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A time-based approach towards cortical functions: neural mechanisms underlying dynamic aspects of information processing before and after postontogenetic plastic processes

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Abstract

Under the assumptions that the entire temporal structure of neuron responses carries significant information and that single cell receptive fields (RFs) and representational maps (RMs) typify representative stages of cortical processing, dynamical properties of RFs and RMs were investigated in three modalities. The resulting time-dependent receptive fields and representational maps are interpreted as specific adaptations to processing of inherently time-variant signals. Based on experimental data about latency differences observed within different hierarchically organized areas of sensory pathways, a time-based concept of temporal distributed processing (TDP) across subcortical and cortical substrates is presented that accounts for dynamic aspects of cortical processing. The high percentage of simultaneously activated neurons makes it rather unlikely that proceeding stages wait until the end of the processing of a previous one. This lack of wait-states is the key feature of the TDP-scheme which poses special emphasis on late response components. To provide sufficient flexibility to slow changing conditions in the environment and individual performance requirements, postontogenetic plastic adaptive processes are assumed to act within this scenario by directly effecting the response dynamics thus altering the entire interareal interactions.

1. Introduction

Over the last years, the exploration of dynamic aspects of brain functions has gained a great deal of attraction. This articles summarizes research about cortical receptive field dynamics and representational map dynamics, and outlines the concept of a time-based processing scheme.

The first part of the article reviews and summerizes previous and most-recent work of our laboratory about receptive field dynamics observed for three different modalities. In the second part, a temporal distributed processing scheme (TDP) is presented that accounts for the described dynamics of RFs and representational maps. Finally, the article deals with plastic reorganizational processes observed in adult mammals, which are referred to as postontogenetic plasticity. These experiments demonstrate a considerable capacity of receptive fields and representational maps to adapt to changing constraints of the environment even after the crit-

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ical developmental periods. Most notable are our latest results about changes of the dynamics of RFs during post-ontogenetic reorganization that could relate normal ongoing processing to plastic adaptive processes of adults. This is the starting point for an attempt to fuse dynamic information processing and postontogenetic plasticity in an understanding of learning and implicit memory functions of cortical systems.

1.1. Levels of description

The research reported here deals with two different processing levels: receptive fields at single neuron level and representational maps. The reasons to follow that doctrine are mainly motivated by pragmatic considerations. Single cells can be measured by single or multiple electrode recordings. Each neuron can be quantitatively studied by exploration of its receptive field properties. In terms of information processing, it provides the window to physical events. In this very broad meaning, receptive fields contain the rules to map physical events into neural activity patterns. As we believe most of such physical events are dynamic in nature, our main interest is in dynamic properties of receptive fields. Cortical neurons have specific response characteristics that are the consequence of their extrinsic excitatory inputs, and of massive intrinsic excitatory and inhibitory connections. There is a fairly clear relationship between receptive fields on one hand and topographic maps on the other hand, as selectively responding cortical neurons are commonly arrayed in topographically ordered representations. Therefore reconstruction of representational maps requires knowledge about geometrical and functional properties of receptive fields, i.e. their size and location within the sensory field and their transfer properties. It is the neighborhood relationship of RFs, their topography, that establishes a systematic spatial representation of environmental aspects: a map. As a consequence, maps and their underlying organization reflect cooperative phenomena among large neuron groups. These considerations make it obvious that there may be other significant levels of processing in between, which has been referred to as columns, assemblies, groups or populations. For the motor system [1] as well as for the Superior Colliculus [2a] it has been convincingly demonstrated that an important step of information processing leads to intermediate representations of information. These representations are more closely related to the overall performance of the system than to single neuron responses. By introducing a new analytical approach to neural data sets, these authors were able to demonstrate that neural populations can represent task-related parameters after transformation of the activity distributions of single neurons into a population representation. Using a time slice technique, it is possible to visualize the emergence and persistence of such representations. A crucial requirement for this type of population analysis is that all cells are measured under identical stimulation conditions. When translated into the constraints of sensory systems, the stimuli have not to be adjusted to the cells RF, but according to a visual field adjusted protocol. We recently initiated experiments to study the applicability of a population coding scheme in the visual system [2b].

The experiments reported in this article were performed in anesthetized rats and cats with recordings made in striate and extrastriate visual areas as well as in primary somatosensory and primary auditory cortices. Besides the apriori importance of studying response dynamics in different modalities, the comparison of differences and similarities found in different modalities offers a unique way of differentiating modality-specific modes of processing from those that are biased by constraints of cortical architecture and cortical processing principles.

1.2. Time scales

Inspection of the crucial time scales in brain functions reveals that there is a gap between processing time scale and that during which reorganizational processes are known to occur. A fast scale of a few to several hundred milliseconds is present in the interspike interval distributions of single neurons following sensory stimulation and is referred to as the temporal structure of neuron responses. Fast changes during postontogenetic plasticity have been reported to occur within minutes during classical conditioning [3], minutes to hours during intracortical microstimulation or pairing paradigms of peripheral stimulation [4–7], and up to several months for reorganizational changes following behavioral training [8–11]. Based on these considerations, the following time scales are subject of this article:

(i) a ten to several hundred millisecond scale, during which intrinsic RF dynamics become apparent;
(ii) a several hundred millisecond to second scale that deals with effects of timing, sequencing and temporal order during subsequent stimulation;
(iii) a minute to hour scale that deals with plastic-adaptive processes that overlays and interacts with the faster scales.

2. Time-dependent receptive fields

2.1. Methodological considerations

Time dependence of receptive field organization was investigated by applying a time slice technique [12,13]. The main idea behind this protocol is to avoid average or maximal measures of neuron responses, but to utilize and to rely on the entire response episodes. First, descriptors of receptive field properties were conventionally measured and calculated [12,13]. Dependent on the modality studied, descriptors used were response planes (visual and somatosensory system), orientation and length tuning (visual system), frequency-intensity planes and frequency tuning (auditory system). Next, time windows or time slices of constant width were chosen and the respective descriptors were recalculated for each time slice. Thus, a temporal sequence of descriptors is obtained which provides information about the instantaneous and actual content of the descriptor (Fig. 1).

All experiments were performed using so-called stationary, on-off type stimulation in order to relate the resulting temporal structure of neuron responses unequivocally to the highly reliable and controllable time course of sensory stimulation which is not possible when moving stimuli are used. Also, the described findings are from an experimental protocol called temporal stimulus isolation. Under these conditions, cells are studied by stimulating them from a zero state condition. Actually, this is the way most studies are done, which requires long interstimulus-intervals (ISIs) of more than 1/2 second. This protocol prohibits interaction between successive stimuli thus warranting that the cell has reached zero state. Therefore, the observed dynamics are interpreted as the manifestation of the intrinsic dynamics of the system, undisturbed by additional dynamics caused by timing constraints of the stimulation [12,13]. So far, little is known about possible differences between zero state conditions and different steady states which can be regarded as perturbations of the system from different base levels. First experiments indicate that the above defined intrinsic dynamics are subject to considerable changes when cells are no longer stimulated from zero state but from various degrees of a steady state introduced by additional timing effects due to short ISIs.

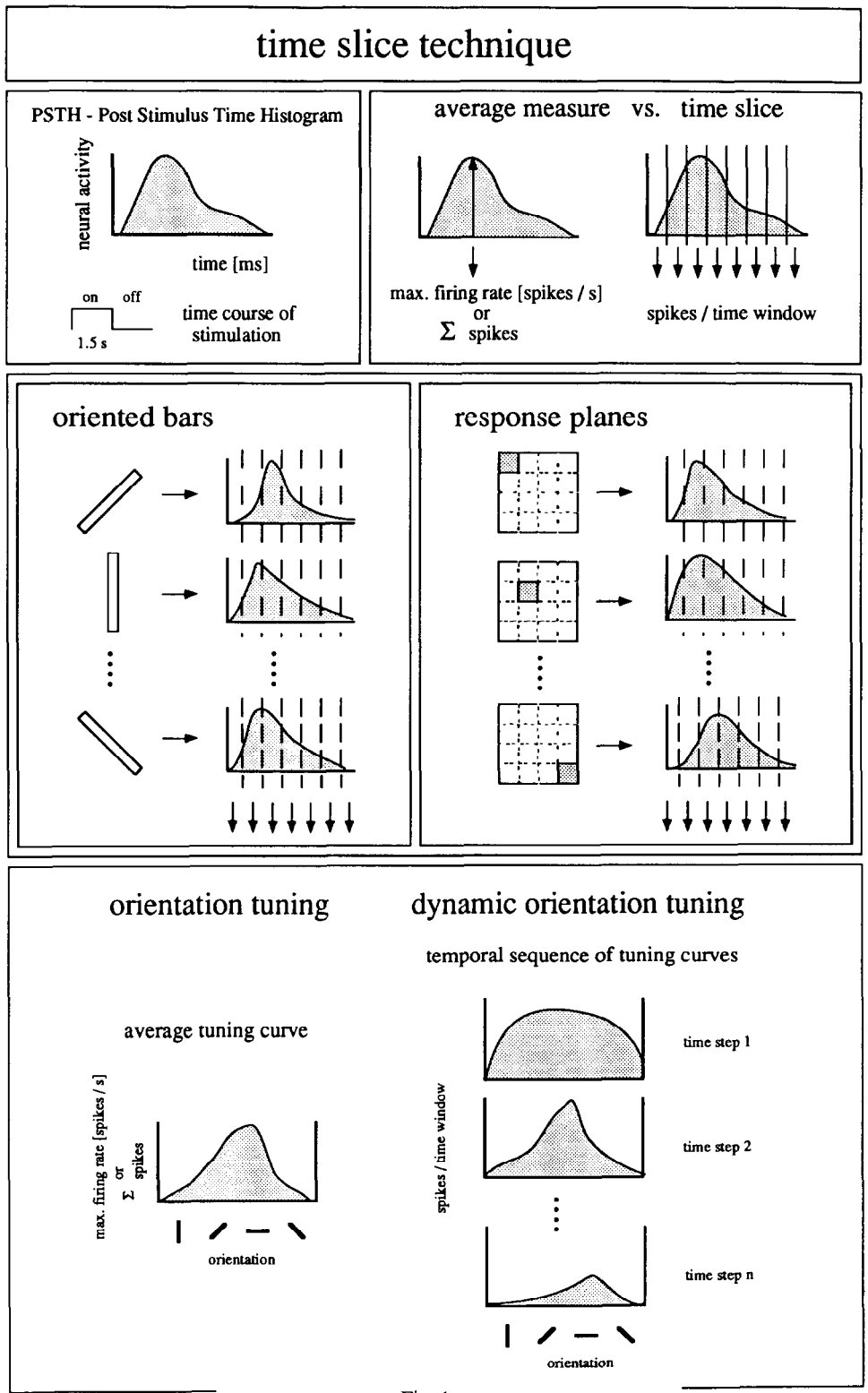

time slice technique
PSTH - Post Stimulus Time Histogram
neural activity
time [ms]
on
off
1.5 s
time course of stimulation
average measure vs. time slice
max. firing rate [spikes / s]
or
Σ spikes
spikes / time window
oriented bars
response planes
orientation tuning
dynamic orientation tuning
temporal sequence of tuning curves
average tuning curve
max. firing rate [spikes / s]
Σ or spikes
orientation
spikes / time window
time step 1
time step 2
time step n
orientation

Fig. 1.

2.2. Survey of time-dependent receptive fields

In this chapter our previous results about RF dynamics in the visual system are briefly reviewed. In addition, more recent findings about similar experiments in the auditory and somatosensory cortex are reported. Details of RF dynamics of the visual system have been described elsewhere [12–15]. The substantial changes of RF organization over time indicate non-separability of space and time [12,13] as well as time dependence of tuning characteristics [12–15].

Most interesting are observations that cortical selectivity such as orientation selectivity or length preference evolves over time preceded by early, unspecific states in which the cell appears invariant to changes of the stimulus. This gives rise to dynamic orientation selectivity and dynamic length preference. Most notable is the match between the emergence of anisotropic RF organization over time and the development of orientation selectivity. Both evolve after a state of isotropic organization during which no selectivity can be found.

Time dependence of auditory RF was investigated in AI of Nembutal anaesthetized cats [15,16]. When RFs were analyzed with the time slice technique, complex diagonal bands of activity across the frequency-intensity planes became visible which were found in equal proportions along the low or high frequency side of the tuning curves. As a rule, these bands were concealed in conventional, time-avaraged tuning characteristics. When the data were re-plotted as frequency-time plots, the time-dependent frequency characteristics revealed frequency transitions and time-dependent multi-peaked tuning properties. Response plane techniques combined with the time slice technique were recently also applied to study RF dynamics of neurons in the hindpaw representation of rat primary somatosensory cortex (SI) [17]. We observed a time-dependent spread of activity resulting in complex spatio-temporal pattern. Most notable was the gradual shift of activity starting at the distal part of the digit representation which then emerged further proximal within the skin representation of the pads or the emergence of focal zones of activity which then spread towards the peripheral portions of the time-averaged RFs, resembling very much the overall spatio-temporal behavior described for the visual and auditory system [15,17]. A schematic overview of dynamic RFs found in three modalities are presented in Fig. 2.

Using reverse correlation methods and time-slice techniques, dynamic receptive field properties have been investigated for several years by a number of groups with different motivations [18–27].

Fig. 1. Illustration of the time slice technique. Neuron responses are collected as PSTHs (post stimulus time histograms) for each stimulus condition separately. Variable time windows (time slices) are used to determine neural activity for each slice (spikes/time slice) instead of using maximal activity or temporal average measures. Tuning curves or reponse planes are then plotted for each time slice. The resulting temporal sequences of RF descriptors display the actual and momentary selectivity of a cell reflecting its time-dependent RF properties.

2.3. Representational map dynamics

Given the above described relationship between RFs and representational maps and, also taking into account the observed dynamic nature of RF organization found in all modalities tested so far, it appears conceivable that comparable dynamics act at the macroscopic level of cortical maps. To unravel those dynamics we initiated studies based on optical monitoring using voltage sensitive dyes (RH 795, RH 414) in the somatosensory cortex of the hindpaw representation. This method allows real-time monitoring of two-dimensional, spatio-temporal activity distributions [28]. Data acquisition windows were set in such a way that a coarse temporal resolution of the time course of the activity distributions could be obtained [15,29].

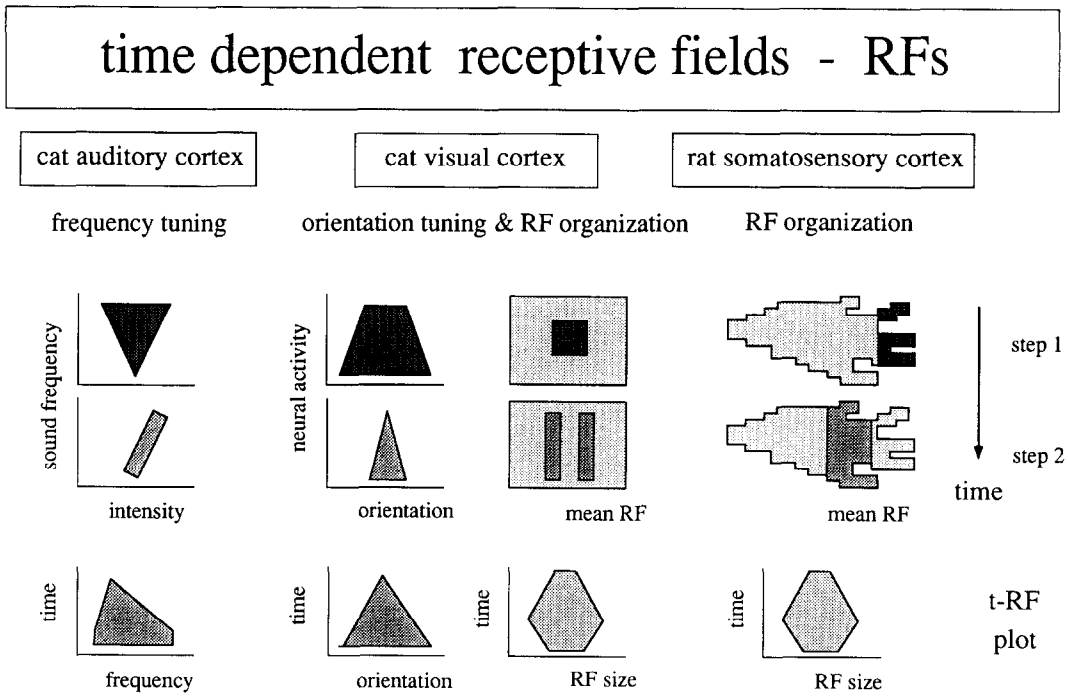


Fig. 2. Schematic survey of types and patterns of dynamic RF behavior observed in three modalities. Upper row sketches the behavior during two successive time steps. Auditory cortex: intensity-frequency plots; visual cortex: orientation tuning and response planes of a visual RF; somatosensory cortex: response planes of a hindpaw RF. In the response planes, the mean, temporally averaged RFs are indicated by light shading. Time-dependent changes of RF locations are given by darker shading. Lower row illustrates plots of RF descriptor versus time (time-soundfrequency, time-orientation, and time-RF-dimensions).

The spatial extent of the representational zones following point-like stimulation at selected skin fields was different when recorded at different times after stimulation. Also, the zone of cortex being activated was considerably larger when longer integration times were used. In this case, the activated area covered the different zones mapped with the short integration times, suggesting similar dynamic properties as described for the organization of single cell RFs.

Our results obtained in the somatosensory and recent work in the auditory cortex [30] in fact revealed the existence of considerable dynamics that are compatible with what is known from RF dynamics. However, the results from both modalities imply much more complicated patterns than would be expected from single cell recordings. The available data suggest wave-like patterns of activity, implying that cortical maps change on a time scale of tens of milliseconds. Any temporal averaging cannot resolve these patterns. Instead, the temporal averaging will melt together small zones of activity, resulting in much larger activity patterns. As these spatio-temporal patterns are reproducible and stimulus specific, they must be regarded as part of a macroscopic processing scheme. Similarly, using optical monitoring combined with spike triggered averaging of neuron activity, Grinvald and co-workers reported on-going, wave-like processes that were present during visual stimulation as well as during episodes of spontaneous, on-going activity [31].

2.4. Common features of RF dynamics and their absolute timing

Time dependence of RFs was studied in three modalities whose organization principles

in terms of neocortical architecture suggest a common mode of processing. As a common feature, two response components could be distinguished which reflect two different states of responsiveness (Fig. 2). So-called early components exhibit a fairly unspecific state which is not or weakly tuned and which is paralleled by a simple, isotropic RF organization. In contrast, the late succeeding state displays a sharp tuning which, in many instances shifts the maximal tuning, and which is characterized by the emergence of an anisotropic RF organization. However, in terms of neural activity, the spike rate during the early state can be much higher than during the late state. This fact provides further evidence for the argument that high spike rates are not necessarily associated with high levels of selectivity [12,13]. Under the assumption that the pronounced temporal structure of neuron responses is in fact used as a time code [32–36], these findings appear not entirely unexpected. In our view, RF properties are not exclusively explained by hard-wired circuitries, but to a considerable degree functionally self-organized through the interaction among many other neurons [12,13]. Besides this dynamic aspect, there are other lines of evidence that support such a view: work about RF plasticity, which is discussed in detail later (see section 5), and experiments about contextual influences [37], which demonstrate a considerable degree of modificability of RF properties. As to the problem of the balance of inhibitory vs. excitatory actions that sculpture RF selectivity, see the detailed discussion in [12].

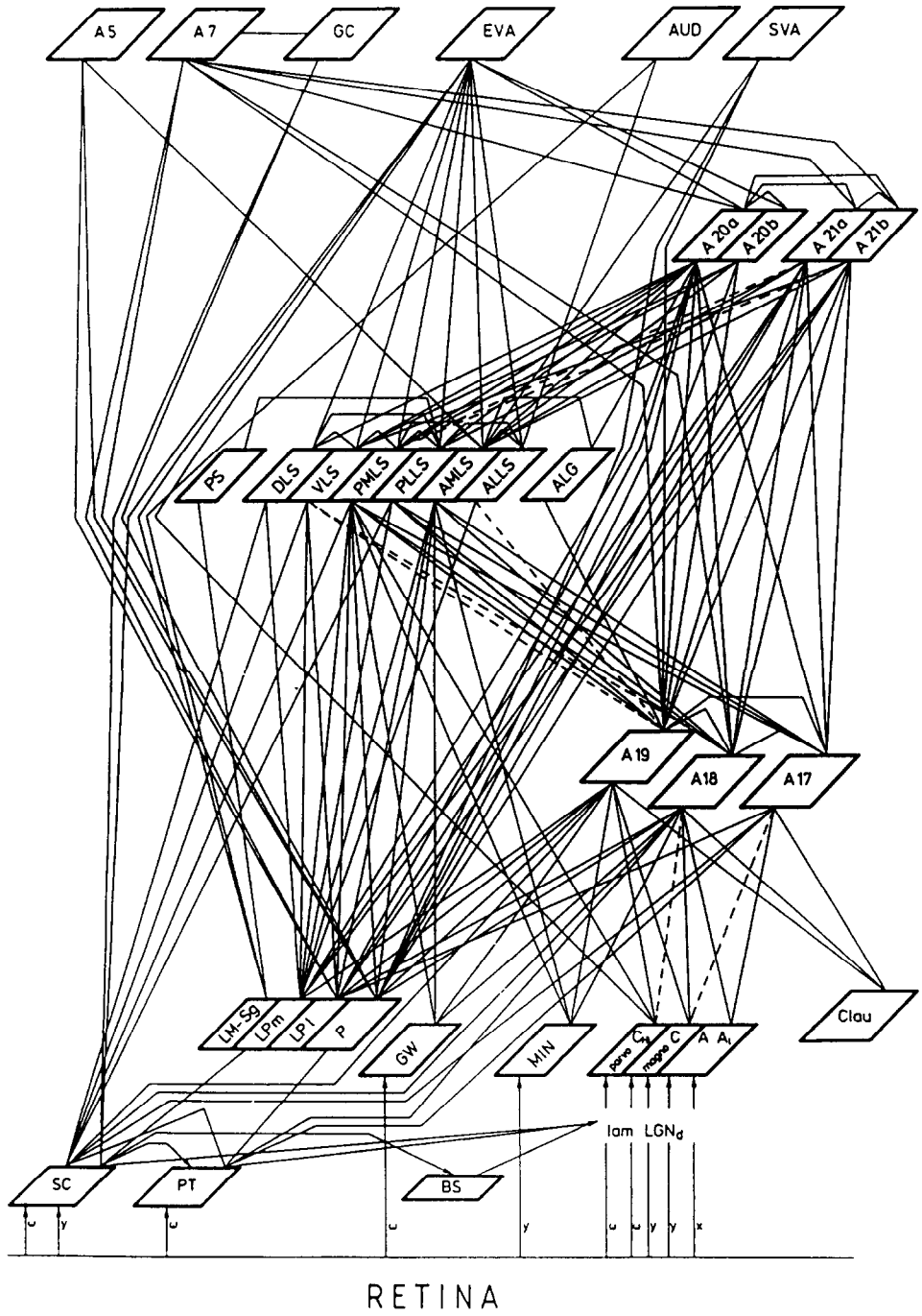
Apart from the obvious similarities of the various RF dynamics, there are also clear differences across modalities which mainly concern the absolute timing of these dynamics. While the time constants of the visual system are in the range of 50 to 200 ms, those of the auditory and somatosensory are much shorter and in a range of 10 to 50 ms.

3. A time-based approach of cortical functions – TDP

3.1. General properties of sensory pathways

Sensory systems of higher mammals represent perfect examples of multi-layer systems. Their architecture consists of sets of multiple stages that constitute heavily interconnected systems of serio-parallel processing which is especially well-documented for the primate visual system [38]. Here, the common properties of a sensory pathway are briefly exemplified in the following for the cat visual system [39,40]. Based on the pattern of thalamo-cortical connections, both areas 17 and 18 in cats are regarded to represent a parallel stage of primary areas directly receiving independent input from the lateral geniculate nucleus (LGN). The same is essentially true for area 19, however, it is regarded to occupy a somewhat more advanced level than areas 17 and 18, because it receives input from the LP Pulvinar complex, which in turn receives midbrain and backprojections from areas 17, 18 and 19. Finally, the suprasylvian areas are on a more advanced, but still intermediate level of processing, as they receive their main input from the LP Pulvinar complex and from areas 17, 18 and 19, while the LGN input remains marginal. PMLS (visual area in the posteromedial portion of the lateral suprasylvian sulcus) is discussed with respect to processing of motion and to its possible analogy to monkey mediotemporal cortex (MT). For the cat system, little is known of areas 20 and 21, which some authors believe to be analogous to monkey inferotemporal cortex (IT), as well as of area 7. The clear hierarchical character as demonstrated for the primate visual system, is not as obvious in cats, though also present (Fig. 3).

In order to understand the absolute timing conditions of processing along these different stages, visual response latencies (peak latencies) and response durations following on-off stimulation were investigated in the LGN (example


A5
A7
GC
EVA
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A 20a
A 20b
A 21a
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ALLS
ALG
A19
A18
A17
LM-Sg
LPm
LPl
P
GW
MIN
C
A
Clau
lam
LGN
SC
PT
BS
RETINA

Fig. 3.

of subcortical processing), in areas 17, 18, 19 (examples of early cortical processing), in area PMLS (example of intermediate cortical processing) and in area 7 (example of higher cortical processing). Based on the above described projectional pattern, it seems conceivable that the areas studied cover at least 3 to 4 different levels of information processing. More details of the experimental procedures are given in [41].

Consistent with the progressive advance of each processing stage, the mean latencies increased. According to the data there is, however, a broad scatter of latencies over a range up to more than 100 ms (Fig. 4). There is also a wide range of response durations. Accordingly, there is a considerable overlap of the time during which neurons are activated suggesting that most of the neurons within different stages of a hierarchically organized sensory pathway are simultaneously active when stimulated (Fig. 5).

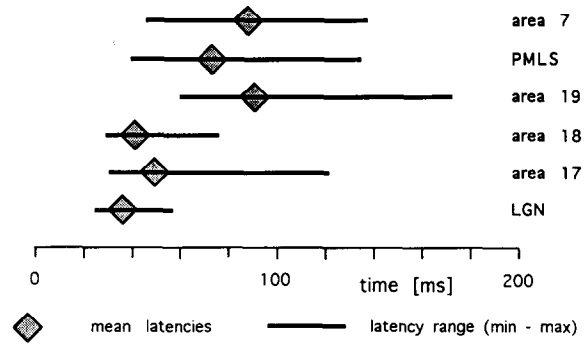

Fig. 4. Visual latencies following stimulation with on-off stimuli (flickered at 0.2 or 0.4 cps) that were adjusted to cover the entire RF of each individual cell (total of 409). For each of the selected stages within the visual pathway, the mean peak latencies as well as the minimal and maximal latencies found for each stage are shown.

Fig. 3. Visual system of the cat as known from anatomical and electrophysiological experiments illustrating the richness of connectivities and hierarchical organization. The different projections of the x-, y- and w- channels are indicated. Dashed lines indicate weak or uncertain projections. Note that many anatomical connections are often not substantiated by functional measurements. Basically all projections shown are reciprocally organized. Abbreviations: A: area; A/A1: A-lamina of LGN; ALG: visual area in the anterior sulcus lateralis; ALLS: visual area in the anterolateral sulcus lateralis suprasylvius; AMLS: visual area in the anteromedial sulcus lateralis suprasylvius; AUD: auditory cortex; BS: brain stem; C: magnocellular lamina of LGN; C1-3: parvocellular laminae of LGN; Cl: Nucl. centralis lateralis; Clau: Claustrum; DLS: visual area in the sulcus lateralis suprasylvius; EVA: visual area in the anterior sulcus ectosylvius; GC: visual area in the gyrus cinguli (area 23); GW: geniculate wing; lam LGNd: corpus geniculatum laterale, laminated, dorsal portion; LM-Sg: lateromedial portion of the suprageniculate complex; LP: Nucl. lateralis posterior; LPi: intermedial zone of the Nucl. lateralis posterior; LPl: lateral zone of the Nucl. lateralis posterior; LPm: medial zone of the Nucl. lateralis posterior; LP-P: Nucl. lateralis posterior - pulvinar complex; LS: sulcus lateralis suprasylvius; MIN: Nucl. medialis intralaminaris; NOT: Nucl. tractus opticus; P: Pulvinar (Nucl. pulvinaris); PLLS: visual area in the posterolateral sulcus lateralis suprasylvius; PMLS: visual area in the posteromedial sulcus lateralis suprasylvius; PS: visual area in the posterior sulcus suprasylvius; PT: pretectum; SC: colliculus superior; SVA: visual area in the sulcus splenialis; VLS: area in the ventral sulcus lateralis suprasylvius. For details of the literature cited see [40].

3.2. No wait-states?

A framework is proposed that incorporates the contributions of feedforward, lateral interactions (excitation and inhibition) and feedback. It is based on experimental data on absolute timing conditions (response latencies and response durations), which we measured in different processing stages of the visual system and which was called Temporal Distributed Processing - TDP.

In the light of the above described findings about response latency differences, the chain of processing across a multi-layered sensory pathway seems to be activated in a temporally continuous fashion. The high percentage of simultaneously activated neurons, makes it rather unlikely that proceeding stages wait until the end of the processing of a previous one. What seems more plausible is a continuous interaction that links together all stages of the processing path including higher-order areas. This is even more obvious in other modalities characterized by much shorter response latencies. As in the case of the auditory system, mean response latencies in primary auditory cortex (AI) are in the range of 10 to 15 ms, giving rise to latency

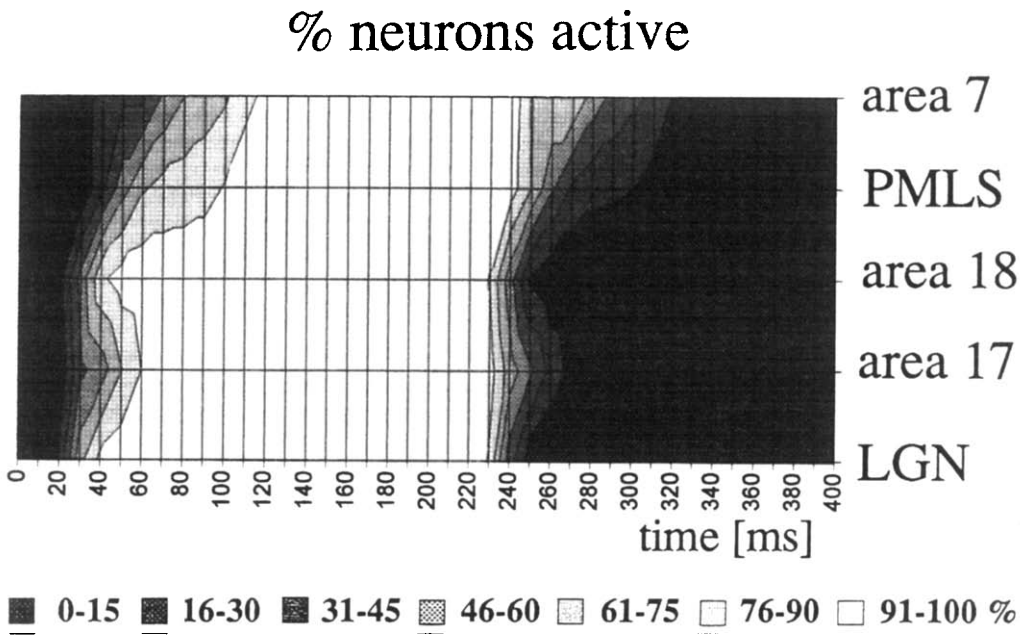

Fig. 5. Flow of information through the visual pathway as based on the latency distributions shown in Fig. 4. Area 19 is not included. According to its latencies, area 19 differs from the other areas and its specific role in information processing is not yet fully understood. In order to calculate the time over which neurons are active following visual stimulation, an average response duration of 200 ms was assumed for all neurons. Shown are the percentages of neurons in each stage that are activated. Based on this flow diagram, a mean transmission time of about 10 to 15 ms can be derived. As this delay is very short compared to the periods of activation, it is concluded that the differences in latencies reflect mainly conduction times and synaptic delays with little emphasis on processing times.

differences between subcortical structures and AI of only a very few milliseconds. Similar considerations hold for the somatosensory system providing further arguments that differences in latencies reflect mainly conduction times with little emphasis on processing times.

3.3. Temporal distributed processing – the TDP-scheme

The basic idea of the TDP concept is grounded on the lack of wait-states. In this scheme, illustrated in Fig. 6, the first available information about external stimulation is fed without delay through the entire pathway which represents the feedforward aspects of the response characteristics. During the continuation of the response, this behavior is repeated. However, after these initial response components, different types of lateral interactions and feedback mechanisms come into play. Among these are the thalamocortical feedback, intracortical feedback and the feedback from other and higher areas. The time required for this action to have an impact on the response characteristics at a given site might be variable for each of the described mechanisms and might depend on the type of stimulation and on the modality. Taken together, these temporally delayed influences modify to a considerable but variable degree the informational content being processed or being represented.

Therefore it seems conceivable that neuronal responses are changed systematically over time making late components completely or at least significantly different from early ones. This is exactly what could be found experimentally: as described, there is accumulating evidence across modalities for time-dependent receptive

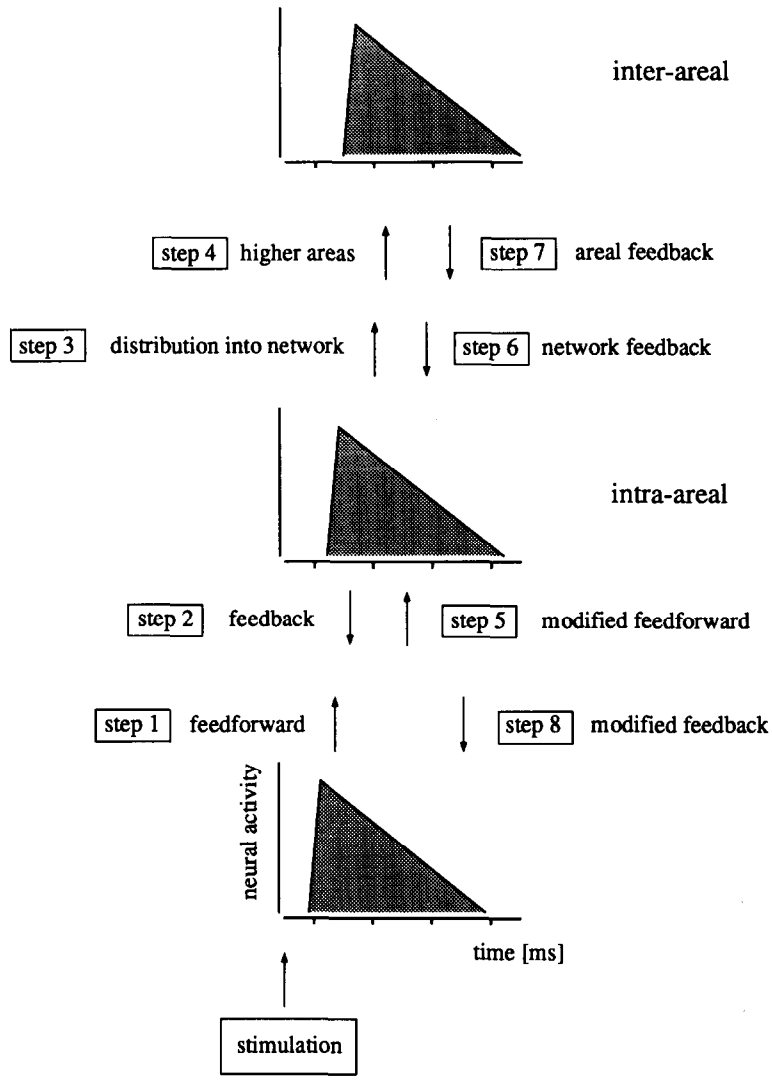

Fig. 6. Schematic illustration of the temporal distributed processing scheme (TDP). Schematic neuron responses are shown as post stimulus time histograms (PSTHs) for different stages of an assumed sensory pathway. Due to the time-dependent action of feedforward components, lateral interactions, different types of feedback and temporally delayed and modified feedforward, the late response episodes are assumed to be significantly altered in their informational content compared to the early parts, independent of their lower firing rates.

field properties, which are highly compatible with the TDP model that explains both late and time-dependent selectivity [12–26]. Inspection of neuron responses following stimulation with complex patterns or faces in IT (inferior temporal cortex which is regarded as an high-end substrate for visual processing), revealed latencies between 80 and 100 ms [36,42,43] which fits remarkably into the outlined framework of the TDP-scheme of a continuous, time-based interareal interaction. In addition, as these experiments were performed in fully awake and behaving animals, they provide an argument that the basic properties of dynamic patterns described in this article are not an artefact of anesthesia.

3.4. Why time-dependent RFs?

Independent of how dynamic RFs are generated, they seem to constitute an essential feature of cortical functions. At a first attempt to clarify their possible functional implications, it seems conceivable that they represent specific adaptations for processing of inherently time-variant signals.

This notion can easily be explored by comparing the range of RF dynamics with typical signal dynamics. In the case of the visual system, motion of either objects or of the system itself represents typical examples of signal dynamics. In the case of the auditory system, frequency transitions of second-order formants in human speech [44] resemble the dynamics observed during the changes of RF organization (Fig. 7). Video analysis of the rat walking pattern revealed time scales of sensorimotor behavior which are fully compatible with those observed during somatosensory RF dynamics. Of course, such matches are only the initial prerequisite for the above described idea of modality-specific adaptations. Further experiments as well as computer simulations will be helpful to elucidate this hypothesis. From a general point of view, an argument can be made in favor of time-variant information processing, because it is essential for many processing tasks to keep information available over a longer period of time. The tasks include integration, prediction, generation of continuity and finally short-term memory functions, with the latter filling the gap between low-level processing dynamics and higher cognitive functions [45–47].

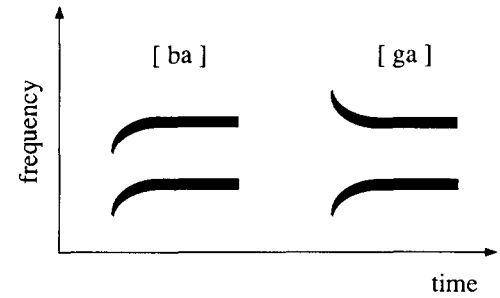

Fig. 7. Comparison of the first and second order formants of the syllables -ba- and -ga-. Their differentiation is based on the differences of the transient aspects of the second order formant only [44].

3.5. TDP implications

TDP treats dynamics of the entire neuron response very specifically, emphasizing late components. Thereby a number of interesting implications are raised. TDP provides a substrate that can be used for routing back memory-related information from higher areas. In view of the recent discussion of memory-related information processing, late response components are most likely to carry such information [48].

TDP has the potential to link remote processing streams that have only very loose relations but have common origins at low levels of processing. The existence of some anatomically based common pathways is the only prerequisite for the emergence of this type of crosstalk, because only a complete anatomical separation would prevent TDP-based interactions. However, in view of the anatomical richness of the projectional patterns and connections, this requirement is easily met. There are in fact many lines of evidence suggesting that such a complete channel separation might be the exception, because of the high probability of feedback [49,50] and the high probability of bifurcation of axons [51], besides the well-documented complexity of a sensory pathway such as the primate visual system with its separation of form and motion [38,52]. Accordingly, considerable crosscouplings can be expected at higher stages due to temporal interaction across all stages. Again, its impacts must be expected to evolve during the late response components. Depending on the specific pathway, this scheme can allow a compartimentation of local vs. remote processing (Fig. 8). Recent work about biochemical properties underlying cortical and subcortical processing revealed specific contributions of the NMDA receptor system to different response

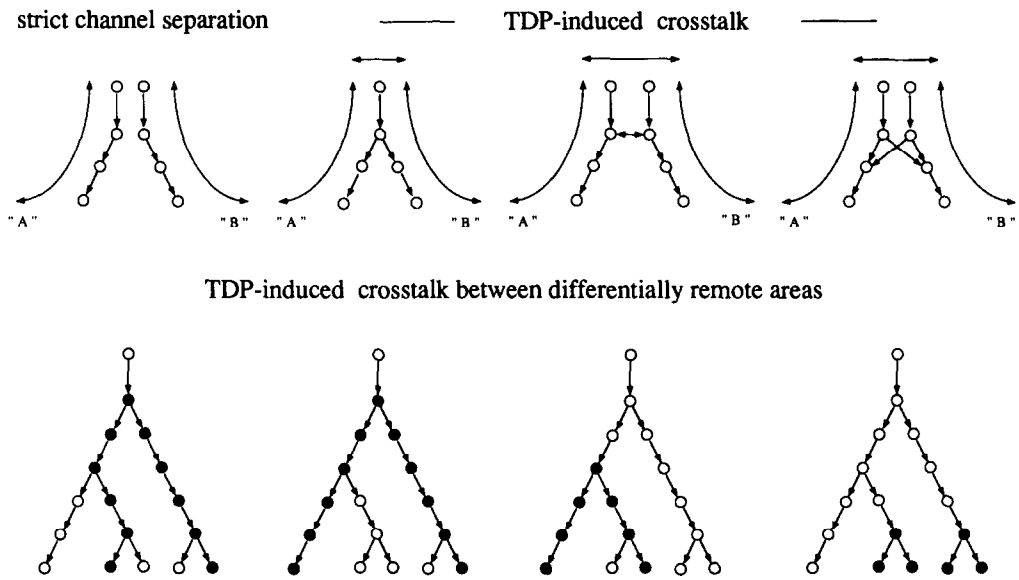

Fig. 8. TDP-based crosstalk in various layouts of multi-layer systems. The form and motion channel as described for the visual system can be assumed to exemplify the two different channels A and B. Top: Crosstalk due to common anatomical pathways that are present at different hierarchical levels. Bottom: Crosstalk between differentially remote areas.

components. Late response components were shown to be highly dependent on NMDA while short latency responses seemed mediated by non-NMDA receptors. Similarily, in the ventrobasal thalamus, the phasic responses were mediated by non-NMDA receptors whereas the long duration components were due to NMDA receptor inputs [53,54]. Late response components as recorded in frog Tectum opticum showed a significantly higher sensitivity to anoxia then early components (Dinse et al., unpublished). While the latter finding is not entirely comparable to cortical processing, together with the NMDA studies there is a basis for a clear distinction between early and late components. Similar arguements can be made based on the findings of the analysis of temporally modulated responses following stimulation with complex signals in IT and area 17 of awake monkeys [36,55,56], see also section 2.4. Also, the low-frequency oscillatory components frequently described for cat visual and somatosensory cortex add another feature of complex late response components whose behavior is different and mostly independent of early responses [12,13,47,57].

It is an intriguing question whether the observed RF dynamics are exclusively cortical in origin and thus a signature of higher cortical processing probably strongly biased by the underlying fairly similar principles of cortical architecture. According to the TDP scheme, similar complex dynamics have to be expected in subcortical substrates due to the inherent temporal interactions. This is in fact suggested by findings on time-dependence and sophisticated RF properties in the visual [18,58], auditory [59,60] and somatosensory [26] subcortical structures. However, at the moment it is unclear whether these properties are due to cortico-thalamic feedback, properties generic to subcortical structures, or both. Neural cooperativity as reflected in correlated activity between neuron pairs has also been shown to be essentially dynamically maintained [61]. Besides fast stimulus-dependent changes, functional connections between neurons have been demonstrated to be dependent on an associative pairing pro-

tocol in behaving monkeys [62]. It appears conceivable that these aspects of dynamic correlations can be covered by TDP.

Considering theoretical and technical applications, the lack of wait-states bears interesting implications for multi-layer models of brain functions that rely on the existence of sequential processing in the sense that some information is extracted at a given stage and the results of that processing are then used as inputs for processing in subsequent stages. As there is a need for many computational tasks to combine a top-down and bottom-up approach, there are several models of visual information processing that rely explicitly on this type of areal interactions [63–65].

Finally, the TDP scheme is certainly not restricted to sensory pathways but might be valid for multi-layer systems in general. It remains to be seen whether retinal processing for example, which is similarily organized within a multi-layer system, follows the predictions made by TDP.

4. Effects of timing, sequencing and temporal order

Systematic variations of interstimulus-intervals (ISI) and the number of stimuli within a stimulus train were used to investigate effects of timing, sequencing and temporal order which reflects the transitions from transient to steady state conditions.

With a second conditioning stimulus, a dominant inhibition was present, characterized by low cut offs at ISIs between 20 and 80 ms. However, this behavior was not replicated when the ISI effects to the third or higher stimulus number were tested. Accordingly, the overall responses depended not only on ISI, but in addition on the number of the stimulus within a train and its ISI condition. Inhibition seen at short ISIs appeared to be uncorrelated with the preceeding response. This leads to the observation that inhibitory action is restricted to certain stimulus numbers thus giving rise to strong sequencing effects [66,67]. What is important in the context of this article is the fact that there are considerable interactions between the described time scales suggesting the existence of substantial functional links.

(1) Intrinsic RF dynamics can be modified by sequencing effects [16, Dinse and Schreiner, unpublished] which is interpreted as a very fast modification compared to plastic-adaptive processes which are on a minute to hour scale.

(2) Temporal transfer properties as seen during given sequencing conditions are subject to considerable changes during plastic adaptive processes [68].

Under natural conditions, stimuli never appear in isolation. Therefore, timing and sequencing impose severe temporal constraints that modulate neuron responses. In this way, response properties are revealed that are not apparent under steady state conditions using solitary stimulation. In addition, the analysis of timing and order effects offer the opportunity for links to behavioral levels, which could be particular rewarding in the auditory domain.

5. Information processing during and after representational plasticity - Survey of postontogenetic plasticity

So far, dynamics of RFs and of representational maps were discussed during normal ongoing information processing of sensory events. During the last years, evidence has accumulated that higher order processing systems are subject to almost continuous alterations which we refer to as cortical (and subcortical) plasticity.

5.1. Why postontogenetic plasticity (POP)?

Neural systems organize behavior according to the environmental conditions. However, the environments and the constraints they impose change on a variety of time scales. Therefore, each system operating in such an environment

must preserve considerable life-long adaptive capacities beyond the critical developmental period for which we introduced the term "postontogenetic plasticity".

During the last years, postontogenetic plasticity was in fact observed in the cortex of many adult species: After circumscribed damage to peripheral receptor arrays of the skin, cochlea or retina, the input-deprived cortical areas are occupied by the representations of neighboring sensory fields after weeks and months of recovery [69–75]. Remodelling of sensory representations following behavioral training, classical conditioning and prolonged natural sensory stimulation suggests that cortical maps and receptive fields are also subject to modification by use [76–82]. The impact of plastic reorganizations, therefore, extends into the field of higher cognitive functions related to learning and memory [82].

5.2. *Fast functional reorganization*

During the last years it has been demonstrated that a few hours of intracortical microstimulation (ICMS) is highly effective to study short-term plasticity, offering the advantage of investigating locally in acute experiments the capacities and constraints of functional plasticity in the adult sensory and motor cortex, regardless of effects from the sensory periphery and the ascending pathways [5–7].

Motivated by the Hebbian postulate [83], our group introduced a pairing protocol of simultaneously applied tactile stimulation (PPTS – paired peripheral tactile stimulation). A few hours of this protocol [80,81] resulted in similar reorganizational changes as reported for ICMS [5–7,68]. As a rule, both ICMS and PPTS induce short-term plastic reorganization which is fully reversible. Early effects can be detected after 15 min, and much greater effects are visible after 2 to 3 hours. The basic methodological approach and the main results are described in [5–7].

So far, representational plasticity has been discussed with respect to geometric aspects of reorganizational changes, i.e. map changes and enlargement of sensory representations. During ICMS and PPTS we additionally observed reorganizational changes of functional aspects of receptive field properties such as frequency and intensity characteristics. Close inspection of the temporal structure of neuron responses during plastic processes also revealed significant changes: (1) there is an increase of correlated activity between pairs of neurons, which is restricted to those cortical zones that underwent reorganizational changes, indicating that neuron interaction is causally related to postontogenetic plasticity [6]. (2) response duration is significantly elongated indicating that the time neurons are active is substantially prolonged. Together with the first observation this indicates that the time of neural interaction has also increased, and (3) the entire RF dynamics are changed. Before we describe our hypothesis about the role of postontogenetic plasticity in relation to learning and implicit memory functions, some basic assumptions and definitions will be made.

6. Learning and normative processing

There is a wide spectrum of disciplines that contribute to our understanding of learning and memory including cellular, biophysical and molecular aspects of psychology and behavioral neuroscience. However, there is surprisingly little known at an intermediate systems level of sensory information processing. This appears especially surprising, as all information that can be utilized for learning and memory functions must be channeled through the early sensory systems.

In a general sense, the modifiability, i.e. the plastic-adaptive capacities that have been described reflects the reorganization of the system following external signals. Therefore, the terms

learning and memory are used as the perturbation imposed by additional external signals. Postontogenetic plasticity can then be used to study the strategies of information processing of sensory inputs during different states of learning related paradigms. One of the crucial questions is how to identify signals that act as perturbation in the above described sense, as they can be part of the overall sensory input thereby changing its meaning and interpretation.

The main difficulties in analysing these adaptational processes arise from two facts:

(1) It is assumed that average knowledge of the world and the specific environment is coded in the type of hardware structure of the brain. Specific constraints as well as completions and adaptations are held within the memory storage. How can these components be separated and identified? Studying the effects of learning requires knowledge about a normative state of the system, a putative control condition. Little is known about these controls and so-called normal states of processing. As each system is continually confronted with incoming information which is used to different degrees for reorganizational processes, a true control state might not even exist at all, meaning that each observed adaptation is a transition from one learned state to another. According to the recent studies in the field of cortical plasticity, each behavioral paradigm changes the underlying system (see also section 8). In this case, again, no control state is available. Moreover, any information available from such an experiment is highly specific and might only hold for these specific situation, making it difficult to draw general conclusions.

(2) Since cortical and hippocampal systems are heavily interconnected, it becomes difficult to assign certain loci that are the substrate for structural or functional changes. TDP adds further support to this assumption that changes measured within a certain processing stage reflect functional reorganization: however, nothing can be inferred about the location at which the alteration of the system actually took place.

The use of variables like spatio-temporal activity patterns as described for time-dependent RFs and representational maps might appear essential to uncover and to understand functional impacts with respect to the generation of plastic changes. As it is conceivable that learning-induced alterations are imposed by feedback mechanisms, their signature within neuron responses can be tiny and therefore difficult to identify. However, TDP provides a framework to allow the separation of direct, signal driven processing from that which is modified by higher-order and significantly preprocessed components which can be expected to contain concepts related to implicit memory functions.

6.1. TDP and POP

Postontogenetic plasticity was so far observed at early stages of processing, i.e. mostly in layers IV of the primary cortical areas suggesting local changes of processing. We must assume, however, that the entire interconnected system of sensory pathways is the substrate in which plastic reorganization takes place.

Analysis of ICMS induced changes at the functional level revealed complicated patterns of adaptation and integration of RF properties that can not be explained in simple terms of inhibition or disinhibition, respectively [7,68]. As described earlier, plastic reorganization affects many aspects of the dynamic features of the temporal response structure. Especially, the early response components are only slightly influenced and changes are mostly restricted to late components.

TDP predicts reorganization to occurr simultaneously in all areas due to the extensive ongoing interactions across all areas. The greatest impact, therefore, should be seen in late components. Accordingly, the local changes observed in primary areas must be expected to be transmitted to remote and higher areas that are more closely related to memory functions. Continu-

ation of a changed sensory input modifies this type of interareal interactions and their dynamics.

In this view, the idiosyncratic nature of RF dynamics reflect the current adaptational profile of an individual organism to cope with the actual requirements of its environment. Under normal conditions, there is a steady state of requirements that prevents the emergence of dramatic changes. Only under conditions that go beyond these steady state limits, can plastic reorganization be revealed experimentally.

However, in spite of the overwhelming evidence for plastic-adaptive capacities, systems must possess some generic stability. With this the requirement of the entire system to perform stable operations despite continuous changes in the environment is meant. One can expect a trade-off between modifiability on the one hand that warrants sufficient flexibility, and stability on the other that enables the system to achieve a state of invariance. Although large scale reorganizations have been reported following large peripheral injuries [84], the limit of about 800 microns encountered in similar fast plasticity experiments [4–7] might reflect a meaningful constraint of short-term plasticity that could provide stability of processing despite all requirements for flexibility.

7. Mapping spatio-temporal activity onto behavioral states

In contrast to the other modalities, the somatosensory system is unique in that it is inherently related to motor action and behavior. This intimate relationship can be utilized in search of interpretations of spatio-temporal activity pattern in terms of behavioral significance and relevance. The main problem is to identify such patterns. The constraints imposed by the somatosensory system on the patterns available are extremely valuable in providing clues to identify them.

The video-based analysis of walking patterns of rats and the time course of representational map dynamics observed for rat extremities match to a surprisingly high degree. Under normal conditions, walking consists of a certain sequence of steps, causally related to a fixed sequence of neural events. It is hypothesized that the spatial and temporal spread of activity anticipate behaviorally relevant patterns, making the expected pattern easier to evolve. It is conceivable that this requires learning to establish the sequence. Accordingly, complex spatio-temporal patterns are a manifestation of highly relevant behavior that is created either during the critical developmental period or during reorganization of the system following postontogenetic plasticity, or both. Either way, RF dynamics link learning and implicit memory functions to normal, continuously ongoing processing. The dynamics represent highly adaptive states based on acquired knowledge that are crucial for facilitating sequences of neural events that can anticipate fixed sequences of behavior-related action. However, as described, these dynamics are highly variable and subject to plastic alterations. From the point of view of this hypothesis, re-learning would be required to establish new spatio-temporal patterns whose temporal order and sequence would represent behaviorally relevant adaptations to changes in the environment or changes in the significance of the environmental events.

Highly overtrained animals might have neural structures that differ decisively from that observed during the beginning of training or without training. Accordingly, behavioral paradigms change the underlying system. It is nevertheless possible to define average representations. It is hypothesized that every individual experiences the same average environment. Only when there are significant deviations from this average environment, plastic reorganization occurs. Since this is to be expected a continuum, minor changes might easily be undiscovered.

8. Implications of POP for understanding neural mechnisms underlying normal, ongoing information processing

Recent work on short-term postontogenetic plastic reorganization of cortical functions has offered new insights in cortical organization. These insights are also beneficial when approaching the problem of normal ongoing information processing. In this sense the investigation of cortical plasticity offers a unique tool. Using various types of manipulations one can artificially create different sets of highly idiosyncratic layouts of cortical and subcortical organizations that utilize different types of processing strategies. Simultaneous assessment of the behavioral performance allows to establish a distinct relationship between the individuals neural representation and its accompanying level of performance [9–11,80,81].

Using a protocol of a few hours of paired peripheral tactile stimulation (PPTS) enabled us to study the relationship between RF size and discrimination performance [80,81]. The considerable increase of RF overlap associated by a loss of fine grained topology as found in acute rat electrophysiological experiments [80] was associated with an increase of the spatial 2-point discrimination performance as found in human psychophysical experiments [81]. Analysis of dynamic response properties revealed that the changes in geometrical aspects as expressed in enlargement of RF size were paralleled by prolonged response durations and changed RF dynamics which became more smooth. It is therefore concluded that the chain of changes includes an enlargement of RF size which causes an increase of RF overlap and an increase of the number of neurons activated by stimulating a selected skin site. Simultaneously, the response duration becomes longer, increasing the time over which the neurons are active. The smoothening of the RF dynamics leads to a more homogenous temporal pattern over time which also leads to a better synchrony of many neurons. As is well-documented from ICMS experiments, fast postontogenetic plastic reorganization alters the correlated activity between pairs of neurons [6]. It seems conceivable that all of these changes taken together are causally related to the increase of performance at a behavioral level. Though the first impression is the dramatic loss of topographic details preserved in small non-overlapping RFs, the resulting large RFs with high overlap that are altogether active over a much longer period of time seem to warrant the engagement of many more neurons than normal. The result is an increase in the level of psychophysic performance. The observed changes of the dynamic response properties suggest alterations of the processing dynamics throughout the entire pathway.

9. Outlook and perspectives

According to our definitions of learning, any sensory input is able to act as perturbation of an assumed normative state. Any information being utilized in this sense must pass different stages of the sensory systems. In higher stages this information is used to generate alterations of these structures which in turn act back to add interpretational constraints at lower stages thus generating specific response dynamics. It is assumed that under normal processing conditions there exists a steady state of requirements which reflect the current adaptational profile of an individual organism to cope with the actual requirements of its environment and which are reflected in the nature of the specific response dynamics. Only excessive deviations from this steady state can lead to measurable changes of the overall response properties with special emphasis on the dynamics.

It is argued that postontogenetic plasticity acts directly on timescales of normal processing by effecting and influencing the temporal structure of neuronal responses. In this view, there are no separate time domains of processing but the en-

vironmental events act directly on cortical information processing by changing and effecting the type and dynamics of interareal interactions.

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