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13 Do Primary Sensory Areas Play Analogous Roles in Different Sensory Modalities?

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We compare the properties of primary auditory, visual and somatosensory cortex in order to discuss whether the extraction and mapping of stimulus features shows equivalencies across sensory modalities. We propose that modality-specific differences in "early" cortical properties are largely a consequence of differences in receptor properties, and that early cortical processes and their implementation are similar across sensory modalities. This view is based largely upon the striking similarities of receptive field organization found in visual, auditory and somatosensory areas with respect to the spatio-temporal distribution of excitation and inhibition. By the same token, inspection of the shape and properties of cortical point-spread functions suggest substantial equivalencies across areas. Analysis of temporal aspects of sensory processing indicates that differences can be attributed to differences in subcortical and peripheral processing, resulting mainly from anatomical constraints and particularities. On the other hand, as exemplified by spontaneous activity and intrinsic oscillatory activity, differences found between cortical layers or those found for state-dependencies, such as wakefulness, attention or sleep, outweigh possible modality and area-specific differences. The common feature of multiple parametric maps observed in early sensory areas might reflect a rather general principle of cortical organization that allows the combination of local operations with a continuous representation of elemental parameters of the environmental scene, maintaining local neighbourhood relationships.

KEYWORDS: auditory, cortical maps, distributed processing, latencies, oscillations, parametric maps, primary sensory areas, receptive fields, receptors, somatosensory, spontaneous activity, temporal aspects of processing, temporal integration, thalamus, vision

1. INTRODUCTION

1.1. Role of Primary Sensory Cortices

What is the role of the representation and processing of the sensory environment in primary cortical fields? How do the principles underlying sensory processing differ among cortical areas? These questions are significant, since the current dominant model of cortex often uses the visual system as a frame of reference, thus, potentially biasing the general view.

To address these questions, we made a comparison between different sensory modalities. The structural framework in different sensory cortices is similar with respect to many aspects (Rockel *et al*., 1980) such as the global arrangement of synapses, axons, excitatory and inhibitory cell types, lamination, as well as vertical and horizontal connections (as discussed in some detail in other chapters). This could lead to the conclusion that the common features of cortical machinery implement algorithms, or a set of universal operations, rather than unique, modality-specific operations. On the other hand, cortical subregions have specific anatomical and physiological distinctions, and critical differences in their functional attributes. The clearest distinctions between subregions of sensory cortex relate to the modality-specificity of receptive field properties and the resulting functional organizations. In fact, visual, auditory, and somatosensory cortex have functional characteristics and parameter representations so different that it may seem unlikely that common cortical processes and mechanisms can subserve such diversity (e.g. see Luria, 1973). However, analysis of the functional properties of cortical neurones, in conjunction with the modality-specific subcortical processes reveals that many sensory cortical attributes reflect analogous, if not identical, local and distributed processing mechanisms. Each modality imposes some specific constraints on these processes and on their functional cortical representation. From a global perspective, we propose that primary sensory cortex in different modalities performs many of the same tasks. The underlying processes are based on analogous operations in different modalities, namely, activity- and correlation-based integration of convergent information by means of well-coordinated excitatory and inhibitory interactions.

1.2. Hypothesis

Different sensory cortices perform similar functions based on common rules in processing elements and mechanisms. Substantive modality-specific differences in peripheral signal properties are transformed subcortically to provide functional equivalency at the cortex. In the cortex, homogeneity of processing is evident in the spatio-temporal arrangement of excitatory and inhibitory interactions. Receptor-specific characteristics that remain at the cortical level are implemented by local arrangements, and not by the basic principles of the processing which is applied.

1.3. Synopsis

We discuss first the parallels and differences between vision, touch, and audition for signal properties of the environmental scene, receptors and receptor organs, and principles of subcortical processing. Here we will emphasize some properties of the auditory system, in order to highlight modality-specific differences in subcortical processes. We, then, compare properties of cortical processing with respect to modality-specific aspects of peripheral processing. We next assess receptive field properties, cortical maps and temporal processing in three primary areas—AI, VI, and SI—to test the notion of a unifying principle of early cortical processing. Next, we summarize experimental findings of cross-modal plasticity that support the idea of general, rather than modality-specific, cortical operational principles. We conclude by discussing briefly some potential consequences for future studies of sensory processing.

2. MODALITY CHARACTERISTICS OF SIGNALS AND SUBCORTICAL SYSTEMS

2.1. The Environmental Scene

Sensory organs scan the surrounding environmental scene in different physical realms, such as electromagnetic waves, air-pressure waves, and mechanical forces. Our interaction with the environment depends critically on the identification of objects within it. Delineation of objects, and formation of frame-independent representations of objects enables us to learn their effects on us, to attach behavioural significance to these objects, and to interact with them (Koffka, 1935; Gibson, 1966). The non-chemical senses—vision, touch, and audition—all have to solve the same problem: analysis of the environmental scene, or identification of objects in complex backgrounds. Characteristic and contingent features in the scene need to be integrated so that object recognition and background perception can occur. For example, features defining a picture of a cat, a sculpture of a cat, or the word "cat", for vision, touch and hearing, respectively, each need to be deconvoluted, coded, analyzed, identified and unified. "High level" processes that deal with the actual analysis of the scene, rely on higher-order correlations in some feature-space and on the comparison with previously stored information about the properties of objects, backgrounds, and events. "Low level" processes, in contrast, extract the information from the receptors, to construct the appropriate feature-space in which the separation of object and background can occur. We argue that the former processes are largely accomplished subcortically, and in the primary sensory cortices. They rely on lower-order correlations among spatial and temporal domains within and across different receptor types and sensory surfaces. The rest of this section refers only to these low-level processes.

2.2. Signal Statistics

Visual, tactile, and auditory objects have a number of properties in common such as edges (definable in space or time), and attributes of their internal features such as colour, texture, and coherent or incoherent frequency and/or amplitude modulations. Object motion relative to the environment, and across the receptor surface, provides data optimal for the extraction of relationships between different object properties. Different physical stimulus dimensions are represented by the nature of receptor organs. Each modality represents the lower-order statistical nature of the signals. Acoustic, somatosensory and visual ecologies share statistical similarities, and embody important differences. Thus, objects that reflect light may also generate and reflect sound, so that the spatial statistics of acoustic and visual environments may have similar scaling behaviour. On the other hand, differences between the visual and acoustic worlds exist: Objects that are visually opaque can be acoustically transparent. In combination with the different generation mechanisms for light and sound, acoustic and visual ecologies may have some different statistical properties that, consequently, entail distinct differences in sensory processing requirements. However, the resulting representational differences of an object by several modalities have to be brought into alignment at some level of processing, in order to allow multi-sensory integration which ensures perceptual unity and consistency in decision-making and behaviour (Stein and Meredith, 1990).

The statistical properties of the modality-specific environments can influence two major aspects of neuronal coding: *what* is represented and *how* is it encoded (e.g. deCharms and Zador, 2000). The *what*-aspect is reflected in the nature of the representational dimensions in feature space, as discussed above. Receptive field analysis (see section 3, below) reveals which features a neurone responds to. Each neurone represents specific values along several feature dimensions, depending on the probability of the occurrence of that stimulus aspect, as well as on the behavioural relevance of that range of values. An important influence of the stimulus statistics on receptive fields is demonstrated in the effect of temporal correlation among independent stimuli. An illuminating example is the effect of the artifical fusion of neighbouring digits of a hand (Clark *et al*., 1988) on its cortical representation. Normally, each finger is mapped in primary somatosensory cortex by non-overlapping receptive fields, that is, the neurones respond to stimulation of one finger alone. After surgical fusion of the skin of two adjacent fingers and extended use of the fused fingers by the monkey, the cortical receptive field boundaries cover both fingers, i.e. the normal discontinuity in the representation of the fingers is altered. This change in receptive field property relates to the high degree of spatio-temporal, correlated input to the fused fingers compared to the uncorrelated input to the fingers when they are used independently. In general, the extraction of spatio-temporal correlations and coherences across the multi-dimensional stimulus space is a critical principle, and underlies many aspects of the generation and representation of feature dimensions related directly to object properties.

Stimulus-response analysis can determine how a cell responds to a stimulus and helps one to understand how stimulus information is coded by the spike train. Approaches from information theory allow one to estimate the precision of the neuronal code, and the quality of the decoding scheme used by neurones and their networks (Nicolelis, 1996; Zhang and Sejnowski, 1999; Doetsch, 2000). This defines *how* environmental information is coded. Several studies (reviewed in Bialek *et al*., 1991; Atick, 1992) have shown that early visual stations, such as the retina and the lateral geniculate nucleus, are optimized—in an information-theoretic sense—for transmitting information about scenes that have natural spatio-temporal statistics. Psychophysical image-discrimination experiments in humans find that performance is best when the pictures have natural second-order spatial statistics (Parraga *et al*., 2000). Similar conclusions have been drawn for the auditory system using a mutual information metric for stimulus and spike trains. Attias and Schreiner (1998) found that neurones in the inferior colliculus of the cat code naturalistic stimuli more efficiently than stimuli with non-naturalistic distributions. Similar results have been found in the auditory systems of frog (Rieke *et al*., 1995) and song-bird (Theunissen and Doupe, 1989). In the somatosensory system problems in evaluating the statistical properties of tactile stimuli have slowed progress.

In combination, these considerations illuminate the idea that many aspects of the natural statistics of the environmental scene are imposed upon, and constrain sensory information processing. Some of these statistical constraints can be quite similar for optical, acoustical, and mechanical aspects of objects, and it is not unreasonable to assume that the neuronal processes underlying vision, audition, and somatic-sensation have developed similar mechanisms to exploit these properties for central nervous representation and coding. Conversely, a number of stimulus characteristics remain very much modality-specific and require special processing strategies to utilize and integrate that information.

Table 13.1.

Parameter	*Audition (A)*	*Touch (S)*	*Vision (V)*
Dimensionality	1	2	2
Laterality	+	–	+
Receptor Types	1	>4	2
Latency	short	short	long

2.3. The Receptors

All receptors have in common the fact that they encode intensity, duration and location of external stimuli. The most obvious distinction between the different sensory modalities are the different designs and spatial arrangements of the receptors that underlie responsiveness to a specific form of physical energy and its transformation into neuronal activity. The auditory system uses essentially a single receptor type, the inner hair cell, to convey information to the central nervous system about air pressure changes. The hair cells are arranged in a single line along the cochlea, that is, the receptor sheet is one-dimensional. Since the ear is a paired organ it provides laterality-specific information to assess correlated activity between the two sides. The eyes are also paired organs. The retina is a two-dimensional receptor sheet with two receptor types (rods and cones). The somatosensory system has a two-dimensional receptor sheet, and uses many more receptor types than vision and audition. More than ten receptor-types serve its function, with four receptors for mechano-sensation alone.

While each modality is highly specific, each modality also shares some properties with the other receptors. The main correspondences are in the dimensionality of the receptor sheet (S = V); in the laterality (A = V); and in the latency (A = S) domain. These parallels imply that each modality has a unique feature that distinguishes it from the others. The receptor-level based differences between the modalities create distinct processing regimes that exploit these properties to optimize feature dimensions for object-oriented scene analysis. The differences in these optimized processing schemes are reflected in the organization and function of the subsequent processing stages. However, the resulting feature maps, despite their many transformations, conserve the plan of the primary receptor sheet, at least up to the primary cortical level.

2.4. Sub-Thalamocortical Processing

Structural design, cell types, local circuits and function of the sub-thalamic processing stages, as well as the number of synapses between receptor and cortex differ, between the three modalities:

Vision: Retina –> Thalamus –> Cortex
Touch: Spinal cord –> Brain stem –> Thalamus –> Cortex
Audition: Spiral Ganglion –> Medulla/Pons –> Midbrain –> Thalamus –> Cortex

In the visual system, several transformations take place before the information arrives in the primary visual cortex. Within the retina, the two receptor types interact with several

local-circuit cells, and give rise to at least two (and likely more) anatomically and functionally distinct pathways. The local circuit cells are a common feature in all modalities, where they modify sensory processing and recombine information internally. The preferred stimulus information conveyed by the two main visual streams differs in various ways, including colour information, receptive field size, stimulus contrast, and temporal aspects (Ungerleider and Mishkin, 1982; Livingstone and Hubel, 1988; Maunsell, 1992; Merigan and Maunsell, 1993; Ungerleider and Haxby, 1994; Hendry and Reid, 2000). In higher mammals, the stream from the retinal ganglion cells reaches the thalamus directly, which then projects to the primary visual cortex. Thus, the main sub-thalamic station which introduces functional varieties and distinctions is at the retinal level, without further brainstem or midbrain processing.

In the somatosensory system, many receptor types encode tactile information. Their pathways remain parallel (that is, they do not converge), as they relay discriminable sensations, including fine touch, vibration, pain and temperature. The slowly adapting system, for example, is essential for tactile form recognition. This division of labour establishes, from the outset, a multidimensional representation of the tactile environment. Overall, the pathways from the receptors to the primary sensory cortical areas—via one brainstem station and the thalamus—provides, through considerable computational effort, a stepwise transformation from an isomorphic representation to a distributed one, in primary somatosensory cortex.

In the auditory system, an even larger amount of task-oriented processing is accomplished below the thalamo-cortical level. Many brainstem stations and one obligatory midbrain nucleus are involved before the information reaches the thalamus and cortex. In addition to frequency coding and information about timing, which originate directly from the activity patterns of the receptor sheet (the Organ of Corti in the cochlea), at least three other basic features have been computed by the time the information reaches the thalamus:

Sound localization: This dimensions uses differences in timing, and in spatial distribution of response strength between the receptor surfaces of the two ears to code spatial position. Unlike the visual and somatosensory system, a direct correspondence between activation of the receptor surface and object position in the external world is not possible. However, the position of an auditory object relative to the position of the two ears, in combination with the physics of sound propagation around the head, evokes unique activity patterns in the two cochleae. Differences in response timing and intensity between the two sides are used to compute the location of a sound source. This computation is capable of locating external sound sources in coordinates that are compatible with those of the other sensory modalities. Thus, in the superior colliculus, auditory space and visual space maps are superimposed (Middlebrooks and Knudsen, 1984).

Spectral integration: In hearing, the extent of spectral integration, or, equivalently, spatial integration in relation to the receptor surface, varies from narrow to broad. However, subsets of midbrain and cortical neurones display properties that are similar to the psychophysical properties of "critical bands" including an integration bandwidth that is insensitive to intensity changes (Ehret and Merzenich, 1988; Ehret and Schreiner, 1997). This property underlies phenomena, such as loudness perception and stimulus discrimination. While it is not understood how this property is extracted, it is not only a consequence of receptor and receptor-surface interactions, but must be generated in

subsequent stations. By the midbrain, this process is essentially completed (Ehret and Merzenich, 1988).

Periodicity: The analysis of coherent temporal modulations across the receptor surface underlies the identification of sound sources (e.g. a particular speaker), the distinction between simultaneously active sound sources ("cocktail party effect"), and it contributes to the perceptual grouping of acoustic objects (ranging, for example, from isolated vowels to words). While the neuronal basis of periodicity analysis is not understood fully, it involves several steps and is largely accomplished subcortically (Langner, 1997).

The many stations of the auditory brainstem probably reflect the number and computational complexity of feature dimension required before reaching the cortex. In contrast, the many receptor types in the somatosensory system, and the complex local retinal processing schemes in vision seem to accomplish the task of generating sufficient feature dimensions without equally extensive brainstem processing. Overall then, the sub-thalamocortical stations compute several aspects from the receptor surface activity, that are optimized for representing and analyzing the environment in a framework that allows further refinement and alignment of the various representations of the external world.

2.5. Thalamus

The thalamus is an obligatory nucleus for all three modalities. It has subdivisions in each modality that segregate sensory information prior to cortical processing, and it is a hub for descending (cortico-thalamic) control. The thalamic nuclei have relatively few cell types, mainly one type of output neurone and one or two types of local interneurone. It often is referred to as a relay nucleus, though this is an oversimplification since each nucleus modulates or transforms the signal passing through it. Indeed, the projections from sub-thalamic stations can remain anatomically and physiologically distinct. Examples of maintained segregation and pathway-specificity include magnocellular (fast-conducting) and parvocellular (slow-conducting) divisions in vision and audition (Hendry and Reid, 2000); tonotopic *vs* non-tonotopic pathways in audition (Winer, 1992); information for eye and ear laterality; cutaneous representation of face and body; slowly and rapidly adapting responses to cutaneous stimulation; and processing of discriminative sensation (high resolution) *versus* epicritic sensation (low resolution but with urgent behavioural qualities), such as pain and temperature sense. A possible reason for such segregation is that the different "channels" need to be optimized spatially and temporally at the cortical input level, for instance for binocular fusion, or higher spectral integration. From this point of view, the sensory thalamic nuclei may serve as staging areas for cortical processing.

An important functional property of thalamic neurones is their high synaptic security, which enables reliable transfer at high temporal precision. Thus, thalamic neurones follow stimulus repetition rates up to >100 Hz with time-locked responses, in somatic sensation and audition. Thalamic function may be less related to local receptive field modification and feature extraction then to state-dependent modulation and gating of activity forwarded to the cortex (for reviews see: Casagrande and Norton, 1991; Winer *et al.*, 1999). Strong modulatory influences from cortical feedback, and many extra-cortical sources have been described (e.g. Steriade and Llinas, 1988). Functionally, such complex modulatory systems may provide state-dependent synchronization or de-synchronization among different

cortical inputs (Traub *et al*., 1999), attentional amplification of receptive field properties (Zhang *et al*., 1997; Yan and Suga, 1999), and, overall, an affective colouring of the sensory experience. These modulatory effects are similar across modalities, suggesting a common operating principle at this gateway to cortex. This also suggests that the content and configuration of the modality-specific information in the thalamus is at an equivalent level of abstraction and integration. Thus, consequences of the modulatory processes imposed on the sensory stream at the thalamus operate on the same level of processing for the three modalities. For an excellent survey of thalamic function, see the review by Sherman and Guillery (2001).

3. MODALITY CHARACTERISTICS OF PRIMARY CORTICAL AREAS

3.1. Receptive Fields

Since its introduction more than 60 years ago, the concept of receptive fields (RFs) has constituted a powerful tool for the analysis of sensory systems. Hartline (1938) wrote: "The region of the retina which must be illuminated to produce a response in a particular nerve cell is termed the receptive field of that cell". Although we perceive the world as unitary, the neuronal elements can analyze only small portions of the environment. Knowing structure, organization and properties of RFs is indispensable for understanding their specific contribution to signal processing and their role in brain function. Consequently, receptive fields are widely used to define and map cortical neural activity into a parametric feature-space derived from either stimulus or computed variables. This analysis allows the characterization of the processing capacities of single cells. Historically, RF properties have been described in terms of "feature-detectors" and filters operating hierarchically at increasing levels of complexity and specificity. Below, some extensions and revisions of this original scheme are discussed. Figure 13.1, depicts characteristics of single cell receptive fields in visual, auditory, and somatosensory cortex. These differ greatly in shape, dimension, and dimensionality. In all of these examples, activity is represented systematically in the parametric space of the respective modality, such as the visual field, the "frequency space", and the skin location. More distinct and refined RF forms emerge in so-called "functional" spaces embedded in the respective modality. Here, neural activity is plotted as a function of a graded variation of a selected stimulus parameter, and the ensuing RFs are often referred to as "tuning curves". This approach allows both quantitative and qualitative analyses of an example of neuronal sensitivity to a given stimulus. Well-known examples include orientation tuning in vision, intensity tuning in audition, and grating resolution in somatic sensation.

Is there a common principle of RF organization despite these dissimilarities? By definition, RFs exist in the parametric space of the respective modality. Thus, the "coordinates" must be different and depend on the parameters under investigation. Inevitably there are substantial and substantive differences, since parameter spaces differ across modalities.

Closer inspection of RFs and tuning curves across modalities reveals at least one common aspect of RF organization: integration of excitatory and inhibitory inputs. Accordingly, the question of a possible common type of RF organization can be resolved by analysis of the spatial distribution and interaction of excitation and inhibition. Figures 13.2 and 13.3 show examples from visual, somatosensory, and auditory cortex. Although the RF structures

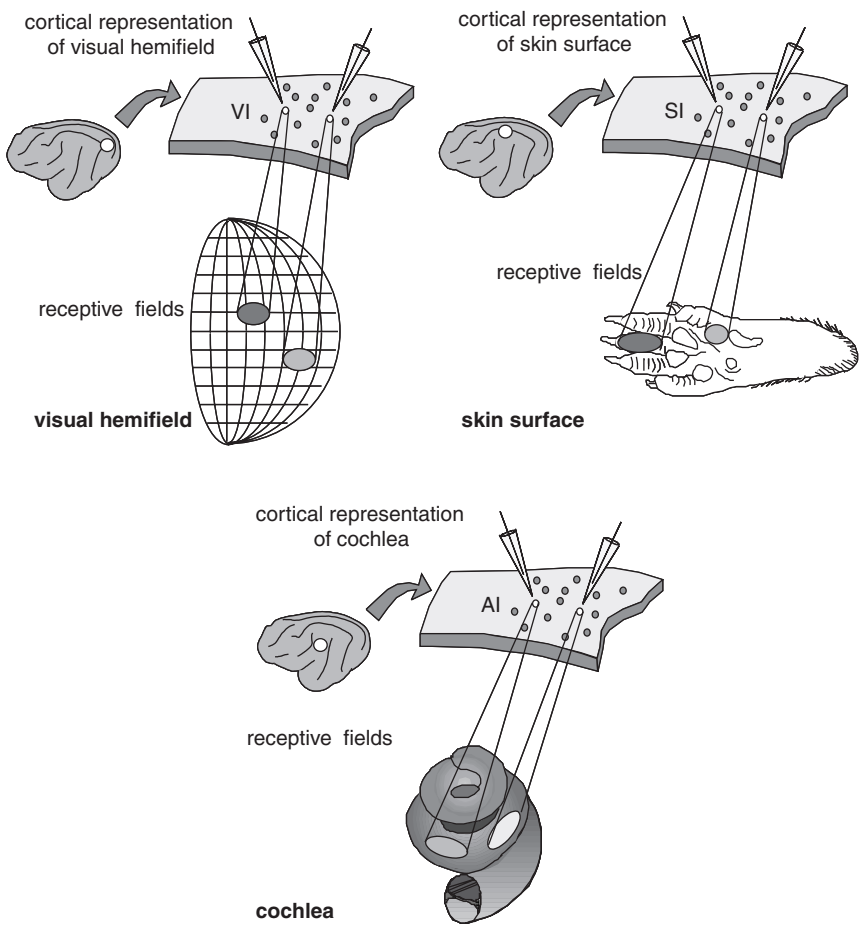

Figure 13.1. Examples of receptive fields (RFs) depicted in parametric space recorded in visual (top left), somatosensory (top right) and auditory cortex (bottom). As a rule, RFs in all modalities cover a certain circumscribed area in visual field, skin surface or frequencies, respectively, thereby providing a "window" to the outside world. Receptive fields are mapped by inserting microelectrodes, into the cortex (usually the middle layers), to record action potentials from single cells or multiple unit activity from small clusters of neurones. The receptive field is defined as that region on the sensory surface where stimulation evokes action potentials. This procedure maps activity recorded in the cortex into the stimulus space, which allows an easy and systematic way of parametric analysis. When moving the electrode to an adjacent location in the cortex, a systematic shift in the corresponding receptive field location will be encountered. A complete topographic map can be obtained when a large number of electrode penetrations is combined in such a way that the penetration coordinates are related to the corresponding receptive field coordinates. The inverse approach is taken when cortical activity distributions are measured. In contrast to the above, a fixed stimulus, ideally a small, "point-like" stimulus, is applied, and the entire activity in the cortex evoked by that stimulus is measured. This type of activity distribution is often referred to as "point spread function—PSF". Technologies often employed for this kind of analysis are optical imaging and fMRI. However, it should be noted that the PSF can be obtained using microelectrodes. In this case, single or multiple neurone activity evoked by the "point-like" stimulus is recorded, and its spatial distribution is derived from a systematic mapping at different locations. In theory, RFs and point-spread functions are the corresponding counterparts of a mapping rule that describes how input is represented in a topographic map. In practice, however, due to differences in threshold and due to particularities in methodological constraints, the two descriptors of cortical representations may yield different results.

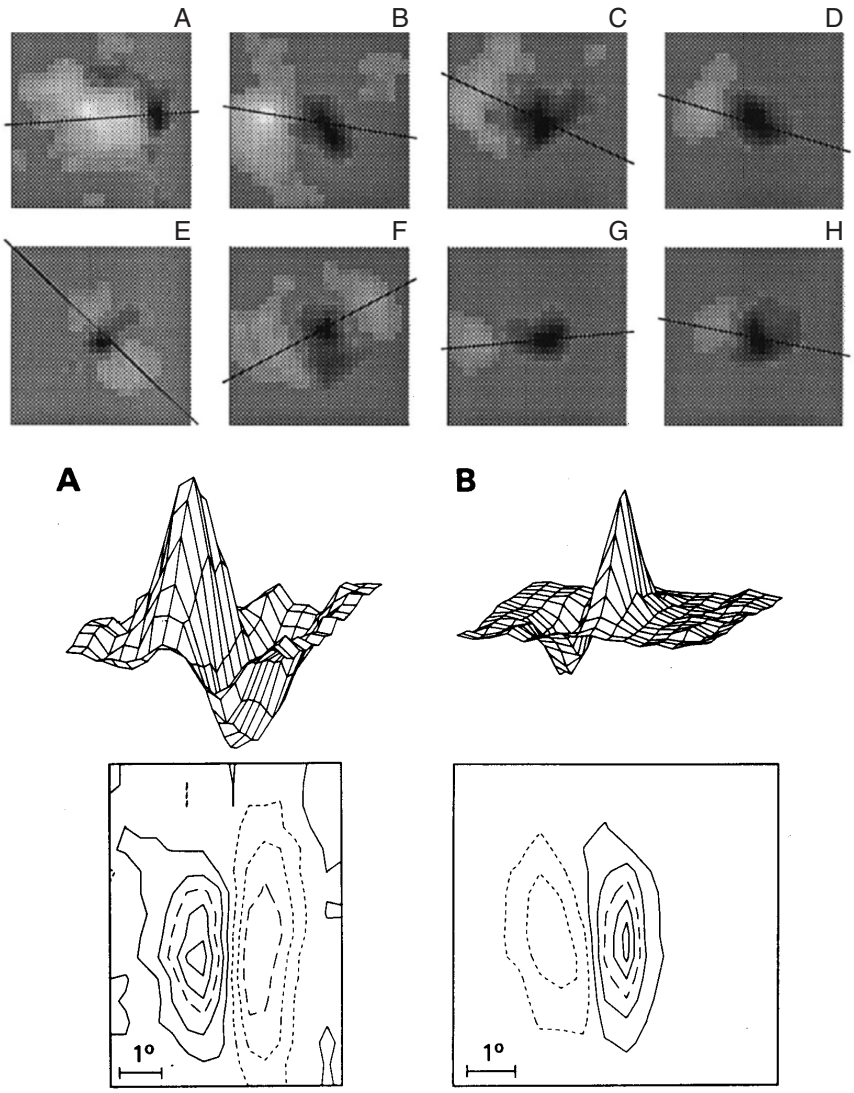

Figure 13.2. Two-dimensional RF profiles recorded in somatosensory cortex (top) and visual cortex (bottom). *Top:* RF structures observed in the hand representation of monkey area 3b. Black indicates excitation, white suppression. The sample RFs are meant to illustrate the wide range of combinations of excitatory and inhibitory areas. A–D and G, H: single inhibitory regions located on the trailing side (i.e. towards the distal aspects of the hand) of the excitatory RF region. E and F: two regions of inhibition on opposite sides of the excitatory region. The line through each RF passes through the excitatory and inhibitory peaks (modified according to diCarlo *et al*., 1998). *Bottom:* Two-dimensional response profiles of 2 typical simple RFs to illustrate variability in sizes, shapes, and placements of individual subregions (modified according to Jones and Palmer, 1987). The letter above each RF corresponds to the one-dimensional profiles shown in Figure 13.3. Reproduced with permission.

vary widely across modalities, they typically have a central region of excitation flanked by surrounding, or offset inhibitory regions (Figure 13.2). The two-dimensional nature of both retina and skin surface makes it challenging to distinguish visual from somatosensory RFs, because the structure of excitatory and inhibitory subregions in RFs of VI and SI

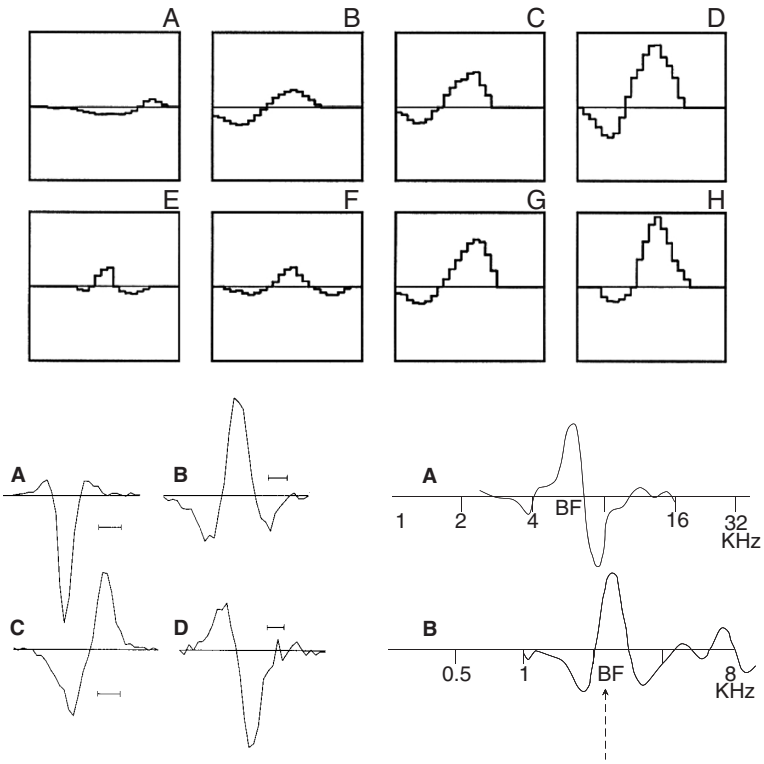

Figure 13.3. One-dimensional RF profiles recorded in somatosensory (top), visual (bottom left) and auditory (bottom right) cortices. The plots display the relative intensities of the excitatory and inhibitory components. Scale bars in bottom left panel indicate 1 degree. BF: best frequency. The letter above each RF in the top and bottom left panels corresponds to the two-dimensional profiles shown in Figure 13.2. Modified according DiCarlo *et al.* (1998) (top), Jones and Palmer (1987) (bottom left), and Shamma and Versnel (1995) (bottom right). Reproduced with permission.

neurones is quite similar (Jones and Palmer, 1987; DiCarlo *et al.*, 1998). An analogous sub-field structure has been described for auditory cortical neurones (Shamma and Versnel, 1987). However, due to the one-dimensional nature of the receptor surface of the cochlea, the RF structure found in AI is also one-dimensional, with inhibitory 'sidebands'. A striking resemblance between RF structures of all three modalities emerges in one-dimensional RF-profiles (Figure 13.3). This demonstrates a common principle of sensory processing, with a complex spatial arrangement of excitatory and inhibitory processes that, together, appear crucial for processing performed in each area.

A next logical step in discerning similarities in RF properties is to study RF organization directly in cortical coordinates, i.e. in the spatial distribution of dendritic activation. Unfortunately, because of technical difficulties, there is very little information available. It has been hypothesized that the often-dramatic forms of functional selectivity might arise from asymmetries and anisotropies at a cellular level. However, in spite of the improvement of anatomical staining techniques, this issue has not been sufficiently resolved. Early papers reported a substantial correlation between cell shape and functional cell types (i.e. "simple" and "complex") in the visual cortex (van Essen and Kelly, 1973; Lin *et al.*, 1979).

In a subsequent study, the dendritic arborizations of horseradish peroxidase-filled cells were reconstructed in three dimensions. There was no consistent relationship between orientation selectivity and the tangential bias of the dendritic tree. The width of the receptive fields was compared to the equivalent "width" of the tangential extent of the dendrites, and there was no significant relationship between the two widths. Accordingly, the tangential arrangement of the dendritic field does not appear to be important in determining the orientation selectivity, or the size of the receptive fields of neurones in the cat visual cortex (Martin and Whitteridge, 1984). Because of its peculiar morphology, the Meynert cell type has been suspected to mediate "direction" selectivity (Livingstone, 1998). In her model, excitatory synapses are activated sequentially along the asymmetric basal dendrites of the large pyramidal cells of Meynert. However, recent modeling studies indicated that even when the electrotonic asymmetries in the dendrites were extreme, as in cortical Meynert cells, the biophysical properties of single neurones could contribute only partially to the directionality of cortical neurones (Anderson *et al*., 1999). Accordingly, the authors suggested that most of the computation of direction of motion, over the range of velocities observed, must rely on network mechanisms, most probably using the local recurrent circuits of cortex.

In a series of studies, extracellular and intracellular recordings were made from neurones in the cat visual cortex, in order to compare the subthreshold membrane potentials, reflecting the input to the neurone, with the output from the neurone seen as action potentials (Douglas *et al*., 1988, 1991; Martin, 1988). The authors failed to find direct experimental evidence for the hypothesis that the selectivity of visual cortical neurones depends on shunting inhibition. More generally, they concluded that the intracellular recordings do not support models of directionality and orientation that rely solely on strong inhibitory mechanisms to produce stimulus selectivity. Taken together, most of the selectivity observed in cortical sensory areas may be functional rather than structural.

Other aspects of cortical processing may be shared by all modalities. These aspects relate to the crucial role of context and nonlinearities. Neurones in primary visual cortex have been characterized with respect to key physical features such as visual field location, orientation, motion direction, ocular dominance, and spatial frequency. These approaches allowed the analysis of neural representations within parameter spaces that are explicitly defined by physical stimulus attributes. However, many visual illusions, such as the perception of illusory contours (Kanizsa, 1976; von der Heydt *et al*., 1984; Ramachandran *et al*., 1994; Sheth *et al*., 1996; Mendola *et al*., 1999), indicate that the visual system must contain representations within parameter spaces without a physical counterpart. This agrees with the observation that single neurones exhibit complex, non-predictable behaviour, dependent on stimulus context (for review see Gilbert *et al*., 2000; Kapadia *et al*., 2000). The complex spatio-temporal response properties are plastic, and can be altered by stimuli outside the receptive field centre, or even outside the classical receptive field (Allman *et al*., 1985; Dinse, 1986; Gilbert and Wiesel, 1990; Sillito *et al*., 1995). Horizontal circuits within the cortex contribute significantly to local cortical processing (Bolz and Gilbert, 1989). Thus, cortical representations of peripheral activity deviate significantly from a simple feedforward re-mapping of sensory space (Ferster and Miller, 2000).

Particularly for the visual system, complex subsystems dedicated either to form or motion processing have been identified (Ungerleider and Mishkin, 1982; Livingstone and Hubel, 1988; Maunsell, 1992; Merigan and Maunsell, 1993; Ungerleider and Haxby, 1994). These pathways originate in the retina and can be traced serially in the visual pathway

up to functionally specific high-level areas. Similar anatomical substrates may exist for the other modalities. However, the actual degree of functional segregation or cross-talk between such subsystems is unknown (Romanski *et al.*, 1999; Recanzone *et al.*, 1999). In any event, the concept of two basic elements of sensory processing—form and motion—holds across modalities. Form is derived from two-dimensional representation of objects, and is best understood in the visual and somatosensory systems. In the auditory system, form contains the one-dimensional frequency space, as well as the time axis, in order to accommodate the spectral-temporal extent and structure of events such as vocalizations.

Objects move relative to the receiver and the background. Movement is represented as a systematic spatio-temporal displacement. Many lines of evidence suggest that the analysis of such displacements is crucial for the processing of objects (Metzger, 1932; MacKay, 1958; Reichardt, 1961; Burr, 1980). In both the visual and somatosensory modalities, perceptual illusions of apparent motion exist (Ramachandran and Anstis, 1983, 1986; Geldard and Sherrick, 1972; Kirman, 1974; Evans and Craig, 1991). In the auditory system, two types of movement can be distinguished: movement across the receptor surface and movement in external space. Frequency sweeps are directly analogous to visual and somatosensory motion with reference to the receptor surface, and result in similar perceptual illusions (e.g. Warren, 1970; Bregman, 1990). However, frequency sweeps that are part of an auditory object (e.g. in formant transitions of stop-consonants, or in diphthongs) are not necessarily equivalent to motion of external objects. Analysis of the motion of an external object in the auditory sense involves a complex interplay of spectral and temporal changes across the receptor surfaces of both ears. Perhaps, the neural machinery for the specialized processing of motion shares similar algorithms across modalities such as directional selectivity and temporal correlation/sequencing of activity across long distances of the receptor surfaces.

From these considerations of response profiles, it follows that RF characteristics, as viewed in a modality-specific framework can obscure the underlying mechanisms, which can be expressed in more general terms, spanning across modalities, such as spatial and temporal interactions of the distributions of excitatory and inhibitory responses.

3.2. Spatial Processing

3.2.1. Cortical maps

Early investigators of sensory cortical areas agreed that these areas re-map certain aspects of the external world, thereby preserving the local neighbourhood relationships in the environment. These representations are known as retinotopic (visual), somatotopic (touch) and cochleotopic (auditory) maps. All constitute systematic parametric representations across cortical space. Given the differences in the respective receptor arrays of the retina, skin and cochlea, these maps differ accordingly in design, and are not a direct, one-to-one representation of the world. This is particularly obvious on a fine spatial scale, where the considerable scatter of RF position is larger than, or in the same range as the required systematic shifts due to a topographic gradient in the map (Hubel and Wiesel, 1962; Albus, 1975; Sutter and Schreiner, 1991). On a larger scale, a clear topographic gradient is present, though distorted. The retinotopic gradient of the cortical map of the visual field is overlaid by other "functional maps". Such maps contain an orderly arrangement

of stimulus attributes for portions of the respective retinal locations (Hübener *et al.*, 1997; Kim *et al.*, 1999) but also exhibit discontinuities that result from the discrete organization of several of such attributes (Das and Gilbert, 1997). Visual functional maps for orientation of moving gratings (Blasdel and Salama, 1986; Swindale *et al.*, 1987; Bonhoeffer and Grinvald, 1991), direction of motion (Weliky *et al.*, 1996), and the spatial frequency of a moving grating (Shoham *et al.*, 1997; Kim *et al.*, 1999; Issa *et al.*, 2000) are now available and undoubtedly yet more such examples will be discovered as our knowledge of cortical representation deepens. In the auditory cortex, there is also evidence for multiple functional maps, that transcend simple frequency representations (Schreiner, 1998; Schreiner *et al.*, 2000). Thus, maps of sharpness of tuning, preferred intensity, direction of FM sweeps, and onset latencies have been suggested. A comparable system for the somatosensory cortex is the spatial segregation of slowly and rapidly adapting mechanoreceptors which form an "overlay" to the general somatotopic cortical map. However, evidence is still scant for other parameter maps analogous to those in audition and vision.

Besides these feature maps, in modalities with a paired arrangement of receptor organs (vision and hearing), there are maps for the inputs from the two organs: ocular dominance maps (Wiesel *et al.*, 1974; LeVay *et al.*, 1978) and binaural bands (Imig and Adrian, 1977; Middlebrooks *et al.*, 1980). No such lateralization maps are known for the somatosensory system. Interestingly, "disparity maps" have been described as an example of higher-order functional maps, that combine the information from the lateralization maps to form an additional parameter space (Burkitt *et al.*, 1998). A similar situation may exist for the auditory cortex where laterality information is readily expressed in binaural bands, whereas explicit maps of spatial information are less obvious (Furukawa *et al.*, 2000).

As noted above, parametric representations must reflect differences of the stimulus spaces. Thus, all maps known in the different modalities differ decisively from one another. A conventional way to obtain insight into the cortical coordinates of these maps is to study the spatial distribution of activation patterns in cortex. The activity pattern can be used to derive the so-called "cortical point spread function" (Fischer, 1972; Capuano and McIlwain, 1981; McIlwain, 1986). In contrast to functional maps, cortical activity is not represented in a parametric space, either by topography or in the stimulus space, but is directly recorded in cortical dimensions (cf. Figure 13.1). Due to technical restrictions, single electrode penetration maps can only reveal an approximate or incomplete picture of the point spread function (PSF). As new imaging techniques—such as optical imaging or the recent development of non-invasive imaging technology for humans such as PET or fMRI—emerge we can derive spatially continuous forms of the PSF, although the measurement itself is necessarily indirect because of the still-uncertain correlation between neural activation and cortical metabolism.

PSFs obtained from activity patterns recorded in VI, SI and AI under comparable imaging conditions with simple stimuli (small squares of light, small indentations of the digit skin surface, and tone bursts, each stimulus applied at moderate intensity) share some properties (see Figure 13.4). As a rule, the simple stimuli used are meant to be an experimentally-feasible equivalent of a "point" on the receptor surface. Although the different stimuli used are not qualitatively scalable, they activate only a small portion of the receptor surfaces. While a direct comparison of absolute size of the PSFs is not possible due to the incomensurate nature of the different stimuli, several basic characteristics of PSFs are shared across modalities:

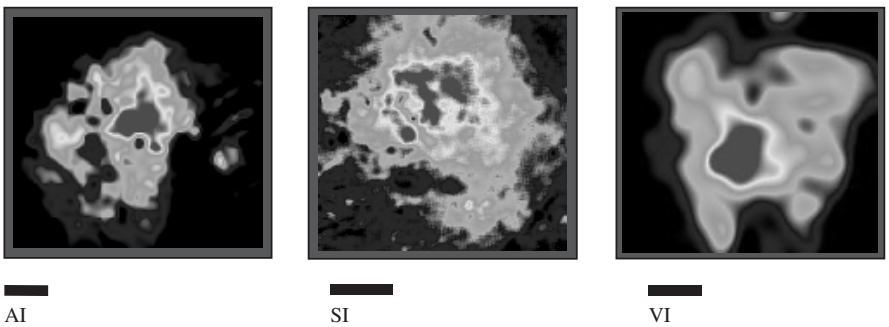

Figure 13.4. Point-spread functions, recorded by means of optical imaging in auditory (left), somatosensory (middle), and visual (right) cortices. AI: tone burst stimulation at 6 kHz delivered at 40 dB SPL, cat primary auditory cortex, scale bar 1 mm. SI: cutaneous stimulation of digit 3 of rat hindpaw, probe diameter, 1 mm, indentation, 250 to 500 µm, rat primary somatosensory cortex, scale bar 1 mm. VI: square of light (0.4 deg visual angle), flashed for 25 ms, luminance 0.9 cd/m^2 against background of 0.002 cd/m^2, cat primary visual cortex, scale bar 0.5 mm. AI modified according to Dinse *et al.* (2000), SI and VI unpublished data of B. Godde, T. Hilger and H.R. Dinse. (*see Color Plate 5*)

1. *size*: PSFs recorded in primary cortices involve a great portion of the total primary area, irrespective of simple, spatially or spectrally restricted stimuli (Grinvald *et al.*, 1994; Das and Gilbert, 1995 (VI); Godde *et al.*, 1995; Chen-Bee and Frostig, 1996 (SI); Bakin *et al.*, 1996; Dinse *et al.*, 1997, 2000 (AI)).
2. *symmetry*: PSFs usually are not simply concentric distributions of activity around the core of the stimulation. Rather, they are spatially highly asymmetric.
3. *compactness*: PSFs are patchy, indicating a non-monotonic decay of activity with distance from the center of stimulation.

While the PSFs recorded in VI and SI are rather similar, the PSFs recorded in AI differ from the others in terms of their shape (cf. Figure 13.4). PSFs for VI and SI are circular, in line with the two-dimensional receptor array arrangement. In contrast, PSFs recorded in AI have an elliptic shape. This might reflect the constraints of the one-dimensional cochlear receptor array, the specific central projection pattern of auditory nerve fibres (Brown and Ledwith, 1990), and specific central circuits. As in the RF comparisons, PSF analyses reveal many similarities once the differences in receptor sheet dimensionality are considered.

3.2.2. Topography and distributed activity

Functional and structural segregation into subregions (patchiness) represents another common property of sensory cortical fields. Many thalamo-cortical and cortico-cortical projections target several, non-contiguous regions. Correspondingly, neurones representing similar functional parameters also tend to cluster in small subregions rather then exhibiting smooth spatial gradients. Such patchiness has been used as evidence against the existence of strict parameter gradients in the various sensory cortical fields. However, considerations of self-organizing models (e.g. Kohonen and Hari, 1999; Swindale, 2000) suggest that both topographical gradients and local patches are necessary consequences of self-organizing algorithms optimized for representing several behaviourally relevant dimensions of environmental scenes. These functional maps are overlaid so as to ensure that many, if not all,

combinations of the different parameters are represented in cortex. Recent theoretical studies show that geometrical factors do not constrain the ability of the cortex to represent combinations of parameters in spatially superimposed maps of similar periodicity. Considerations of uniform coverage suggest an upper limit of six or seven maps. A higher limit, of about nine or ten, may be imposed by the numbers of neurones or minicolumns available to represent each feature within a given cortical microdomain (Swindale, 2000; Swindale *et al.*, 2000). Thus, several feature dimensions can be expected to be represented across VI, AI, and SI. The set of all values in a given dimension is not equally represented; ranges that are especially important for behaviour are expanded (Suga, 1984; Recanzone *et al.*, 1993). To provide the optimal range of combinations between different information-bearing parameters, complex spatial relationships between the various parameter maps are necessary (Obermayer *et al.*, 1990; Swindale, 1991). This general principle is evident in the gross similarity of maps in the different sensory cortical fields. From this point of view, each neurone, and each location in VI, AI, and SI can be understood as representing a specific set of many independent variables in the sensory environment. Topographically, each location on the cortical surface corresponds to a specific intersection of several systematic maps. Mathematically this forms a response vector, with specific direction and length in a multi-dimensional parameter space (e.g. Lennie, 1998). Based on anatomical studies (Lund *et al.*, 1993), similar conclusions have been drawn: the size-match between axonal patches and dendritic arbors should result in a maximal diversity of dendritic sampling (Malach, 1994).

There is agreement that physical attributes of sensory stimuli are encoded as activity levels in populations of neurones. Reconstruction or decoding describes the inverse problem, in which the physical attributes are estimated from neural activity. Reconstruction methods have been regarded useful, first in quantifying how much information about the physical attributes is present in a neural population, and second, in providing insight into how the brain might use activity arising from many neurones (Nicolelis, 1996; Zhang and Sejnowski, 1999; Doetsch, 2000).

Most of what we know in the visual cortex about functional maps, beyond orientation preference, comes from optical imaging techniques. This method allows the simultaneous assessment of entire maps, covering many square millimeters of cortex. Functional maps are calculated by finding, for each cortical location, the preferred parameter value, viz., that causing the largest change in light absorption. This approach employs a particular reconstruction scheme to decode information from the averaged activity distribution. It implicitly assumes that thresholded activity reveals pertinent aspects in brain functioning. However, this "winner-takes-all" approach is only one possible functional interpretation of distributed neural activity.

Are there alternatives? Recently, it became evident that a critical step for the investigation of how distributed cell assemblies process behaviourally-relevant information is the introduction of data analysis methods that could identify functional neuronal interactions within high-dimensional data sets (cf. Nicolelis, 1999). In fact, the introduction of the multi-neurone/multi-site recording technique made it possible to record from a large number of neurons simultaneously, even in awake and behaving animals (Abeles, 1991; Nicolelis *et al.*, 1997). This approach allows the exploration of dynamically-maintained distributions of activity, including aspects of cooperativity between neurones, on a single trial basis. For example, in a study devoted to exploring the representation of tactile information in three areas of the primate somatosensory cortex (areas 2, 3b and SII), small neural ensembles (30–40 neurones) of broadly-tuned somatosensory neurones were sufficient to identify correctly the

location of a single tactile stimulus on a single trial (Nicolelis *et al.*, 1998). Interestingly, each of these cortical areas could use different combinations of encoding strategies, such as mean firing rate, or temporal patterns of ensemble firing, to represent the location of a tactile stimulus. Thus, several distinct ensembles of broadly tuned neurones, in different regions of the somatosensory cortex contain information about the location of a tactile stimulus. In contrast to functional maps, distributed representations are characterized by poor selectivity of their constituents, and accordingly, little topographic specificity. Instead, it is assumed that each neurone contributes, in a weighted form, to each possible stimulus configuration.

Another (albeit related) approach was recently introduced in order to account for population activity at the level of spikes, recorded in early areas of sensory cortex. The goal was to visualize and to analyze cortical activity distributions, in the coordinates of the respective stimulus space, in order to explore cooperative processes (Dinse *et al.*, 1996; Jancke *et al.*, 1996; Kalt *et al.*, 1996; Erlhagen *et al.*, 1999; Jancke *et al.*, 1999; Jancke, 2000). Instead of asking how accurately the parameter of, for example, stimulus location can be reconstructed or decoded, the main interest was on analyzing interaction-based deviations of population representations, dependent on defined variations of stimulus configurations. Despite the fact that very different types of stimuli were employed, (squares of light *versus* indentations on the digit of the hand), comparable distance-dependent interactions could be demonstrated for visual and somatosensory cortex. This, again, suggests modality-independent modes of processing and representation of distance-dependencies (Dinse and Jancke, 2001a).

Taken together, there is convincing experimental evidence that sensory cortices contain large pools of neurones that act in concert to represent aspects of the outside world. Depending on the methodology used, the outcome emphasizes either the aspect of "parametric maps" or the notion of "distributed representations". In this scenario, parametric maps are often regarded as a mass activity-based feature detector, i.e. a rather robust representation of certain parameter regimes, invariant against further contextual influences. Accordingly, this view provides some problems concerning how plastic adaptive capacities can be implemented. The notion of "distributed representations" allows a higher degree of flexibility, at the cost of a less rigid representation of feature spaces. On the other hand, it has even been suggested that distributed representations might reflect a lack of orderly representational maps. Only further experiments and more refined techniques will solve these conceptual discrepancies in functional mapping. However, there are no clear modality specific differences in these general questions regarding principles of cortical organization.

3.3. Temporal Processing

Many aspects of temporal processing across modalities can be compared rather directly, because the time-axis reflects an absolute measure, rather than a parametric distribution of activity which would allow differences between modalities in input energy. We will now consider response latencies, repetition rate coding, RF-dynamics (i.e. the spatio-temporal, or spectro-temporal organization of RFs), and oscillatory behavior.

3.3.1. Response latencies

Cortical response latencies are basically determined pre-cortically, by the kinetics of the receptors, by subcortical processing and by properties of the propagating axons. There are

considerable differences in the temporal properties of the different receptors, and in the number of subcortical stages, which in turn results in significant timing differences across modalities. Axon properties such as myelination and size are comparable across modalities (Brown, 1987; Hunt and McIntyre, 1960). For the visual system, fast and slow conducting fibres constitute two segregated information channels that may play differing roles in form and motion processing (Ungerleider and Mishkin, 1982; Dreher *et al.*, 1976; Bullier and Henry, 1980; Petersen *et al.*, 1988). By contrast, segregated pathways in the somatosensory system that also may contribute to form and motion processing, that is, neurones with slowly and rapidly adapting responses, are not distinguished by different conduction times (Tremblay *et al.*, 1993).

Comparing cortical response latencies across modalities reveals significant differences, even given the uncertainty of comparing and scaling the stimuli (see above discussion of Point spread function). In any case, auditory and somatosensory latencies have the shortest latencies (ranging 10 to 20 msec), and visual latencies are the longest (40 to 60 ms). The somatosensory system has an unusual property: cortical latencies vary with skin position (in contrast to the ears and eyes, which have a fixed distance with respect to the cortex). Response latencies to hindleg stimulation can be twofold longer than latencies following vibrissa or foreleg stimulation. Thus, latencies in S1 reflect the distance between skin site and cortex. Other cortical factors such as synaptic integration and threshold behaviour may contribute to response latencies. Such factors probably do not contribute significantly to timing differences of peripheral and subcortical origin.

The significant differences across modalities in the time at which sensory information arrives in the cortex provide a clear modality-specificity. However, it also poses a problem when information from different modalities has to be combined to yield an integrative, behaviourally-meaningful output. This raises the question of how information from different modalities is combined. In one possible scenario, the slowest modality could set the pace (for an account on insula contributions to auditory-visual interactions via short-latency connections with the tectal system see Bushara *et al.*, 2001). Compensatory effects on sensory processing in blind subjects provide some insights. Late components of auditory event-related potentials (ERPs) have shorter latencies in blind than in sighted humans (Naveen *et al.*, 1998; Niemeyer and Starlinger, 1981; Röder *et al.*, 1996). In auditory discrimination tasks ERPs show an enhanced amplitude recovery in blind subjects as compared to normal sighted subjects, indicating an improved ability to process fast sequences (Röder *et al.*, 1999). Studies on the speed of language processing revealed a similar superiority for blind people, as compared to normal subjects (Röder *et al.*, 2000). On the other hand, the texture segmentation and visual search capacities in deaf subjects did not exceed that of age-and gender-matched hearing subjects. Rather, deaf school children showed deficits in visual processing, which were partially compensated in adult deaf subjects (Rettenbach *et al.*, 1999). These findings from blind and deaf subjects indicate that sensory deprivation has no general effect on processing times, resulting either in acceleration or deceleration. The data are compatible with the hypothesis that the multi-sensory processing speed in normal subjects arises from integrative processes, which are dominated by the slowest information stream. Once the modality with the longest latencies is removed, sensory processing is accelerated.

3.3.2. Repetition rate coding

Temporal integration, as expressed in repetition rate coding or sequence representation, is the capacity of cortical cells to respond to consecutive stimuli. In the periphery and the

thalamus many neurones in each modality can follow high repetition rates, of more than 100 events/s. In contrast, cortical cells usually have a low-pass characteristic which limits the following of more than 10 to 20 events/s, in all modalities (Movshon *et al.*, 1978; Creutzfeldt *et al.*, 1980; Foster *et al.*, 1985; Simons, 1985; Philipps *et al.*, 1989; Nelson, 1991,a,b,c; Gardner *et al.*, 1992; Reid *et al.*, 1992; Merzenich *et al.*, 1993; Brosch and Schreiner, 2000; Krukowski, 2000). It has been proposed that specific properties of the NMDA-receptor channel kinetics mediate this reduction in stimulus-following capacity (Thomson and West, 1993; Crair and Malenka, 1995; Denham, 2000; Krukowski, 2000). In addition, GABAergic mechanisms might contribute to this property (Dykes *et al.*, 1984) as well as fatigue and depletion of synaptic transmission (Chance *et al.*, 1998, Galarreta and Hestrin, 1998; Wang and Kaczmarek, 1998; Buonomano, 1999, 2000). Presumably, these all act in concert to constrain the representation of fast event sequences in the cortex. Further work shows that active behaviour such as exploration can modulate the temporal processing capacities, compared to passive stimulation (Fanselow and Nicolelis, 1999; Moore *et al.*, 1999), and that plastic reorganization alters and modifies temporal processing (Kilgrad and Merzenich, 1998; Buonomano, 1999; Dinse and Merzenich, 2002). Thus, in the cortex there is a significant reduction in repetition frequency response compared to subcortical processing. Such uniformity is another argument for homogeneity of cortical sensory processing across modalities.

3.3.3. RF-dynamics

It has been known for decades that RFs have complex spatio-temporal behaviour (in the visual cortex) or spectro-temporal behaviour (in the auditory cortex) involving the time domain. This is seen, when the complete temporal profile of neurone responses is assessed (de Boer and Kuyper, 1968; Podvigin *et al.*, 1974; van Gisbergen *et al.*, 1975; Aertsen and Johannesma, 1981; Eggermont *et al.*, 1981; Krause and Eckhorn, 1983; Jones and Palmer, 1987; Shevelev, 1987; Best *et al.*, 1989; Dinse *et al.*, 1990; for an update of more recent results see: Eckhorn *et al.*, 1993; DeAngelis *et al.*, 1993; Dinse, 1994; Wörgötter and Eysel, 2000; Dinse and Jancke, 2001b; Dinse, 2001). The substantial changes in RFs over time indicate a significant interaction of space and time—or of spectrum and time—as well as temporal dependence of tuning characteristics (Dinse *et al.*, 1990, 1991; Dinse and Schreiner, 1996; Ringach *et al.*, 1997; Ghazanfar and Nicolelis, 2001). Dynamic RFs are a common denominator in all sensory modalities. Their basic dynamic properties are influenced by aspects of latencies that reflect subcortical processes and by aspects of response duration. Response duration is governed by feedforward, feedback, and lateral interactions (von Seelen *et al.*, 1986; Krone *et al.*, 1986; Dinse, 1994; Dinse and Schreiner, 1996; Omurtag *et al.*, 2000).

These interactions constitute an essential and unifying feature of cortical functions. Another interpretation of RF dynamics attempts to link cortical processing dynamics and dynamics of the environment (Dinse *et al.*, 1993; Dinse, 1994; Wiemer *et al.*, 2000). Sensory signals typically have complex time-variant properties, which are manifested on a variety of time scales, that may be reflected in the dynamics of RFs. In the auditory system, one can differentiate timing based on the period of syllable sequences, in the range of hundreds of ms, from the duration of consonants and formant transitions, in the range of only 10 to 20 ms, from onset information, whose precision is in the millisecond range (for single events). In the visual system, the timing schedule provided by eye movements also imposes ecologically relevant dynamics. For the somatosensory system the movement of

objects across the receptor surface reflects largely the velocity of limb movements relative to the objects (in the range of hundreds of milliseconds) and, by vibrational correlates, also reflects the texture properties (in the range of tens of milliseconds). RF dynamics may represent specific adaptations for processing inherently time-variant signals specific for each modality. A common feature of cortical signal processing would undergo some specific adaptations to match the requirements of the signal space.

3.3.4. Oscillations

Perhaps the most widely recognized but least understood electrophysiological activity of the cerebral cortex is its characteristic electrical oscillations, which comprise a broad spectrum of periodic events from high-frequency oscillations (30–90 Hz, the so-called gamma range) to frequencies as low as seconds or minutes (besides ultradian and circadian rhythms). Stimulus-evoked oscillatory responses in the 10 Hz range have been studied for several decades at cortical and subcortical levels (Bishop and O'Leary, 1936; Chang, 1950; Andersen and Andersson, 1968). However, at present the analysis of these low frequency oscillations is purely phenomenological, and it is uncertain whether the different low-frequency patterns seen in different brain regions have common origins and functions, despite their temporal similarities (Dinse *et al.*, 1990; Kopecz *et al.*, 1993; Ahmed, 2000; Cotillon *et al.*, 2000; Miller and Schreiner, 2000). Accordingly, their functional role remains obscure. Low-frequency oscillatory events are phase-locked to sensory stimulation, which explains their appearance as distinct oscillatory peaks in post-stimulus-time histograms (PSTHs). They cover frequencies between 5 to 20 Hz, encompassing several EEG bands. A detailed analysis of area- and modality-specific properties of low frequency oscillatory patterns recorded in 4 visual cortical areas, as well as in AI and SI (Dinse *et al.*, 1997) found low-frequency oscillations in all areas. These differed in probability of occurrence, and each area had a characteristic frequency range of its own. Thus, in VI, frequencies ranged from 8 to 22 Hz, in AI from 6 to 10 Hz, and in SI from 10 to 20 Hz. Accordingly, the phenomenon of low-frequency oscillations is very general and found in all areas. There is a striking uniformity of the overall pattern, but there are substantial differences in the sequence and timing of the individual oscillatory peaks, differences that reflect an area-specific signature of the oscillations. Interestingly, human auditory and visual EPs also differ in their amplitude-frequency characteristics: Frequency maxima for visual stimuli were significantly higher than for auditory stimuli (Schurmann and Basar, 1999). Recent inactivation experiments in AI revealed that both the auditory thalamus, and the auditory sector of the thalamic reticular nucleus, but not the auditory cortex, have a role in the genesis of a specific type of low frequency stimulus-evoked oscillations (Cotillon and Edeline, 2000). The tendency to oscillate can be modified through external stimuli with appropriately chosen spatio-temporal properties (Miller and Schreiner, 2000). These findings suggest a common drive or origin of this oscillatory behaviour, that is modified by localized parameters.

High-frequency gamma oscillations were described first for the olfactory bulb by Freeman and co-workers (Freeman, 1968; Freeman and Skarda, 1985; Eeckman and Freeman, 1990). They have since been found in visual (Eckhorn *et al.*, 1988; Gray *et al.*, 1989), auditory (Franowicz and Barth, 1995; MacDonald and Barth, 1995; Sukov and Barth, 1998) and somatosensory (MacDonald and Barth, 1995; Jones and Barth, 1997; Hashimoto, 2000) cortex, and they have gained much attention due to their possible involvement in

"feature binding" and higher cognitive processes (Eckhorn, 1994; Singer, 1998; Sauve, 1999). In contrast to low-frequency oscillations, high-frequency oscillations are not stimulus-locked, so they are only detectable in single trial analyses, or by computation of the power spectra of spike trains, and not in PSTHs that are based on a temporal averaging. High-frequency oscillations cover a wide frequency range, from the higher beta range (~20 Hz) to >100 Hz. There is debate about the stimulus-specificity of these oscillations and uncertainty about the features and states that drives them optimally. While moving bars of light or moving gratings drive high-frequency oscillations strongly, flash stimuli are unable to induce oscillations, although they have the same perceptual relevance (Tovee and Rolls, 1992).

Several studies have emphasized the importance of high-frequency oscillations in tasks relevant to behaviour, and there is ample evidence for a task-specific emergence of such oscillations (Hamada *et al*., 1999). Comparing oscillations across several neocortical areas shows that the spatial patterns formed by synchronous activity change when the contingency of reinforcement is reversed, vary with respect to stimuli, and had a dependence on context and learning, as seen in the olfactory bulb and prepyriform cortex (Barrie *et al*., 1996). In monkeys performing a motion-discrimination task, significant temporal correlations exist between simultaneously recorded pairs of neurones, in areas MT and MST and other extrastriate cortical areas. Interestingly, temporal decorrelation of MT and MST neurones could be used to detect the stimulus, but synchronization did not convey specific information about its direction of motion and was, thus, unlikely to contribute to behavioural performance (de Oliveira *et al*., 1997).

While the functional role of this type of oscillation remains unresolved (Eeckman and Freeman, 1990; Ghose and Freeman, 1992; Kirschfeld, 1992; Tovee and Rolls, 1992; Kirschfeld *et al*., 1996, Ghose and Freeman, 1997; Singer, 1998; Engel *et al*., 1999), it is clear that even single cells display complex patterns of oscillatory behaviour across the whole frequency spectrum (Nunez *et al*., 1992; von Krosigk *et al*., 1993; Gray and McCormick, 1996; Jones *et al*., 2000). Accordingly, the origin of high-frequency oscillations is usually considered as a combination of cellular and network properties. For the present purposes, there appear to be no modality-specific effects, since high frequency oscillations are found in all areas discussed. The variability from cell to cell, or across behavioural states certainly exceeds any modality-specific aspect. However, comparative studies across modalities might reveal more specific insights into the functional role and relevance of cortical oscillatory patterns.

3.4. Spontaneous Activity

The most conspicuous neural activity in sensory cortices occurs in the absence of sensory stimulation. The interpretation of this "spontaneous" activity, as either random background noise, or as functionally-relevant signal, has remained controversial. The high level of spontaneous discharge emanating from the retina, the cochleae, and several mechanoreceptors may reflect true noise, since it is believed to result from the stochastic nature of transmitter release from the receptors (Koerber *et al*., 1966; Rodieck, 1967). On the other hand, it has been argued that "ongoing activity" in higher brain centres might contain codes for global states and conditions, that reflect meaningful aspects of brain function, as yet unknown to the experimenter, and usually uncontrolled (Perkel and Bullock, 1968; but see: Miller and Schreiner, 2000). Spontaneous activity has also been shown to play an

important role in creating and maintaining connections in the developing nervous system (Shatz and Stryker, 1988; Penn *et al.*, 1998). Straightforward ways of analyzing spontaneous activity are to utilize spike count and frequency, while more sophisticated tools include analysis of interval distribution. In the case of a completely random series of action potentials, the interval distribution follows a Poisson-process. As neurones are characterized by refractory periods, such processes are more adequately described as renewal processes (Cox and Miller, 1965; Moore *et al.*, 1966; Perkel *et al.*, 1967; Wilbur and Rinzel, 1983). Even after decades of extensive study there is still controversy about the nature of the underlying interval distribution, as well as the nature of variability and stationarity (Softky and Koch, 1993; Shadlen and Newsome, 1998; Nawrot *et al.*, 2000). However, perhaps more importantly, spontaneous activity in central nervous stations can show pronounced deviations from the predictions of a Poisson-process, as reflected in spontaneous oscillations.

A general scheme holds that the spontaneous activity is lowest at cortical levels, but increase successively when one descends a sensory pathway. According to Herz and coworkers (1964), retinal ganglion cells discharge at >30 spikes/s, geniculate (thalamic) neurones at about 15 spikes/s, and visual cortical cells at about 5 spikes/s. Similar conditions have been reported for auditory and somatosensory system (Kiang *et al.*, 1965; Goldstein *et al.*, 1968; Willis *et al.*, 1975; Peschanski *et al.*, 1980), although skin receptors can vary more widely in terms of spontaneous activity (Bergmans and Grillner, 1969; Dykes, 1975; Johnson and Hsiao, 1992).

There is some agreement that the dynamic state of the brain is reflected in the level and character of spontaneous activity (Evarts *et al.*, 1962; Noda and Adey, 1970; Burns and Webb, 1982; Miller and Schreiner, 2000; Steriade, 2000), which appears to hold across modalities. For example, increasing depth of anaesthesia leads to decrease of spontaneous firing rates from 2.5–11 Hz during light anaesthesia, to 0–2.5 Hz in deep anaesthesia (Armstrong-James and George, 1988). This implies that the level and character of ongoing-activity is subject to substantial modifications, making it difficult to assign a characteristic pattern of spontaneous activity to a given area. In fact, there are very few studies devoted to unravelling possible modality-specific aspects of spontaneous activity (cf. Eggermont, 1990). Swadlow (1990) published a series of papers on ongoing activity in awake rabbits, recorded in different cortical areas. He classified cortical recording sites according to layer and projection pattern. For the forelimb representation of somatosensory cortex he reported discharge frequency differing substantially between laminae, by a factor of 5, with highest rates found in layer V. Similar lamina-specific differences were found in visual cortex recordings in the same preparation (Swadlow, 1988). Interestingly, intra-areal comparison of the forelimb and vibrissae representations in the somatosensory cortex confirmed laminar differences, but these differences were higher—up to a factor of 15—in the vibrissae representation (Swadlow, 1989). According to these data, differences in spontaneous discharge rate appear comparable between areas for a given layer, but can be large across layers, or within a single sensory representation. Average spontaneous activity recorded in the motor cortex was about 11 Hz ranging from 0.4 to 26 Hz (Glass and Wollberg, 1973). These authors reported a slight correlation with cortical depth suggesting that this might be due to layer-dependent variation in excitability or richness of dendritic arborization.

With regard to higher-level areas, prefrontal cortical areas are involved in the temporal organization of behaviour, and are discussed in relation to working memory (cf. for reviews Fuster, 2000; Goldman-Rakic, 1996). Spontaneous activity levels typically are in the range of about 5 Hz (Harden *et al.*, 1998; Gulledge and Jaffe, 1998). One key aspect of

working memory functions consists of the temporary holding of goal-relevant information about sensory stimuli, even if that information is no longer present at the time of response generation. In this sense, prefrontal neurones have the property of "memory cells", in being active during delay periods, suggested by changes in firing rates. Accordingly, the level of ongoing activity is strongly modulated, by a factor of 10, in a highly task-specific way. However, it should be noted that data about comparable firing rates do not imply that variability and interval distributions are comparable as well.

Independent of the level of spontaneous activity, the instantaneous frequency undergoes dramatic variation on a very short time scale (Werner and Mountcastle, 1963; Tolhurst and Movshon, 1983; Holt *et al*., 1996; Gutkin and Ermentrout, 1998), which is also true for stimulus-driven activity (Tomko and Crapper, 1974; Schiller *et al*., 1976; Manley and Mueller-Preuss, 1978; Heggelund and Albus, 1978; Vogels *et al*., 1989). Recent development of real-time imaging made it possible to monitor large-scale spatio-temporal changes of cortical activity on a millimeter scale, and at a millisecond time resolution, by means of voltage-sensitive dyes (Lieke *et al*., 1989). Recording both ongoing and light-evoked spatio-temporal activity patterns in cat visual cortex revealed that the variability of evoked activity appeared deterministic, resulting from the dynamics of ongoing activity. It has been suggested that these dynamics might reflect the instantaneous state of cortical networks. In spite of the large variability, evoked responses in single trials could be predicted by linear summation of the deterministic response and the preceding ongoing activity (Arieli *et al*., 1996). Tsodyks *et al*. (1999) were able to demonstrate that the firing rate of a spontaneously active single neurone depends strongly on the instantaneous spatial pattern of ongoing population activity in a large cortical area. At the level of cortical maps, very similar spatial patterns of population activity were observed both when the neurone fired spontaneously, and when it was driven by its optimal stimulus. Accordingly, these studies provide a direct link between spontaneous activity and cortical representations arising from sensory stimulation. The processes underlying the transformation of random and uncorrelated peripheral activity to central spontaneous activity (that can show spatial and temporal correlations) remains to be resolved.

In conclusion, spontaneous activity is a typical characteristic of primary cortical areas. It appears comparable in frequency, particularly when compared to sensory periphery or subcortical stages which all discharge at a much higher frequency. Spontaneous activity at the cortical level does reflect different neurological states and functional properties of neuronal assemblies. There is little evidence for modality-specific characteristics. It remains to be seen whether the striking correlation of the dynamics of spontaneous activity pattern with the organization of sensory processing exists in non-visual modalities as well.

4. CROSS-MODAL PLASTICITY

We have noted some functional and potential conceptual similarities between primary sensory cortical areas. It should then be possible, in principle, to substitute one cortical area for another, if the machinery and the implemented processing algorithms in different sensory cortices are indeed the same (or at least very similar). Building on work by Frost and Metin (Frost and Métin, 1985; Métin and Frost, 1989), Sur and colleagues (Sur *et al*., 1990; Sharma *et al*., 2000; von Melchner *et al*., 2000) tested this hypothesis directly (see also the chapter by S. Pallas, this volume). In immature ferrets, they eliminated the

auditory input to the auditory thalamus, and redirected retinal fibres to the auditory portion of the thalamus, which in turn projected to the auditory cortex. The auditory cortex, completely deprived of auditory input, but supplied with information originating in the retina, developed functional properties resembling VI receptive fields and topographies. Single cells were tuned for direction- and orientation-selectivity, and showed organized retinotopic and orientation maps (including "pinwheels"). Moreover, horizontal connections in the rewired and remodelled AI were more like those in normal VI than those in normal AI. The rewired animals responded to visual stimulation as if they experienced vision, and did not treat such stimuli as an auditory event (von Melchner *et al*., 2000).

If the experiment involved auditory input to the deafferented VI, there remains the question of which auditory input is necessary to change VI into a replica of AI. It appears unlikely that input from the auditory nerve alone would suffice to generate all AI properties in VI, since major feature dimensions are not yet computed at this peripheral level. Rather, the output from the midbrain station, the inferior colliculus, would seem to be the more appropriate input to the visual thalamus needed to induce the formation of functionally correct AI properties in VI. It alone has an equivalent set of basic feature dimensions to generate a sufficiently complete and computationally accessible cortical representation of sound. This proposition awaits direct experimental investigation.

The elegant experiments described above provide direct evidence that different cortical processing systems may be interchangeable, and are capable of implementing the processes and algorithms used in other modalities. Since developmental and reorganizational plasticity undoubtedly was involved in the process of "rewiring" the auditory cortex (e.g. Buonomano and Merzenich, 1998), the experiments do not prove that the same algorithms are implemented in AI and VI, but only that AI can implement the VI algorithms. Furthermore, the experiments show that sensory and perhaps perceptual qualities are modality-specific, and not cortical field-specific. Such findings strongly support the hypothesis proposed at the outset of this chapter, that the different primary sensory cortical fields can be viewed as analogous structures anatomically, and perhaps more importantly, functionally.

5. GENERAL CONCLUSION AND PREDICTIONS

We have reviewed evidence germane to the hypothesis that the different sensory modalities perform similar tasks, under similar statistical constraints imposed by sensory input, with the same structural elements, and, possibly, similar circuits: The common task is to transform receptor images to cortical representations of external objects preparatory to action. While the peripheral sensory systems have different structural adaptations at the receptor level, the neuronal implementations of the required algorithms at the early cortical level show much congruence and may be interchangeable between modalities.

The main lines of argument in support of this notion were as follows:

(a) *Functional and structural heterogeneity in the subcortical systems:* The role of the subcortical system may be understood as a transformation of receptor surface information into a multi-dimensional parameter space. This process adapts the different sensory streams to a thalamo-cortical stage that applies common schemes for information processing and modulation. The activity across a receptor surface codes information about local and global correlations in the scene, shown by coactivation

and sequential activation of the receptors. This permits higher-order stimulus correlations, including contextual events, to be integrated in this process. Multiple subcortical systems construct relevant, functionally-independent feature dimensions. Since the nature of the stimuli and the corresponding receptors differ, the nature of these subcortical processing stages also differs between the modalities.

(b) *Functional and structural homogeneity in the thalamo-cortical system:* The role of the thalamus and primary sensory cortex is, according to this view, to establish a compatible representation of different feature dimensions, that allows extraction of object form, attribute, and location relative to the background, for an analysis of the environmental scene. Subsequent sensory cortical areas use these base features to analyse the global features of objects and to establish object representations that become less dependent on the perceptual frame-of-reference. Furthermore, higher processes establish the relationship of objects to the environment and the self, perform multi-sensory integration, assign and evaluate the behavioural significance according to context, and as a basis for action.

(c) *Computational homogeneity in the thalamo-cortical system:* At the thalamo-cortical interface a similar set of operations is implemented that involves thalamo-cortical, cortico-cortical and cortico-fugal network interactions. The main mechanisms of these algorithms include the spatio-temporal arrangement of excitatory and inhibitory processes in columnar and horizontal networks, that operate on spatially- and temporally-related streams of input.

While only few of the actual processing schemes have been dissected and modeled in detail, the processing that is accomplished at the thalamo-cortical level appears to be largely a local, differentiating analysis, as opposed to a global, integrative one. A case in point is the contrast-independent processing of orientation-selectivity of visual cells (for review see Ferster and Miller, 2000; Anderson *et al*., 2000). The algorithms used in this task are based on local correlations and anti-correlations of inputs, as expressed in local excitatory and inhibitory circuits. Such computations use temporal and spatial information arising from peripheral receptors. Correlations among the activity in the receptor space are exploited to establish computationally-useful and independent dimensions, that are representative of external objects and scenes, and not just the receptor-surface activity. These computed entities may serve several needs of central processing: (i) They precede a general representation of the external world; (ii) They are a basis for the determination of object form and position; (iii) They create reliable and stabilized feature properties, as reflected in the intensity and contrast invariance of orientation tuning in the visual cortex, or in independent tuning properties of some auditory neurones in the presence of background noise ; (iv) Such computed features allow subsequent multi-sensory integration, by transcending a pure receptor representation of the sensory events; (v) Finally, they allow the assignment of significance to particular environmental conditions, and ultimately, the emergence of different perceptual attributes and the initiation of behaviour. Certain of these tasks may take place beyond the primary sensory field.

(d) *Multi-sensory integration:* The integration of information from several sensory modalities has many advantages for the individual, including increase of salience, removal of ambiguities, and unified object characterization and perception (e.g. Stein and Meredith, 1990). To accomplish such integration, the information from the different modalities has to be represented at an equivalent level of abstraction, and in

compatible frames-of-reference. Many aspects of multi-sensory integration take place after the early cortical representation suggesting that major aspects of representational equivalence have been established at that level. For example, it has been demonstrated that auditory-visual stimulus-onset asynchrony activates a large-scale neural network of insular, posterior parietal, prefrontal, and cerebellar areas (Bushara *et al.*, 2001) permitting auditory-visual interaction phenomena such as the ventriloquist, and the McGurk illusions. Subsequent processing can then employ similar mechanisms for similar tasks. Furthermore, it would be advantageous if attentional and emotional modulation of these representations takes place at equivalent stages of processing, to maintain compatibility between sensory systems. The common nature of the modulatory influence at the thalamus suggests that the early cortical processing operates at equivalent levels across the three modalities (cf. Sherman and Guillery, 2001).

(e) *Cross-modal equivalence:* The induction of visual receptive field properties and map organization in AI after re-routing of sub-thalamic channels convincingly demonstrates that the normally-observed functional differences between early sensory cortical areas is not a consequence of immutable field-specificity but largely due to subthalamic preprocessing. The processing capacities in the primary cortical fields therefore have the same potential for expressing specific algorithms. However, they can function somewhat differently according to the actual input.

From these general principles of cortical processing equivalencies, a number of specific predictions can be made. Among them are the following:

- Given the joint 2-dimensionality for vision and touch, functional maps should be present in SI that are comparable to the many aspects described for VI, including orientation sensitivity, and direction selectivity.
- The emergence of spatial frequency maps (relative to the receptor sheet) should also be a common factor. Spatial frequency in the visual system can be regarded as equivalent to the spacing of frequency bands in the auditory system. Given that this aspect is coded in functional maps in VI and AI, a corresponding spatial-frequency coding scheme should be present in SI.
- The visual cortex shows a relationship between spatial frequency maps and orientation maps. A similar relationship could be predicted for the somatosensory cortex. (One should keep in mind that map expression and map interrelations can be quite weak on a local and cellular scale.)
- Ocular dominance bands in the visual cortex have a specific relationship to orientation maps and, perhaps, to spatial frequency maps. Cortical domains with low spatial frequency tend to lie in the centre of the ocular dominance columns (Hübener *et al.*, 1997). Accordingly, the position of binaural bands and spatial frequency/bandwidth distribution in auditory cortex may show a systematic relationship as well.
- The inhibitory push-pull mechanisms invoked for contrast-independent orientation selectivity (Troyer *et al.*, 1998) may also be found in somatosensory orientation processing and, perhaps, in auditory processing of spectral-shape information.
- "Feature maps" are not invariant, resistant to variations of stimulus configuration, context or timing parameters. For example, direction selectivity of visual neurones is strongly dependent on the direction of a moving texture background (Orban *et al.*, 1987; Dinse and Krüger, 1990). Also, in SI and AI, there is evidence that spatial/spectral

and probably also temporal topography can be modified substantially by behavioural discrimination training (e.g. Recanzone *et al*., 1992, 1993; Wang *et al*., 1995; Beitel *et al*., 1999). The cortical mechanisms that govern these processes should hold for all modalities.

The common feature of parametric maps observed in early sensory areas might reflect a rather general principle of cortical organization and function, potentially holding also for all other cortical areas. The fundamental processing step consists of a local operation, modified (contextually) by long-range connections. As this type of processing is performed within a two-dimensional sheet, it warrants the combination of local operations based on excitatory and inhibitory interactions, with a continuous representation of parameters, maintaining local neighbourhood relationships. While local processing obeys *per se* rules of proximity, the two-dimensional sheet allows one to define proximities of various kinds. For sensory areas, the "representation" of the outside world implicates both two-dimensionality, and proximities within the various types of physical worlds. In this sense this scheme is highly intuitive for early cortical representation, where it is reasonably clear what is represented. However, this scheme has been shown to hold also for intermediate states: An example is the highly specialized and detailed maps as described by Suga and coworkers in echolocating bats (e.g. Suga, 1984). Because of the highly specialized ultrasound environment of bats it was possible to deduce and then to identify higher-order maps that contain ordered representations of echo frequency and echo delay.

The main problem in higher cortical areas arises from the fact that the behaviourally or computationally relevant parameter space is unknown and, in principle, is difficult to deduce. The nature and properties of such parameter spaces need to be determined to understand cortical processing outside the primary sensory or motor domains. For example, it is likely that there are highly abstract parameter spaces representing a profile of a face in terms of its emotional expression. In any case, the basic principle is to compute and assemble behaviourally relevant aspects of proximity, or similarity and dissimilarity in the projected parameter space.

In principle, "parametric mapping" can be regarded as equivalent to "distributed processing". Differences that have been pointed out between these two concepts are mainly methodological, and arise largely from peculiarities of the reconstruction algorithms (e.g. the optical imaging-based feature maps are just due to an "iceberg effect", by ignoring a large portion of neural activation). While "parametric-mapping" is more intuitive because it relates directly the sensory representations to known physical features, we believe that the concept of "distributed representation" encapsulates better the representational and computational principles expressed in the brain, and this concept holds equally in lower (or early) and higher cortical areas.

The appearance of modality-specific differences and modality-independent properties of brain organization and function offers an opportunity to investigate systematically the underlying functional and structural constraints and consequences. Among the questions that can be addressed from a more general point of view are the following: What is the basis and consequence of modality-specificities? Why and how are certain general aspects of cortical processing modified in particular ways? What is the consequence of such modifications for the evolution of higher brain functions in humans?

The emphasis of common structures, mechanisms, and operational goals in primary sensory cortex, in support of the notion of functional equivalency, does not imply a perfect

correspondence across areas. An evolutionary advantage and consequence of the apparent homogeneity of cortical organization is the richness in potential network characteristics that can be realized. The substrate for cortical processing can apply in a flexible manner, during development and learning, to a wide range of environmental and behavioural conditions. However, the influence of these conditions on the different modalities may be quite similar. In any case, it remains to be seen whether the local circuit interactions and functions are identical in different modalities or merely constitute similar classes with different solutions in each modality. We are now ready to discover the local network properties and the algorithms which are implemented for a number of primary cortical processes in different modalities. A refinement of the modality-comparative approach to this difficult but exciting and fundamental problem of brain function could decipher this mystery.

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