SYMPOSIUM REPORT

Computing with thalamocortical ensembles during different behavioural states

Miguel A. L. Nicolelis

Departments Neurobiology and Biomedical Engineering, Center for Neuroengineering, Duke University Durham, NC 27710, USA

A series of recent studies have indicated that ensembles of neurones, distributed within the neural structures that form the primary thalamocortical loop (TCL) of the trigeminal component of the rat somatosensory system, change the way they respond to similar tactile stimuli, according to both the behavioural strategy employed by animals to gather information and the animal's internal brain states. These findings suggest that top-down influences, which are more likely to play a role during active discrimination than during passive whisker stimulation, may alter the pattern of neuronal firing within both the distinct layers of the primary somatosensory cortex (S1) and the ventral posterior medial nucleus (VPM). We propose that through this physiological process, which involves concurrent dynamic modulations at both cellular and circuit levels in the TCL, rats can either optimize the detection of novel or hard to sense stimuli or they can analyse complex patterns of multiwhisker stimulation, during natural exploration of their surrounding environment.

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Corresponding author M. A. L. Nicolelis: Box 3209, Room 327 Bryan Research Building, Duke University, Durham, NC 27710, USA. Email: nicoleli@neuro.duke.edu

The trigeminal component of the rat somatosensory system is widely recognized as a versatile and invaluable experimental model to investigate the principles of development (Rice, 1995), anatomical organization (Woolsey & Van der Loos, 1970), physiological properties (Chapin & Woodward, 1981; Simons, 1985; Connors & Gutnick, 1990; Silva *et al.* 1991; Nicolelis & Chapin, 1994; Ghazanfar & Nicolelis, 1999), coding strategy (Simons & Carvell, 1989; Ahissar *et al.* 1997; Fee *et al.* 1997; Ghazanfar *et al.* 2000), and plastic potential (Nicolelis *et al.* 1993; Castro-Alamancos *et al.* 1995; Polley *et al.* 1999*a*) of sensory systems in mammals. As a result, this sensory system has been scrutinized by a variety of powerful techniques, such as *in vivo* and *in vitro* patch clamp recordings (Zhu & Connors, 1999; Petersen & Sakmann, 2000), intra- and extracellular recording (Markram *et al.* 1995; Nicolelis *et al.* 1997; Markram, 1997), and optical imaging (Masino & Frostig, 1996; Kleinfeld & Delaney, 1996; Sheth *et al.* 1998; Polley *et al.* 1999*a*,*b*). More recently, chronic multisite, multielectrode recordings in freely behaving animals have been employed to characterize, for the first time, the simultaneous activity of distinct populations of neurones that define the main thalamocortical circuit of the rat somatosensory system (Fanselow & Nicolelis, 1999). This new experimental paradigm has provided a unique opportunity to correlate the physiological properties of thalamocortical neural ensembles with the main behaviours employed by rats to extract tactile information from their surrounding environment.

By employing multielectrode recordings in freely behaving rats we have recently obtained physiological and behavioural data supporting the hypothesis that the thalamocortical loop dynamically adjusts its physiological mode of operation, at both cellular and circuit levels, in accordance with internal brain states and the specific behaviours used by rats to explore their surrounding environment. Here, we briefly review the evidence that supports this hypothesis. A series of papers published elsewhere summarizes this argument in greater detail (Nicolelis & Fanselow, 2002; Krupa *et al.* 2004*a*; Gervasoni *et al.* 2004).

The rat somatosensory thalamocortical circuit

Figure 1 summarizes the circuit that defines the main thalamocortical loop of the trigeminal component of the rat somatosensory system (Fig. 1*A*). Ascending action

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potentials resulting from mechanical stimulation of the whiskers travel to the trigeminal brainstem complex and the reticular formation. Projections from the trigeminal brainstem complex terminate on neurones in the VPM thalamus. In the rat, the VPM thalamic nucleus contains only one type of neurone, excitatory cells that project mainly to layer IV (CTX IV) of the primary somatosensory cortex (SI). On the way to the cortex, the axons of VPM also give off a projection to the thalamic reticular nucleus (RT). VPM and RT neurones also receive dense ascending cholinergic projections from the brainstem reticular formation (RF) (Hallanger *et al.* 1987). These projections can excite VPM cells through nicotinic and M1-type muscarinic receptors (Zhu & Uhlrich, 1998; Plummer *et al.* 1999), but inhibit RT cells *via* M2-type receptors (Carden & Bickford, 1999).

A major source of descending projections in the thalamocortical loop originates primarily in layer VI of SI cortex (CTX VI) (Fig. 1*B*). The distal dendrites of VPM neurones are densely innervated by these projections, which activate both ionotropic and metabotropic glutamate receptors. On their way to VPM, cortico-thalamic projections also give off branches to RT neurones. The RT consists exclusively of inhibitory neurones, which project either to the VPM nucleus, where they terminate near the cell bodies where they activate $GABA_A$ and $GABA_B$ receptors, or locally within RT. The rat VPM nucleus is unique in that, unlike other main thalamic nuclei in rats and in other species, it does not contain intrinsic inhibitory neurones. Due to this lack of inhibitory interneurones, RT neurones are the only source of GABAergic inhibition in the rat VPM (McCormick, 1992).

Although considerable anatomical and physiological data indicate that top-down inputs may have a significant effect on mechanisms of tactile information processing (Mignard & Malpeli, 1991; Roelfsema *et al.* 1998; Hupe *et al.* 1998), the nature of these descending influences even on the primary thalamocortical loop of the rat somatosensory system remains poorly understood. As a rat actively samples a tactile stimulus, particularly one involving salient associative memories, several higher-order processes that would not be activated by random passive stimuli, delivered in either anaesthetized or paralysed animals, will likely be engaged. For instance, the animal's state of attention, motivation, sensory-motor integration and reward expectation are all likely to

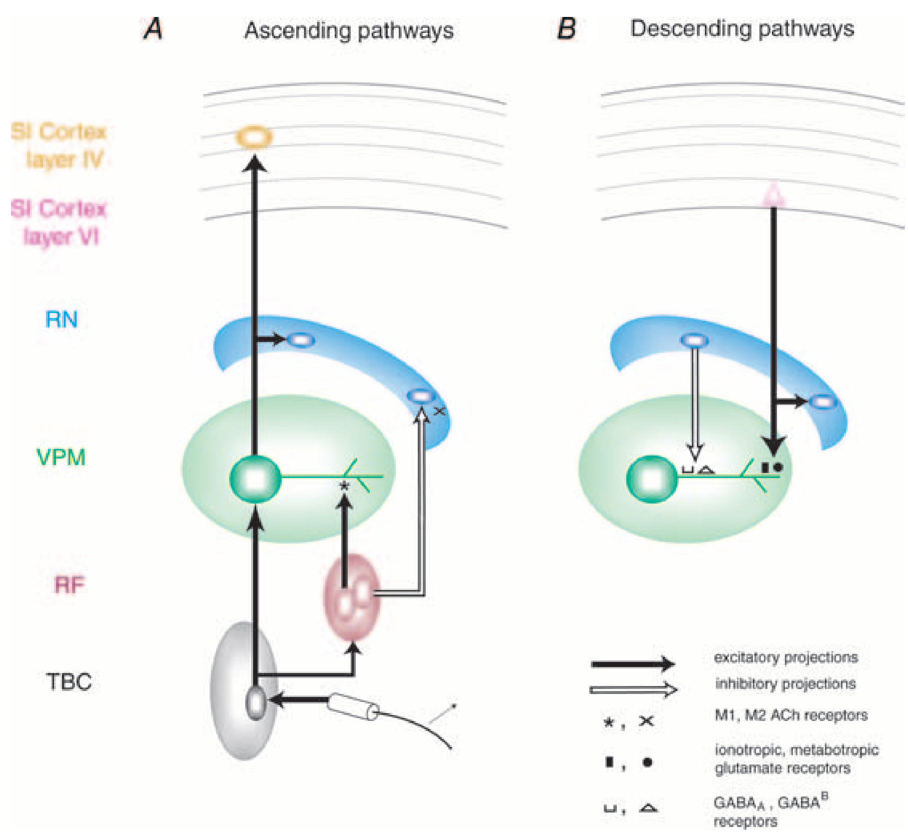

Figure 1. Schematic diagram of the main rat thalamocortical loop
A, diagram of the main ascending pathways. *B*, diagram of the main descending pathways. From Nicolelis & Fanselow, 2002. Reproduced with permission (http://www.nature.com.nn).

influence the nature of the tactile responses generated by thalamocortical neurones. However, what effect these, or other, higher-order processes might have on mechanisms of tactile processing in rat SI remains largely unknown.

Over the past decade, our laboratory has performed a series of experiments in which chronic recordings of the simultaneous activity of ensembles of thalamocortical neurones were obtained in freely behaving rats engaged in a variety of tasks (for a review see Nicolelis & Fanselow, 2002). In our first studies, we measured how the tactile responses of ensembles of single neurones located in S1 and VPM of the thalamus varied according to three basic behaviours exhibited by rats. The first of these we refer to as the 'quiet' behaviour, in which rats are standing or sitting still and there is no movement of the whiskers (Fanselow & Nicolelis, 1999; Nicolelis *et al.* 1995). The second is known as the 'whisker twitching' behaviour. During this behaviour, rats are also standing or sitting still, but twitch their whiskers in very rhythmic, small amplitude movements at a rate of 7–12 Hz (Semba *et al.* 1980; Semba & Komisaruk, 1984). The third behaviour, referred to as 'whisking', occurs when rats move their whiskers back and forth in large-amplitude sweeps at a rate of ~4–6 Hz. Rats use these whisking movements to repeatedly put their whiskers in contact with surfaces or objects so they can gather tactile information as they actively explore their environment (Carvell & Simons, 1990). During the quiet and whisking behaviours, there is no large-scale, coherent neural activity among the cells in either VPM or SI, and the activity is thus referred to as 'desynchronized'. In contrast, the whisker twitching state is accompanied by a highly synchronous 7–12 Hz oscillatory neural activity (Semba *et al.* 1980; Semba & Komisaruk, 1984) (Fig. 2*A*), which appears first in the rat SI cortex and later in the VPM thalamus (Nicolelis *et al.* 1995; Fanselow *et al.* 2001). Shortly after the onset of this oscillatory neural activity in the thalamocortical loop, rats start producing the rhythmic, small amplitude whisker twitching movements characteristic of this behaviour, which are phase-locked to the neural oscillations (Semba & Komisaruk, 1984; Welker, 1964).

Overall, we observed that the tactile responses of both S1 and VPM neurones can vary significantly in several ways as a rat shifts between these three behavioural states (Fig. 2*A* and *B*). First, when a single tactile stimulus is presented, e.g. one brief deflection of a whisker, the probability of a neuronal response is largest during the quiet behaviour, smaller during whisking, and lowest during whisker twitching (Fig. 2*B*). Second, following the stimulus, there is a robust inhibitory period lasting ~75 ms during the quiet behaviour. This poststimulus inhibitory period is shorter during whisker twitching, relative to the quiet behaviour, and is substantially shorter during whisking (Fig. 2*C*). Finally, when pairs of stimuli are presented, the ability of a neurone to fire in response to the second stimulus in the pair is dependent on the interstimulus interval and the animal's behavioural state. During the quiet and whisker twitching behaviours, if the interstimulus interval is less than 75 ms, the probability of VPM and SI neurones responding to the second stimulus in a pair will be very small (Fig. 2*B*). However, during whisking, the probability of a response to the second stimulus of a pair is only reduced if the interstimulus interval is 25 ms or less. Thus, the ability of VPM and SI neurones to respond reliably to rapidly repeated stimuli is correlated with the duration of the poststimulus inhibitory period, which differs according to behavioural state.

Analysis of the firing properties of thalamocortical cells (Fanselow *et al.* 2001) in these behaving rats has shown that during the 7–12 Hz oscillations observed in the whisker twitching behaviour, VPM and S1 neurones fire bursts of action potentials substantially more frequently (average of once every 7.2 s) than during the quiet (average of once every 45.5 s) or whisking (average of once every 28.6 s) behaviours (Fig. 2*D*). Moreover, signals directed from SI to VPM are significantly more coherent during whisker twitching episodes than during the other two behavioural states (Fig. 2*E*). In addition, inactivation of the SI cortex *via* local infusion of the $GABA_A$ agonist muscimol, abolished whisker twitching movements, 7–12 Hz oscillations and bursting activity in the VPM. These results suggest that during whisker twitching the SI cortex exerts a powerful rhythmic influence on VPM neurones and that these descending cortical signals are required for the emergence of 7–12 Hz oscillations, the bursting activity observed in VPM during these oscillations, and the genesis of the whisker twitching behaviour.

These results led us to propose that the *active* use of whiskers, in multiple types of whisker movements, is integral to processing tactile stimuli in rats. Indeed, our hypothesis proposes that two distinct types of whisker movements serve as differential dynamic 'filters' to process specific types of incoming tactile information that result from whisker stimulation. The second global operating principle we proposed is that, as with the determination of receptive field properties and maps in SI and VPM (Krupa *et al.* 1999; Ghazanfar *et al.* 2001), the asynchronous convergence of ascending and descending projections in the thalamus is critical for generating the animal's range of sensory processing strategies. When this circuit arrangement is combined with the range of intrinsic cellular properties of cells in the thalamocortical loop, a complex and dynamic system emerges, which is capable of quickly shifting its physiological properties in order to maximize the type of tactile information sampled by a particular active exploratory behaviour. Finally, we hypothesized that internal changes in brain state would significantly impact on the way ensembles of

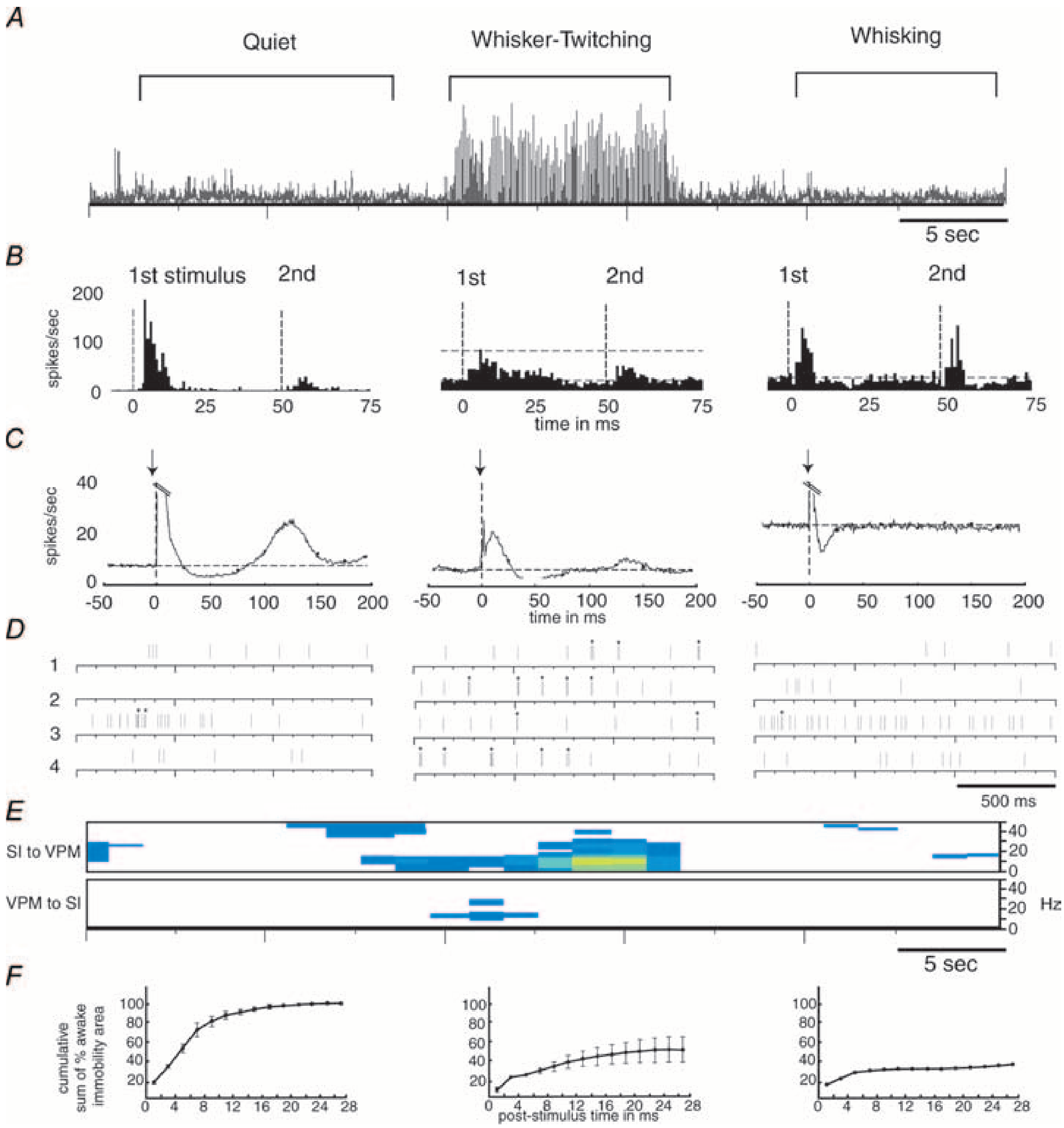

Figure 2. Neural activity in VPM thalamus during three behavioural states
A, a continuous 50 s trace of the first principal component of neural ensemble activity in VPM across quiet, whisker twitching and whisking behaviours. *B*, responses of single VPM neurones to the presentation of two infraorbital nerve stimuli with an interstimulus interval of 50 ms (stimuli presented at bold dotted lines; horizontal dotted lines indicate baseline firing level). *C*, average peristimulus time histograms (PSTHs) of neural activity in VPM neurones before and after one stimulation of the infraorbital nerve (note that the peaks of the responses to the stimulus have been truncated so the lower-magnitude activity can easily be seen; stimuli presented at bold dotted lines; horizontal dotted lines indicate baseline firing level). *D*, rasters showing the activity of four single units in VPM during each behaviour. Bursting activity is identified by asterisks above each raster. *E*, amount of partial directed coherence observed during each of the three behaviours. The top panel is for partial directed coherence from SI to VPM, the bottom panel from VPM to SI. Colour indicates the intensity of the coherence, white indicating none and yellow indicating the highest level of coherence. *F*, cumulative sum of amount of cortical area activated by a single infraorbital nerve stimulus. Values are normalized to the maximum activated area in the quiet state. From Nicolelis & Fanselow, 2002. Reproduced with permission (http://www.nature.com.nn).

thalamocortical neurones respond to incoming tactile stimuli.

Together, these principles illustrate that the rat somatosensory system does not merely play the role of a 'passive observer' of the environment. Instead, it can choose from multiple functional modes in order to actively examine and analyse tactile inputs from the world, based on expectations built throughout a life of whisking.

Layer specific tactile responses in the rat S1 during active tactile discrimination

A recent series of experiments further highlighted the profound differences in tactile information processing that exist across the layers of the S1 cortex when rats engage themselves in active whisker discrimination, *versus* serving as passive recipients of comparable tactile stimuli (Krupa *et al.* 2004*a*). In these experiments, Krupa *et al.* recorded the activity of ensembles of single neurones through different layers of the barrel region of S1 in five rats that were trained to perform a whisker-dependent tactile discrimination task (Krupa *et al.* 2001*b*, 2004*b*). The task required rats to actively sample a variable-width aperture with their large facial whiskers, and then signal whether the aperture was 'narrow' or 'wide' (Fig. 3*A*). Video analysis showed that rats approached and sampled the aperture in a very repeatable, stereotypical manner, using only their large facial whiskers to contact the aperture (Fig. 3*B*). Single-unit activity was recorded through all layers of SI with chronically implanted, movable arrays of high impedance microwire electrodes. Electrodes were orientated perpendicular to the cortical surface so that recordings along an individual electrode track were from the same cortical column. This allowed neural activity recorded at different depths through individual cortical columns to be compared.

A total of 317 units were recorded bilaterally in the barrel region of S1 while the rats performed the active tactile discrimination: 114 units in supragranular layers; 105 in layer IV; and 98 in infragranular layers. Sixty-seven per cent (212) of these units displayed significant modulations in firing rate as rats performed the tactile discrimination: 37% (78) showed significant increases in firing (excitatory responses); 26% (56) decreased firing (inhibitory responses); and 37% (78) had multiphasic responses consisting of combinations of increases and decreases. The overall percentage of responsive units per layer did not differ significantly (64% in supragranular layers, 70% in layer IV, and 66% in infragranular layers).

These responses were compared with the activity of 244 units recorded in the S1 of 10 additional rats that received several different forms of passive whisker

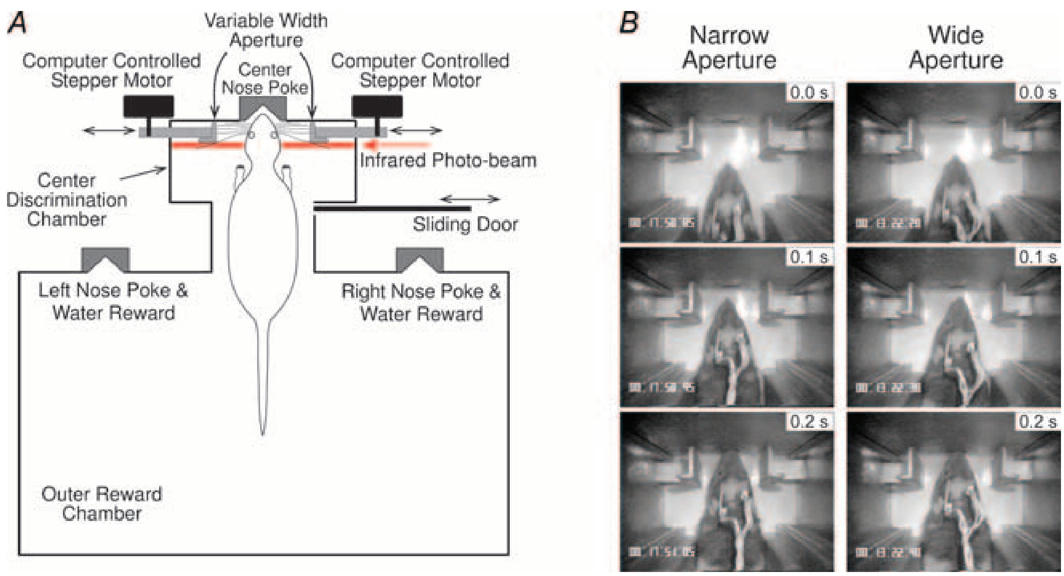

Figure 3. Active tactile discrimination task
A, schematic diagram of the behavioural apparatus. Trials begin when the sliding door opens. Rats enter the centre discrimination chamber and sample the variable width aperture with their facial whiskers. Rats then poke their nose into either the left or right reward nose poke to receive a water reward: left nose poke if the aperture was narrow (60 mm), right nose poke if wide (68 mm). Immediately after, the sliding door closes and the aperture is randomly reset to wide or narrow. The next trial begins 30 s later. *B*, video frame captures showing a rat approaching and sampling the Narrow and Wide aperture. The 0.0 s frame (top-most frames) shows the rat breaking the infrared photobeam; the middle frame (0.1 s later) shows the whiskers initially contacting the aperture; bottom frame (0.2 s) shows the whiskers fully contacting the aperture. From Krupa *et al.* (2004). Reproduced with permission.

stimulation designed to simulate the spatio-temporal dynamics of whisker deflections that occurred during the active discrimination. Three of the rats received patterned ramp-and-hold stimulation of 16 individual whiskers with a multichannel whisker stimulator (Krupa *et al.* 2001*a*, 2004*b*) while lightly anaesthetized (Fig. 4*A*). Three rats were habituated to calm, head-fixed restraint and received similar, patterned ramp-and-hold stimuli (Fig. 4*A*) while fully awake (Wiest & Nicolelis, 2003; Krupa *et al.* 2004*b*). Four rats received bilateral whisker stimulation with a movable aperture while lightly anaesthetized or restrained and fully awake (Fig. 4*B*). This moving aperture (same size as the aperture in the active discrimination) was accelerated across the facial whiskers at velocities and trajectories that replicated the whisker deflection dynamics that occurred during active discrimination (Krupa *et al.* 2004*b*).

Excitatory responses displayed a distinct shift from phasic activation during passive stimulation to tonic activation during active discrimination. This tonic activation (Fig. 4*C*) consisted of sustained increases in firing-rate with a mean duration (Krupa *et al.* 2004*b*) that was significantly different across cortical layers: supragranular layers, 282 ± 29 ms (mean ± s.e.m.); layer IV, 207 ± 16 ms; and infragranular layers, 339 ± 19 ms; ($F_{2,54} = 8.8$, $P < 0.001$). The magnitude of tonic responses (Krupa *et al.* 2004*b*) during active discrimination also varied significantly across layers: supragranular layers, 7.0 ± 0.7 spikes per trial; layer IV, 4.3 ± 0.5 spikes per trial; and infragranular layers, 9.5 ± 1.1 spikes per trial; ($F_{2,54} = 10.6$, $P < 0.0005$).

In contrast, passive ramp-and-hold whisker stimulation (in either anaesthetized or awake, restrained rats) or moving aperture stimulation (in anaesthetized or awake rats) evoked excitatory responses that consisted of relatively brief, transient increases in activity (Fig. 4*D* and *E*). The mean excitatory response durations and magnitudes evoked by these passive stimuli are summarized in Fig. 4*F*. Response duration during active discrimination was highly significantly different from each of the passive stimulation conditions ($F_{4,85} = 59.2$, all $P < 0.0005$; Tukey's HSD. The same was true of the response magnitude measure ($F_{4,85} = 29.9$, all $P < 0.00001$, Tukey's HSD. In short, excitatory activation of S1 by passive whisker stimulation was fundamentally different in nature than S1 excitation evoked by the active discrimination. Several additional lines of evidence indicate that this shift from phasic to tonic activation during passive and active stimulation (as well as several other functional differences, described below) could not have resulted solely from variations in whisker deflection dynamics during passive and active stimulation (Krupa *et al.* 2004*b*).

Another functional difference between active and passive stimulation was a significant shift in the relative balance between excitatory and inhibitory responses. Only 7% of S1 units responded to the ramp-and-hold or moving aperture passive stimulation with either purely inhibitory responses or inhibitory followed by excitatory activation; the remaining 92% responded with either purely excitatory or excitatory followed by inhibitory activity, results consistent with earlier studies (Simons, 1978; Swadlow, 1989; Brumberg *et al.* 1999; Sachdev *et al.* 2000). Moreover, there was no significant difference in the percentage of inhibitory responses evoked by the different passive stimuli delivered to either anaesthetized or awake, restrained rats. In contrast, nearly half (49%) of S1 units responded during the active discrimination with either a purely inhibitory response (26%) or a response that was initially inhibitory followed by an excitatory phase (23%). The mean duration of inhibitory responses during the active discrimination (246 ± 21 ms) was significantly longer than the duration of inhibitory responses evoked by the passive stimuli (12.4 ± 1.8 ms); ($t(12) = 9.9$, $P < 0.0001$). During active discrimination, purely inhibitory responses were evenly distributed across layers: 33% in supragranular layers, 36% in layer IV and 31% in infragranular; inhibitory–excitatory responses were asymmetrically concentrated in the granular layer: 23% in supragranular, 54% in layer IV, and 23% in infragranular. Collectively, these different inhibitory responses indicate that the activation dynamics of S1 following passive whisker stimulation are fundamentally different from during active discrimination. Passive multiwhisker stimulation causes a predominately excitatory deviation from prestimulus baseline activity, whereas similar stimulation during active discrimination evokes almost equally balanced excitatory and inhibitory shifts from baseline.

The functional nature of these actively evoked inhibitory responses was examined using an artificial neural network, based on the learning vector quantization (LVQ) algorithm (Krupa *et al.* 2004*b*). Results revealed that information about different aperture widths is encoded simultaneously by excitatory *and* inhibitory responses in S1 (see LVQ Based Analyses in Krupa *et al.* 2004*b*). Further, LVQ-analysis of ensemble activity in different layers indicates that layer-specific tactile coding mechanisms may be engaged during active discrimination. For instance, single-trial prediction of wide and narrow apertures by infragranular ensembles was significantly more accurate than supragranular ensembles (Krupa *et al.* 2004*b*).

Finally, cortical columns displayed significantly different functional properties during active discrimination and passive stimulation. S1 recordings in monkeys, cats, and rats show that responses within a column evoked by passive stimulation share similar functional properties of place (all units have a common receptive field locus), and mode (all units respond to similar stimulus modalities) (Mountcastle, 1957; Powell & Mountcastle, 1959; Simons, 1978; Chapin, 1986;

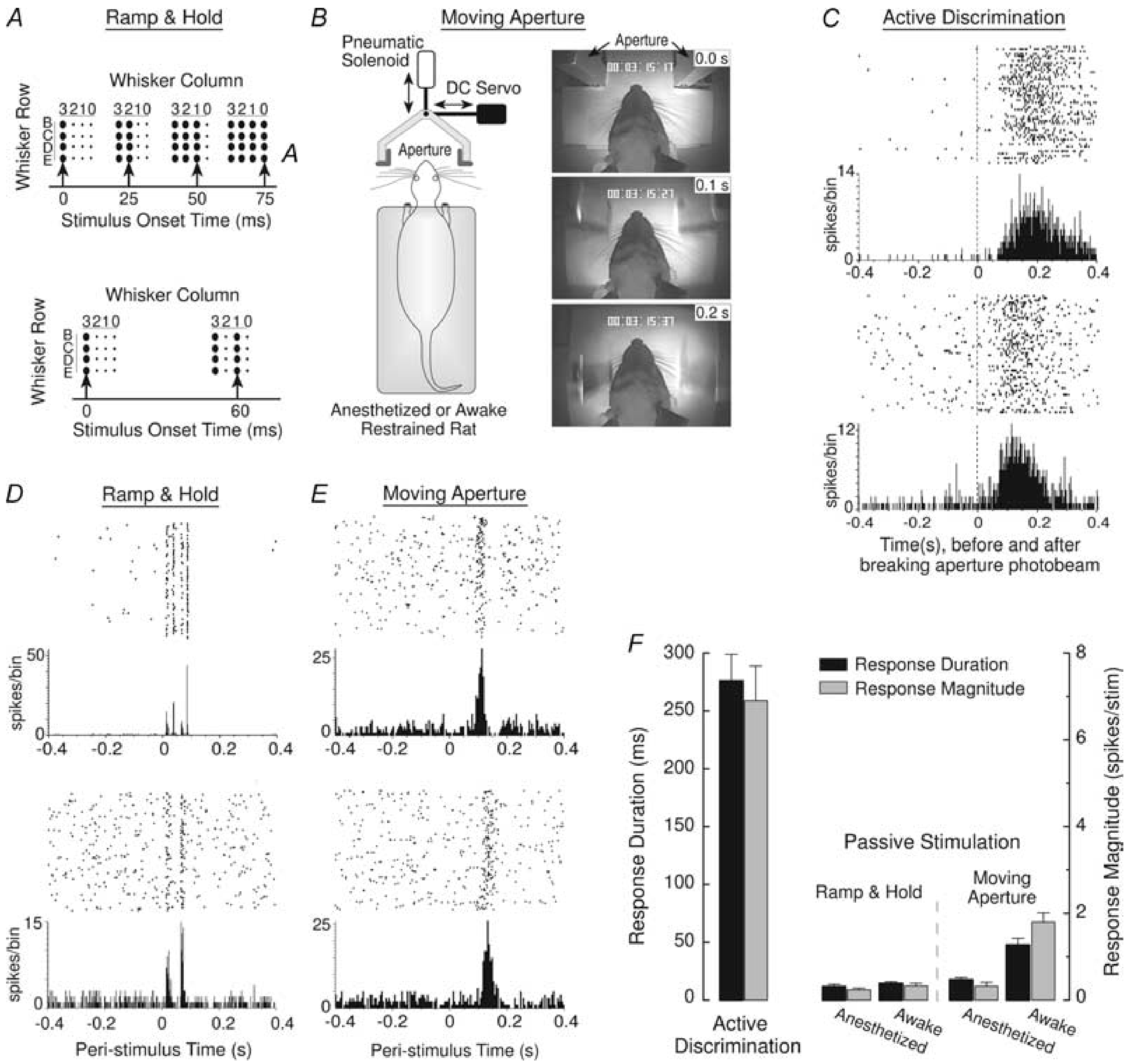

Figure 4. Passive stimulations and neural response properties
A, upper schematic diagram: pattern of multiwhisker ramp-and-hold passive stimuli delivered to anaesthetized rats. Large black dots represent stimulation of a particular whisker. Upward arrows show stimulation onsets. Lower schematic diagram: stimulation pattern of the awake, restrained rats. *B*, left, schematic diagram of the moving aperture stimulus. Aperture is accelerated across the facial whiskers (with variable onsets and velocities) by the pneumatic solenoid and also simultaneously deflected laterally in varying amounts by the DC servo in order to accurately replicate the range of whisker deflection dynamics that occurred during active discrimination. Right, video frame captures showing an example of the aperture moving caudally across the whiskers of an awake restrained rat while simultaneously deflecting laterally 5 mm (to the right) over a 200 ms interval. *C*, representative single-unit responses showing long-duration, tonic activation during active discrimination. Upper portion of each panel is a raster plot where each line represents a consecutive trial in a recording session and each dot is a unit spike; lower portion of each panel shows summed activity for all trials in 5 ms bins. The 0 time-point represents the moment that rats disrupted the aperture photobeam (Fig. 1). *D*, representative single-unit responses evoked by passive ramp-and-hold stimulation of 16 whiskers in lightly anaesthetized rats (upper panel) and by passive stimulation of 8 whiskers in awake, restrained rats (lower). The 0 time-point represents stimulus onset. *E*, representative single-unit responses evoked by moving aperture stimulation of awake, restrained rats (0 time-point represents onset of aperture movement). *F*, mean (+ S.E.M.) excitatory response duration and magnitude evoked during the active discrimination and by the different passive stimuli delivered to anaesthetized or awake restrained rats. From Krupa *et al.* (2004). Reproduced with permission.

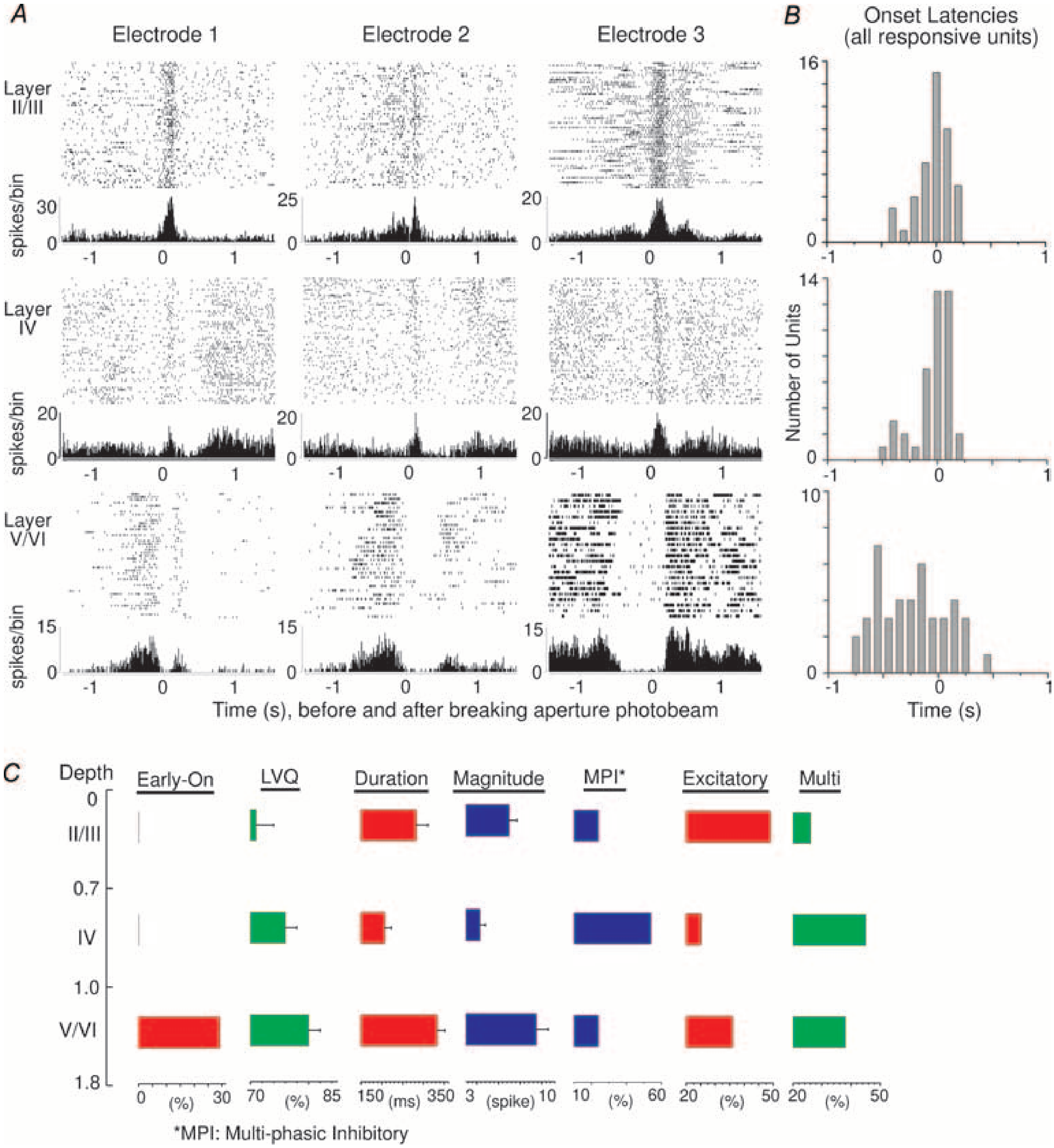

Figure 5. Neural response properties during active discrimination
A, examples of single-unit responses recorded at different depths along 3 different electrode tracks during the active discrimination (wide aperture). Units recorded in infragranular layers respond significantly earlier than units in more superficial layers and before whiskers contact the aperture. *B*, distribution of onset-latencies for all responsive cells recorded in the different layers during active discrimination. *C*, summary diagram showing significant major effects across layers during active discrimination. The Early On column shows the percentage of units showing early onsets per layer. LVQ: mean (+ S.E.M.) performance of the LVQ for populations recorded at the different depths. Duration: mean (+ S.E.M.) excitatory response duration. Magnitude: mean (+ S.E.M.) magnitude of excitatory responses. MPI: distribution of units with multiphasic responses that began with an inhibitory phase. Excitatory: percentage of units with excitatory responses. Multi: percentage of multiphasic units. From Krupa *et al.* (2004). Reproduced with permission.

Armstrong-James *et al.* 1992; Brumberg *et al.* 1999). In contrast, during the active discrimination described here, 36% of infragranular units began responding significantly before the rats' whiskers contacted the aperture during active discrimination. More importantly, these units began responding significantly earlier than units recorded directly above them in supragranular or granular layers (Fig. 5*A*). Onset latencies between supragranular and granular layers did not differ significantly (Fig. 5*B*). In contrast, onset latencies of infragranular units were significantly earlier than units in the more superficial layers (Tukey's HSD, $P < 0.0005$).

These early responsive units in infragranular layers appear to represent a functionally different class of neurones. First, early responses were not seen in layer IV, indicating that the afferent source(s) of these responses was not ascending thalamic input. Second, video analysis of rats performing the task shows that these responses occurred as the rats were moving towards the aperture, although no distinct tactile stimuli appeared to contact the whiskers. Third, the duration of these early responses was significantly longer than responses of other infragranular units that responded only when the whiskers contacted the aperture (see Krupa *et al.* 2004*a*). Finally, the whiskers on one side of the face of one rat were cut prior to a behavioural recording session. Early onset responses were still observed in the infragranular layers contralateral to the whisker cut. Together, these results indicate that the early onset units are not activated by whisker stimulation directly. As such, these early onset responses do not appear to share the same functional properties of place and modality as units recorded more superficially in the same cortical column.

In summary, numerous functionally significant differences in S1 activity were observed in different cortical layers as rats performed an active tactile discrimination (Fig. 5*C*). Moreover, fundamental differences in the functional nature of S1 activity were observed during active discrimination and passive whisker stimulation. These results suggest that S1 receives significantly different afferent input during actively acquired and passively delivered stimuli. These differences do not appear to result exclusively from changes in bottom-up ascending input to S1. Instead, during active discrimination, top-down influences may also affect tactile processing in S1. For instance, the early onset units were only observed in infragranular layers and not layer IV, indicating that these responses did not arise from ascending thalamic input. Because motor cortex (M1) sends a significant projection to S1 infragranular layers (Miyashita *et al.* 1994; Zhang & Deschenes, 1998), these early onset responses might represent modulation from MI as rats initiate the discrimination. Also, excitatory response durations and magnitudes in supra- and infragranular layers were substantially greater than those in layer IV during active discrimination, indicating that the non-granular laminae received additional excitatory input from sources other than ascending thalamocortical input. Possible sources of this input include the secondary somatosensory cortex (Koralek *et al.* 1990; Jackson & Cauller, 1998) and the contralateral SI (Olavarria *et al.* 1984; Koralek *et al.* 1990; Shuler *et al.* 2001; Shuler *et al.* 2002), both of which innervate the non-granular laminae.

Conclusions

Evidence obtained under a variety of experimental conditions indicates that tactile responses produced by ensembles of S1 and VPM vary according to the animal's behavioural strategy and internal brain state. Functional differences observed in the rat thalamocortical loop during active *versus* passive stimulation also indicate that passively evoked tactile responses constitute a relatively poor predictor of the processing mechanisms operating in the mammalian somatosensory system during active discrimination.

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