Research report

Sensory cortical dynamics

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Abstract

Sensory cortical networks are commonly regarded as stable, changing only in the face of prolonged alteration of sensory input. There is increasing evidence, however, that the functional connectivity of cortical networks changes significantly, but reversibly, in response to conditions of sensory stimulation similar to those encountered in everyday life. In this review, we provide examples of sensory cortical dynamics at the single neuron and neural population levels. The dynamics detected at both levels of experimental observation suggest that a brief exposure (tens of milliseconds to tens of seconds) to sensory stimulation is accompanied by changes in the capacity of cortical networks to process and represent environmental stimuli. Candidate cellular mechanisms and the potential benefits of such stimulus-driven, rapid, and fully reversible sensory cortical dynamics are discussed. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Although understanding of the neural basis of perception is far from complete, it is clear that the computations that underlie perception are carried out quickly, a necessity if the challenges posed by an ever-changing environment are to be met successfully. For instance, Thorpe et al. [47] demonstrated that humans can make sensory decisions—determining whether or not a complex scene contains a particular element—in less than 200 ms. Given the rapidity of this decision, it seems likely that cells involved in processing the information needed for this task rely primarily on rapid synaptic neurotransmission (e.g. AMPA and NMDA receptor mediated excitatory neurotransmission, and GABA$_A$ receptor mediated inhibitory transmission). Traditionally, fast neural computation is viewed as occurring in essentially stable or 'hard-wired' networks; that is, networks whose processing characteristics are independent of their recent history of activation. On a much longer time scale (e.g. days or years), it has been established that cortical networks can undergo substantial changes in functional connectivity in response to prolonged alterations in the pattern of sensory drive (i.e. experience-based cortical plasticity, [5]). These long-term changes in functional connectivity are believed to involve changes in synaptic efficacy and/or axonal sprouting.

These two views of the information processing characteristics of primary sensory cortex—a fixed circuit capable of rapid processing, and a plastic network capable of long-term change—are conventionally regarded as distinct features of cortical networks. The two extremes, however, may not be as dichotomous as is commonly believed. Rather, we propose that they form opposing ends of a continuum of functional states that can be expressed by primary sensory cortex, each state having information processing capacities maximally consistent with the properties of the stimuli the network processed in a preceding temporal interval. Central to this alternative view is the idea that a stimulus applied either continuously or intermittently at a sufficient rate evokes an orderly temporal continuum of functional states in primary sensory cortex. We refer to the hypothesized temporal progression of functional network states associated with temporally extended sensory stimulation as 'cortical dynamics'. The available experi-

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mental evidence leads us to believe that natural sensory stimulation evokes cortical dynamics which (1) occur over a time scale of tens of milliseconds to many minutes; (2) are associated with an orderly temporal progression of changes in the receptive field properties of primary sensory cortical neurons; and (3) involve a repertoire of linked cellular mechanisms, each requiring unique conditions for its activation, and each exhibiting a distinct time course of operation.

In this brief review, we present evidence obtained using both single neuron and neuronal population recording methods which supports our concept of sensory cortical dynamics. We also introduce a substantial literature describing cellular mechanisms with attributes compatible with short-term, reversible, use-dependent changes in sensory cortical networks. We conclude with a discussion of the potential functional benefits of cortical network dynamics.

2. Single neuron dynamics

Contrary to the view that the response properties of primary sensory cortical neurons are fixed in the short term, there is considerable experimental evidence that the selectivity and response characteristics of sensory cortical neurons evolve continuously during the presentation of a stimulus. For example, the selectivity of individual sensory cortical neurons has been shown to change dramatically and rapidly (in tens of milliseconds) after stimulus onset. Sugase et al. [45] reported that the first 50 ms of the response of neurons in macaque inferior temporal cortex conveys global information about the visual input provided, while the same neurons encode much finer information about the stimulus later in the response. Specifically, the authors found that stimuli consisting of pictures of various faces elicit a robust transient response, but only faces with particular expressions could drive a neuron to fire for up to 500 ms after stimulus onset. Similarly, Dinse et al. [10] reported that for more than 50% of the neurons in cat primary visual cortex (V1), orientation tuning is largely absent during the period of high frequency firing typically elicited < 60 ms after stimulus presentation, but develops progressively in the next 20–40 ms (for similar findings see references [37,43]; Celebrini et al. [8] report contradictory results). Dinse et al. [10] also found that the receptive field size and end-stopping properties of striate cortical neurons exhibited rapid dynamics (i.e. their value depended on the time after stimulation at which the measurement was made). These results led Dinse et al. [10] to conclude that V1 cortical neuron 'selectivity evolves from an early state of non-selectivity'. It is important to note that changes in RF properties on the time scale of tens of milliseconds may in some cases reflect delayed inputs arising from other cortical

regions (e.g. feedback), from neurons in the same cortical region (e.g. inputs relayed via long-distance horizontal connections), or from feedforward inputs which arrive with different latencies (e.g. low contrast information in the visual system evokes responses in cortical neurons with a longer latency than high contrast inputs).

The reports that the selectivity of visual cortical neurons undergoes substantial and progressive modification with time after stimulus onset have much in common with published findings on the response of primary somatosensory cortical (SI) neurons to skin brushing or vibrotactile stimuli. Lee and Whitsel [25] studied the response of single SI neurons in monkeys to repetitive brushing stimuli applied to the hairy skin of the forearm. They found that when the interval between successive brushing stimuli was less than 5 s, the mean firing rate of some units decreased progressively across multiple presentations of the stimulus while that of other neurons gradually increased. Importantly, these changes in SI neuron firing rate were frequently accompanied by changes in receptive field dimensions and/or directional selectivity. In a more recent study of SI neurons in both cats and monkeys, Whitsel et al. [53] used sinusoidal cutaneous flutter stimulation with a duration between 2–30 s. At stimulus frequencies between 10–25 Hz, but not at higher-frequencies (e.g. 50 Hz), SI neurons that receive their principal input from RA-type skin mechanoreceptors were found to become better entrained with continuing stimulation of the receptive field center (Fig. 1). Such dynamic modifications in the capacity of SI RA neurons to signal direction of stimulus motion across the skin, or frequency of vibrotactile stimulation within the frequency band 10–40 Hz, are apparently mediated by central nervous system mechanisms because similar effects do not occur in the response of skin mechanoreceptive afferents whose receptive field is stimulated in the same way [25,52].

Consistent with the results from SI cortex, Muller et al. [33] reported that a brief (500 ms) presentation of a sinusoidal grating resulted in stimulus-specific adaptation of V1 cortical neurons such that the response of the same cell to a second presentation of the stimulus applied a short time later (1–3 s) was reduced. This rapidly occurring adaptation had the consequence that the orientation tuning of V1 neurons was sharpened significantly by the adapting stimulus.

Other studies have investigated the effects of longer periods of sensory stimulation (lasting for several tens of seconds) on the response properties of neurons in primary sensory cortex. Studies of sensory cortical dynamics on this time scale have shown that such stimulation is accompanied by substantial changes in the selectivity of individual neurons. For instance, pre-exposure of the receptive field ('adaptation') of a V1 neuron to gratings of a specific spatial frequency was
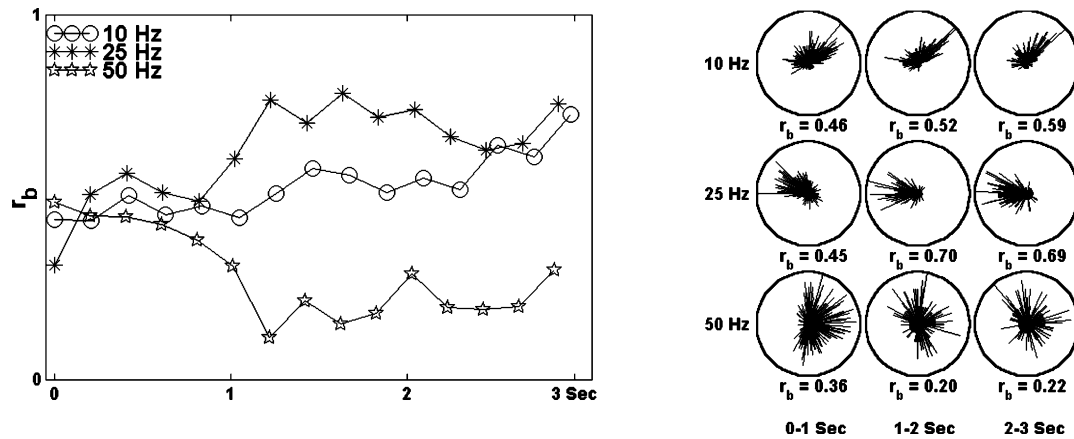
Fig. 1. *Left*: Neural entrainment as a function of time for an RA-type SI neuron. Neuronal entrainment was estimated using r_b, a measure of dispersion in the phase of spike firing derived using circular statistics (see [52] for details). Note that the entrained response to sinusoidal vertical skin displacement stimulation—indicating the neuron's capacity to signal stimulus frequency using a periodicity code—changed systematically after the onset (at time 0) of 10, 25 or 50 Hz stimulation. The temporal evolution of entrainment is different at the different frequencies of stimulation—at 10 and 25 Hz entrainment increased progressively during stimulation, but entrainment decreased at 50 Hz. *Right*: Rows of polar plots for each frequency of stimulation illustrating the dispersion of phase of spike firing within selected time periods ($0-1$, $1-2$ and $2-3$ s after stimulus onset). The degree to which this neuron's spike discharge activity was phase-locked to the different frequencies of vibrotactile stimulation was not different between $0-0.5$ s after stimulus onset, but became increasingly different with continuing stimulation. As stimulus duration increased the neuron became more strongly entrained to both the 10 and 25 Hz stimulus, but its capacity to signal 50 Hz stimulation degraded. The RF of this cell was restricted to the volar surface of the tip of digit 3 on the contralateral hand. Peak-to-peak amplitude of all stimuli was 350 μm. All stimuli were applied to the RF center using a 5mm diameter cylindrical probe. In the absence of stimulation the probe indented the skin by 0.5 mm

shown to lower the neuron's subsequent response to similar gratings, but not to gratings of differing spatial frequency [32,40]. Thus, exposure of the receptive field to a grating of a given spatial frequency systematically alters the spatial frequency tuning of V1 neurons. Recovery from adaptation occurred over several minutes. Analogous effects have been reported for the temporal frequency tuning of V1 neurons [41], for the direction selectivity of neurons in V1 and in area MT [14,30,35], and for orientation tuning in V1 [12]. These changes in selectivity appear to involve a stimulus-specific change in contrast gain. Following the presentation of a high contrast stimulus, a V1 cortical neuron's contrast sensitivity function shifts towards higher contrasts; that is, the neuron becomes insensitive to stimuli of low contrast. Similarly, adaptation to low contrast makes the neuron sensitive to low contrast stimuli, but causes the response to saturate over a wide range of high contrast stimuli [34]. Following adaptation to a particular high contrast pattern, contrast sensitivity is reduced for stimuli similar to the adapter but largely unaffected for other stimuli [32], thus giving rise to the specificity of adaptation effects. Importantly, changes in contrast gain exhibit interocular transfer and are not observed in the lateral geniculate nucleus, lines of evidence strongly suggesting that this effect is attributable to cortical mechanisms [3].

Sensory stimulation lasting for periods as long as several minutes has been found to alter the response properties of primary sensory cortical neurons for up to tens of minutes. These modifications in RF properties

are so long lasting that they blur the usual distinction between the reversible changes described in the preceding paragraphs and those long-term (essentially permanent) changes regarded as cortical plasticity. For instance, Pettet and Gilbert [36] investigated the receptive field properties of V1 neurons following the presentation of an artificial scotoma: a uniform pattern of moving bars interrupted by a blank region that covered the receptive field of the neuron being studied. Following several minutes of exposure to this condition, most neurons recorded in V1 of anesthetized cats showed a dramatic increase in receptive field size (by a mean of 5.2 times). Interestingly, when a V1 neuron that had undergone such a receptive field expansion was stimulated inside its classical receptive field, the receptive field expansion disappeared more rapidly (usually within several minutes) than in the absence of such stimulation. This finding may indicate that recovery from the effects of repetitive stimulation is an active process in which the network returns more quickly to its initial state when a new stimulus appears than when it is left to recover passively. In a later study, Das and Gilbert [9] found that when the same conditioning protocol was carried out repeatedly in the same cell, the receptive fields tended to get locked in an expanded state, suggesting that the dynamics induced by their artificial scotoma were sufficient to induce long-term, essentially permanent changes in the functional connectivity of V1 cortex. Minutes-long sensory stimulation has also been shown to alter the orientation tuning of V1 neurons [12]. Specifically, presentation of an oriented

drifting grating to a V1 neuron for 10 min was shown to shift the optimum orientation away from the orientation of the adapting stimulus, due both to a reduction of the neuron's responses to stimuli with an orientation similar to that of the adapting stimulus and to enhancement of the response to orientations different from the adapting stimulus.

In summary, there is abundant experimental evidence that the presentation of a sensory stimulus can substantially but transiently alter the response properties of sensory cortical neurons. The effect of persistent stimulus drive continues for some time after stimulus withdrawal; that is, sensory stimulation appears to leave a persisting 'trace' in sensory cortex. In general, longer exposure to a sensory stimulus leads to a stronger modification of sensory cortical neuron response properties, and a larger and more persistent trace.

3. Population dynamics

While evidence concerning stimulus-driven dynamics in single sensory cortical neurons has been accruing for decades, detailed information about the temporal evolution of the neuronal population response to persistent or repetitive sensory stimulation has become available only within the past few years. In general, these studies have shown that the changes in response observed at the single-cell level are paralleled by substantial and orderly dynamics occurring at the level of the responding cortical neuronal population. Tommerdahl et al. [48,50] have reported that the spatial extent of the intrinsic optical signal elicited in SI cortex decreases with a characteristic time course during a 10 s, 25 Hz vibrotactile stimulus. The decrease in the size of the activated SI area is frequently accompanied by an increase in intrinsic optical signal strength in a local region at the center of the stimulus-activated cortical field. Interestingly, Tommerdahl and colleagues find that the particular form of SI cortical population dynamics depends on the type of stimulus drive provided. For instance, the initial response of cytoarchitectonic area 3b to 25 Hz flutter, to 200 Hz vibration, or to noxious skin heating stimulation of the same skin site is strikingly similar [48–50]. At later times, however, obvious differences among the population responses were found to emerge. Specifically, the response to 25 Hz flutter stimulation in area 3b shrinks in size, but with continuing stimulation is relatively well-maintained in magnitude. The response to both 200 Hz vibration and to noxious skin heating stimulation, on the other hand, dissipates rapidly and, in many instances, disappears altogether. The optical signal at the end of 200 Hz or skin heating stimulation frequently has a polarity opposite to that widely believed to be associated with neuronal excitation, perhaps indicating global SI neuronal inhibition.

The finding that the size of the responding SI cortical population decreases during persistent stimulus drive has been reported in other functional imaging studies. In a voltage-sensitive dye optical imaging study of rat barrel cortex, Kleinfield and Delaney [21] found that repetitive stimulation of a single whisker initially activates an extensive cortical region, but that within ∼1.2 s of stimulus onset the spatial extent of the pattern shrinks rapidly. The reduction in the spatial extent of the signal was due largely to a loss of signal from more peripheral parts of the responding cortical territory while the signal intensity of the central area remained unchanged. Cannestra et al. [6] found that the response measured by intrinsic signal optical imaging or intravascular fluorescent dye imaging in human and rat somatosensory cortex decreases during continuous sensory stimulation (10 s). Interestingly, a second presentation of an adapting stimulus led to a signal of substantially reduced intensity, while the post-adaptation presentation of a novel stimulus evoked a signal in the same cortical territory which was near-normal in both areal extent and magnitude.

Population recordings using scalp electrodes have provided data consistent with findings obtained using functional imaging methods. Kelly and Folger [20] reported that EEG driving responses recorded from the scalp of a human subject during the presentation of repetitive cutaneous flutter stimulation underwent pronounced changes in amplitude and topographic organization during the 4 s period of stimulus delivery. The topography of the response evoked by flutter stimulation of a given locus on digit 2 evolved rapidly toward that evoked in the same subject by direct periodic microstimulation (using a percutaneous microelectrode) of a single RA-type afferent fiber that innervated the same skin region. Kelly and Folger [20] also reported that this topographic shift in the EEG response was accelerated by increasing stimulus amplitude or frequency, and by decreasing the time interval between stimulus presentations. Collectively, these findings indicate that the mechanism responsible for the shift in the spatial locus of the cortical response is sensitive to stimulus conditions, and that its effects may dissipate slowly after the termination of skin stimulation. Magnetoencepholography (MEG) recordings in humans have revealed a similar stimulus carry-over or 'memory' effect. In a study of echoic memory Lu et al. [26] required subjects to compare the loudness of an auditory probe stimulus with that of a standard stimulus. Performance was found to depend strongly on the time interval between the presentation of the probe and the standard stimulus: the loudness match was best for short intervals and decreased with longer intervals, with performance level reaching a plateau for

inter-stimulus intervals of ~ 8 s. The authors found that the strength of the N100 component of the MEG evoked by the probe stimulus (the component of the signal that appears 100 ms after stimulus onset) was reduced when it was preceded by the standard stimulus. Most importantly, the time course of recovery for the amplitude of the N100 component matched closely that of the psychometric performance curves of the subjects; that is, the amplitude of the N100 component was unaffected by the preceding standard stimulus for interstimulus intervals greater than ~ 8 s. The authors concluded that subjects' performance relies on a form of short-term sensory memory which is manifest as a trace that persists in primary sensory cortex after termination of the standard stimulus.

In summary, a diverse set of neuronal population recording studies using a variety of technical approaches (optical imaging, EEG, MEG) shows that repetitive or persistent sensory drive reliably causes a substantial reduction in the size of the responding cortical neuronal population and an altered response to subsequent stimulation, particularly if subsequent stimuli are similar to the adapting stimulus. These population-level observations are thus strongly consistent with the evidence obtained in studies of single cortical neuron dynamics.

4. Mechanisms of dynamics

That the response properties of sensory cortical neurons undergo substantial transient stimulus-driven change is not surprising given a rich substrate of potential cellular and synaptic mechanisms which could contribute to these dynamics. For instance, the response of a neuron to even the most basic stimulus—the injection of depolarizing current into the soma—depends on its recent activity. Due to the presence of calcium-activated potassium channels, the firing rate of pyramidal cells during depolarizing current injection rapidly decreases. As a result, if depolarizing current injection is preceded by a period of neural discharge and associated calcium influx, it will evoke a lower spike firing rate than after a period of quiescence. Intracellular recordings in invertebrates have shown that the activation of a calcium-dependent hyperpolarizing current induces 'forward-masking', the ability of a sensory stimulus to make a cell unresponsive to subsequent stimulation [44]. Modeling studies suggest that a similar effect may occur in cortical pyramidal cells [51]. Recently, a sodium-dependent potassium conductance has been found to be activated by persistent sensory drive in cat striate neurons [38]. This current appears to underlie the tens-of-seconds long postsynaptic hyperpolarization [7,39] which may, in turn, mediate long-lasting changes in the contrast gain of visual cortical neurons [34].

The effects of repetitive stimulus drive need not be exerted solely via ion channels located in the somal membrane. The presence of a rich diversity of voltage-gated ion conductances in dendrites could form a substrate for activity-dependent modification of cortical neuron response properties (reviewed in Magee [27]). For instance, repetitive backpropagation of action potentials into the dendrites of cortical pyramidal neurons has been shown to lead to prolonged sodium channel inactivation (requiring 2 s for 80% recovery; [19]). Since dendritic sodium channels are involved in boosting distal synaptic input [24], inactivation of these channels would be expected to reduce the efficacy of distal excitatory synaptic inputs. In general, the manner in which dendrites process inputs depends strongly on the state of their active conductances. Since recent activity can alter the state of these conductances, the manner in which a distributed pattern of synaptic input to the dendrites is converted to somal action potential firing would be expected to undergo substantial modification during and following an extended period of stimulation.

In addition to the modulation of postsynaptic membrane conductances, repetitive stimulation can also cause substantial transient changes in synaptic efficacy, a subject of intense recent experimental and theoretical interest [1,28]. The nature of the change in efficacy appears to depend on the type of cell targeted by the synapse: synapses between pyramidal cells depress while pyramidal cell-inhibitory interneuron synapses facilitate [29,46]. As a result of the different adaptation properties of synapses on excitatory and inhibitory cells, the relative strength of excitation and inhibition in a cortical circuit would be expected to change during persistent stimulus drive. Interestingly, synaptic depression not only varies among cell types, but also has been shown to occur more rapidly in some cortical pathways than others. Specifically, Gil et al. [15] found that synaptic depression is more pronounced in thalamocortical than corticocortical synapses, indicating that the relative strength of these two pathways may change during prolonged activity.

Persistent activity can activate receptors and signaling pathways not recruited by briefer periods of stimulus drive. For example, repetitive high-frequency activity, but not single or low-frequency presynaptic events, can activate presynaptic metabotropic glutamate receptors, which inhibit further neurotransmitter release, a form of dynamic feedback inhibition [42]. The activation of metabotropic glutamate receptors may contribute to contrast adaptation in cat striate cortex [31]. Similarly, presynaptic GABA$_B$ receptors are activated only when repetitive activity causes an accumulation of GABA which spills out of the synaptic cleft [18]. Neurotransmitter spill-over may also allow repetitive activity in one set of synapses to modulate subsequent activity in a

different set. In the cerebellum, for instance, GABA accumulation induced by repetitive activity in the granule cell parallel fiber system has been shown to inhibit subsequent heterosynaptic input to Purkinje cells [11].

In addition to changes in the state of single neurons or synapses due to their own activity, there are a number of mechanisms which can affect the responsivity of neuronal populations. Such population-level effects can arise due to changes in the extracellular concentration of ions (principally potassium, but potentially other ions as well, including calcium; see [13]). We have recently found that stimulus-driven changes in the cellular micro-environment differentially modulate the efficacy of inputs to different locations on a pyramidal cell dendrite (Fig. 2). Specifically, we found that repetitive layer VI-white matter (WM) stimulation substantially increases the efficacy of layer II/III horizontal input to layer V and layer II/III pyramidal neurons in vitro, but causes a profound reduction of the efficacy of layer I input [22]. The dynamic modulation of these two types of inputs lasts for several tens of seconds after the termination of the repetitive conditioning stimulus. The potentiation of layer II/III EPSPs was due to a stimulus-driven increase in extracellular potassium. The differential modulation of layer I and II/III input suggests that the efficacy of different sources of input to a cell
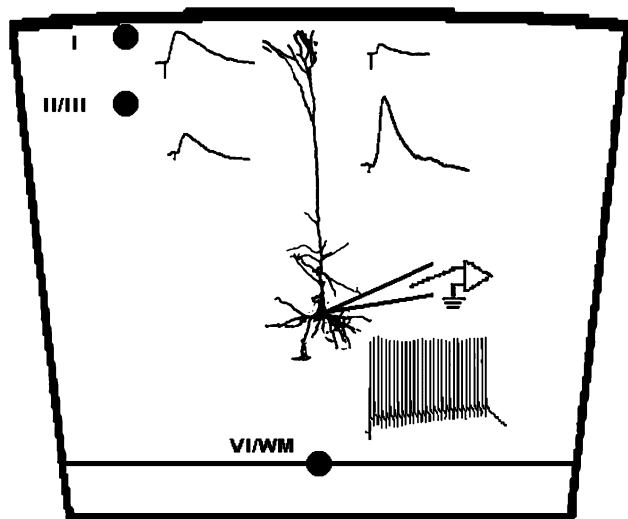

Fig. 2. The effect of a repetitive stimulus train (3 s of stimulation at 10 Hz; delivered at the layer VI/WM border as indicated by the filled circle) on layer I and layer II/III EPSPs recorded in layer V pyramidal cell. The EPSPs elicited by electrodes in the upper layers (position indicated by filled circles) before the stimulus train are shown to the *left* of the cell; those elicited after the stimulus train are shown to the *right*. Layer I EPSPs are reduced in amplitude following repetitive stimulus drive at the layer VI/WM border while layer II/III EPSPs are strongly potentiated. The response of the cell to the layer VI/WM conditioning train is shown in the lower right.

(e.g. feedback vs. horizontal input) changes during repetitive feedforward stimulus drive.

In summary, recent cellular level observations strongly suggest that the response of a sensory cortical network to a given input will depend strongly on the recent history of activity in that network. Persistent, but not transient, patterns of stimulus drive recruit a number of receptors and ion channels which remain active over a time scale extending from hundreds of milliseconds to many seconds. Although the specific way in which each cellular mechanism contributes to the single-cell dynamics discussed in the previous section remains to be ascertained, it is abundantly clear that sensory cortex contains a rich repertoire of mechanisms capable of mediating changes in neuronal response properties both during and following temporally extended stimulus drive. From the perspective of cellular neurophysiology, cortical dynamics provide a potentially important context for gaining improved understanding of the contributions to cortical function of receptors and signaling mechanisms whose time course is too slow to contribute to fast neurotransmission based information processing.

5. Benefits of sensory cortical dynamics

The available experimental evidence suggests that by affecting the response properties of cortical neurons, stimulus-driven dynamics alter substantially the information processing characteristics of cortical networks. There are several, interrelated functional benefits which may be provided by cortical network dynamics. In essence, all of the suggested benefits propose that stimulus-drive causes a rapid and stimulus-specific optimization of the network. First, although fewer cortical neurons would participate in signaling the properties of a persistent sensory stimulus, those that continue to participate would signal stimulus properties less ambiguously. In other words, by reducing the coding redundancy in the cortical neuronal population, recent sensory history enables a reduction of the number of neurons that must be recruited to solve a particular processing task [2,33]. A reduction in the size of the responding population would, in turn, reduce the metabolic cost associated with information processing [23]. Second, cortical dynamics could allow for the temporal integration of sensory information. While perception can be remarkably rapid, performance on difficult sensory discrimination tasks improves with the duration of exposure to a stimulus or following an appropriate priming/adapting stimulus (e.g. [4,16,17]). While these performance improvements could be due to a simple strategy of integrating a constant (non-dynamic) signal over time, an alternative possibility is that dynamic, adaptive changes in the information

processing capacities of sensory cortical networks might be responsible. In this view, the improvement in performance would be directly linked to the stimulus-driven changes in single-neuron tuning properties discussed previously. Third, a functionally significant advantage of stimulus-driven dynamics is that it could allow sensory cortical networks to be both broadly-tuned (capable of processing a diverse set of inputs and of making associations among them) and capable of processing a particular type of input rapidly and efficiently. Thus temporally extended sensory stimulation may convert an initially broadly-tuned sensory cortical network to a circuit dedicated to efficient processing of the type of input that the network has experienced most recently. Finally, dynamics could allow sensory cortical networks to better capture subtle changes in the environment. This ability could be afforded, for instance, by simple stimulus-driven changes in cortical gain. By allowing neurons to adjust their response range to the mean level of the ongoing stimulus, gain control allows neurons to signal effectively small changes in a stimulus parameter using their limited dynamic range. More complicated cortical network dynamics, such as changes in the interactions between cells due to increased mutual inhibition, could allow for better detection of novel associations among stimuli [2].

6. Conclusion

Stimulus-evoked sensory drive transiently alters the response properties of individual sensory cortical neurons and modifies the size of the responding neuronal population. The alterations that accompany temporally extended sensory stimulation are fully consistent with the biophysical characteristics of the somal and dendritic compartments of cortical neurons and the properties of cortical synaptic neurotransmission. Sensory cortical dynamics may result in the significant enhancement of the capacity of single neurons and of neuronal populations to encode information about prevailing stimulus conditions. It is not yet possible to assign specific cellular mechanisms to particular single neuron or neural population dynamics, nor can one rigorously specify the contribution(s) to perception of any of the expressions of cortical dynamics identified to date. Despite these limitations, the available evidence requires rejection of the ideas that prominent changes in sensory cortical organization only occur with prolonged manipulations of sensory drive and that the information processing characteristics of sensory cortical networks are fixed over the short term.

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