appears to be connected to the representational function.

An illustration of these ideas results from the study of different types of animal behaviour; e.g. predation, territorial and sexual behaviour. In these situations a specific sequence of behavioural acts occurs which has been selected out of a set of possible behaviours directed towards certain goals and based upon interpretation of the sensory environment and expectation of its development. If a frog attempts to catch a flying insect he has to match his intended jump to the extrapolation of the trajectory of the insect. The explanation of the actual behaviour of the frog can only be given by an embedding of these facts among the possible alternative forms of behaviour e.g. a different type of jump at a different moment of time. This selection of behaviour results from the characteristics of an active model of the environment carried by a creative neural system forming a representation of the perceptual-behavioural interaction of the animal and its environment.

It is in this direction that we attempt to find an approach to analysis and interpretation of multi-unit recording considered as an observation of neural activity patterns.

6 Analysis and Interpretation of Neural Activity Patterns

The fundamental assumption is that the analysis and interpretation of stimulus associated multi-unit recording should be based on the description of the brain as a creative representational system generating an internal model of the perceptual and behavioural environment present in the past and persistent in the future.

The experimental data given by multi-unit recordings form an observation of the nervous system on the level of the process. In order to gain insight in the nervous system as such we try to make a connection with different levels of the system. One of these connections is the relation of process and structure: how to go from the correlation measured in the neural activity to the connectivity present in the neural structure? This is an inverse problem, well-known in the field of system identification and parameter estimation. Under certain conditions, including qualitative information concerning the system and complete observability of the state variables, it may be possible to compute the behaviour of the system in a forward way and to invert these equations in order to determine the parameters (Johannesma and van den Boogaard 1985, van den Boogaard et al. 1985). A more inspired approach has been taken by Gerstein; in a paraphrase it can be stated as follows:

1. Make an assumption on the ontogenesis of the system in relation to its process.
2. Model the system in a qualitative form.
3. Observe the activity patterns belonging to this system.
4. Project a development on the model based on the ontogenetic principles in combination with the observed processes.
5. Assume that the asymptotic structure of the time-variant model reflects the time-invariant structure of the neural population.

Compare the contribution of Aertsen et al. in this Vol.

This approach as a form of adaptive system identification is interesting and looks promising. Based on the ideas of different levels of systems, including the nervous system, two observations can be made.

In the first place all anatomical and physiological information available a priori should be included in the initial abstract form of the model. If equations of the type of Eq. (4.3) do apply, they may well be used, moreover then the initial condition on W should not be $W(0) = 0$ or random but based on assumptions and observations e.g. using the (relative) positions of the micro-electrodes.

In the second place the view of the nervous system as a representational system implies that the model for the nervous system as generated in this procedure forms a model of reality. If the model of reality, the brain, has developed in a natural environment of sensory stimuli and behavioural patterns then it may be preferable to have the development of the model of the brain occur in a comparable situation. This leads to the conclusion that natural stimuli and active behaviour may well be a necessary condition for a successful imitation of the ontogenesis of a neural population.

In these considerations we see an interaction of the syntactical analysis of a neural population (structure \leftrightarrow process) and the semantical level (process \leftrightarrow function). This idea also appears fundamental to the notion of a *neural assembly*: a population of neurons connected in such a way (structure) that their activity pattern (process) corresponds to a meaningful element in the sensory-motor space (function) (Braitenberg 1977, Palm 1982). If this description, as given in Sect. 5, is accepted, then the study of a neural assembly should be made as a multi-level investigation of structure, process and function of neural populations.

The “gravitational clustering” approach starts from the syntactic level concentrating on neural interaction and trying to deduce connectivity (structure) from correlation (process); in a later stage stimulus related arguments (function) become relevant. Now we shall sketch a complementary approach starting on the semantic level as given by the relation of sensory stimulus and neural activity. In fact the ideas are focused upon the neural base of perception.

Apart from introspection, the perceptual value of sensory stimuli can be measured by behavioural responses in relation to sensory stimuli. The normal procedure is the presentation to a subject, animal or human, of pairs of sets of

stimuli, which are selected in such a way that these can barely be discriminated among each other and ask or force the subject to make the discrimination. This leads to the “just noticeable difference” (j.n.d.) for sensory stimuli; these j.n.d.’s can be used as a metric in sensory space. The sensory space together with the metric or resolution from the j.n.d. has the mathematical form of a “tolerance-space” and may be considered as the perceptual space. The characteristics of the perceptual space may well depend on the situational context of the experiment and on the motivational state of the subject. However, giving confidence to experimental psychology and/or ethology we assume this perceptual space to be known in principle.

A central question for the interpretation of neural activity in sensory parts of the nervous system is the definition, both formal and operational, of the perceptual value of neural activity. We propose the following definition:

the percept associated with a neural activity pattern is the optimal estimation of the sensory stimulus which can be made by an external observer which has knowledge both of the structure of the nervous system and of the characteristics of the stimulus ensemble.

Here the notion of “optimal” is defined as a least square distance of percept and stimulus in technical context and as a minimal perceptual distance in a behavioural context. The perceptual metric has to be based on meta-physiological information e.g. from behavioural studies. This definition is analogous to the situation of an observer who knows his apparatus and the general characteristics of his environment and then searches for the best interpretation of his observations.

The percept as defined here is not a physical entity as such but an interpretation by the investigator projected upon his experimental data in the context of his insight into the behavioural relevance. When the neural activity pattern forms the internal map of the sensory stimuli, then the percept is defined as the optimal inverse map from neural activity back to the sensory stimulus. If the mathematical description of the nervous system, as far as involved in this sensory task, can be formulated as well as the description of the sensory environment, then the inverse map can in principle be derived making use of the Bayes’ relation for conditional probabilities. For a reactive model of the peripheral part of the auditory system this has been investigated mathematically and by computer simulation (Johannesma 1981).

The percept associated with a given neural activity pattern z is denoted as the sensory interpretation of neural activity (SINA) and in first approximation defined as the appropriate superposition of single unit receptive fields (SURF) of those neurons which are active. In general receptive fields, visual and auditory, will be spatio-spectro-temporal entities which may be regarded as points or regions in sensory space. For a reactive neural population the SURF is a properly defined entity which can be measured e.g. by cross-correlation of sensory stimulus and single unit neural events. It may be clear that the SURF is

described in sensory space (adequate or optimal stimulus or stimuli to activate a neuron); as such it forms already an example of inverse mapping. The SINA is intended as a generalisation of the SURF for multi-unit activity. However, as far as our insight goes, the SURF is only defined for a reactive population, while the SINA, being intended for the functional description of a neural assembly, is related to a creative population. A solution for this vicious circle is a sequential approximation under the assumption of convergence to an appropriate asymptotic solution. The verification of this assumption needs further mathematical analysis, numerical simulation and application to electrophysiological data.

Before the precise description of the SINA a final assumption is made concerning the interrelation of structure, process and function in the nervous system. It is based on the ideas presented in Sect. 4 and the definition of reactive and creative as given in Sect. 3. The assumption is as follows:

- Reactive aspects of the nervous system (convergence and divergence of connections) take care of the *representation* of the sensory environment directed toward *precision* and *reliability* (signal/noise).
- Creative aspects of the nervous system (lateral and recurrent connections) take care of the *transformation* of the representation of the sensory environment directed toward *plausibility* and *relevance* (figure/ground).
- The interplay of reactive and creative operation is under control of central parts of the nervous system which are influenced by external and internal factors.
- Reactive aspects are relatively insensitive, creative aspects are relatively sensitive for composition of the stimulus ensemble and state of the animal: the more natural the state of the animal and the characteristics of its environment are, the more creative the nervous system behaves.

On this base a description in formal and a prescription in operational terms of the SINA reads as follows:

1. Induce a perceptually alert state in the animal under investigation.
2. Present in alternating way two stimulus ensembles:
the first one with form but without sense:
e.g. random elements of the sensory biotope in random order
the second one with form and with sense:
e.g. natural selections of the sensory biotope.
3. Measure the stimulus associated multi-unit neural activity pattern $\{z_k(t), k = 1, K\}$ for both stimulus ensembles.
4. Compute the SURF for the first stimulus ensemble by correlation of sensory stimulus and neural events:
e.g. by second order correlation for the auditory system

$$X_k(\mathbf{r}, \omega, \tau) = \int dt X(\mathbf{r}, \omega, t - \tau) z_k(t)$$

where $X(\mathbf{r}, \omega, t)$ is the spatio-spectro-temporal characterisation of the stimulus ensemble.

5. Construct the SINA for both stimulus ensembles by an appropriate superposition of the receptive fields of the active neurons

$$\Xi(\mathbf{r}, \omega, t) = \sum_{k=1}^K \int d\tau X_k(\mathbf{r}, \omega, \tau) z_k(t - \tau)$$

6. Display the spatio-spectro-temporal image of stimulus-ensembles presented to the animal as well as the image of both stimulus-ensembles as constructed on the base of the associated neural activity pattern.
7. Investigate the hypothesis that the SINA of the sensible S.E. is transformed compared to the SINA of the non-sense S.E. in the direction of greater realism; the figure-ground effect should be much stronger.

A comparable experiment would be to choose a single stimulus ensemble where the stimuli gradually change from a given natural stimulus through an intermediate stage to a different natural stimulus. In this situation we expect a phase-transition in the neural activity pattern such that the associated SINA abruptly changes from one percept into the other; also hysteresis type of effects may occur.

A neural assembly may then be defined as a creative population of neurons which contribute to the generation of

- figure out of ground
- percept out of stimulus
- sense out of fact.

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