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Gating of the sensory activity within barrel cortex of the awake rat

Abstract In rat barrel cortex, evoked potentials (EPs) to vibrissa stimulation can be divided into two distinct classes according to the relative contribution of their principal components. Our experiments support the notion that these components can be attributed to activation of two pyramidal cell populations: supra- and infragranular. With well-habituated stimuli EPs are dominated by a component related to the supragranular cells (class 1). However, the first reinforcement of vibrissa stimulation in the classical aversive paradigm favours the appearance of EPs dominated by a component characteristic of infragranular cells which matches with activation in the surround zone of the barrel field (class 2). Similar dynamic changes of the relative occurrence of the two EP classes follow other aversive stimuli, including pressing the animal's ear and restraining a whisker. We hypothesize that neuromodulatory action elicited by contextual stimulation activates all neurons in the principal barrel column, including those providing an output to the surrounding barrels. In the classical conditioning paradigm this mechanism may lead to experience-dependent changes within the intracortical network.

Key words Evoked potentials · Principal components · Cortical column · Information processing · Contextual gating

Introduction

The vibrissa-to-barrel sensory pathway is the most studied neural network after the visual system of mammals (see Jones and Diamond 1995). The relatively simple architectonics of barrel cortex in rodents (Woolsey and Van der Loos 1970; Welker 1971; Simons 1978; Armstrong-James and Fox 1987) offer an excellent possibility of investigating the columnar organization and function of the sensory cortex (Mountcastle 1978). Intracellular studies in unanesthetized rats have shown that striking a single vibrissa evokes EPSP with trisynaptic latency in neurons of the corresponding barrel, and this excitation spreads within 3–4 ms throughout the barrel column (Carvell and Simons 1988). By measuring extracellular spike activity under light anesthesia, Armstrong-James et al. (1991) have shown that excitatory surroundings of the receptive fields of rat's cortical barrel cells are almost entirely building by intracortical connections. It was then proposed that this surround was formed by intracolumnar flow of excitation: the thalamic input first reaching the layer-IV cells could consequently be transmitted to the surrounding barrels either horizontally or through the pyramids in layers II and III (Armstrong-James et al. 1992). On the other hand, the layer-V pyramidal neurons were proposed to exert a descending control over the cells in the posterior thalamic group (POm), which in turn would prime the cells intercalated between cortical columns, thus allowing further spread of intercolumnar activity (Diamond et al. 1992b).

The flow of sensory information between the adjacent barrels has been proposed to be used in normal behavior for comparing incoming sensations from neighboring points, according to the needs of dynamic cortical calculations, which may further lead to modification of the barrel cortex network (Simons 1995). To verify such a hypothesis, one needs to study the circuit in behaving animals. We have chosen the technique of recording gross potentials from the barrel cortex of awake rats during a classical conditioning situation. This old technique still gives the best time resolution and additionally allows parallel monitoring of synchronized activity of pyramidal cells in supra- and infragranular layers (Di et al. 1990; Musiał et al. 1998b), the main output cells for the cortical barrel column.

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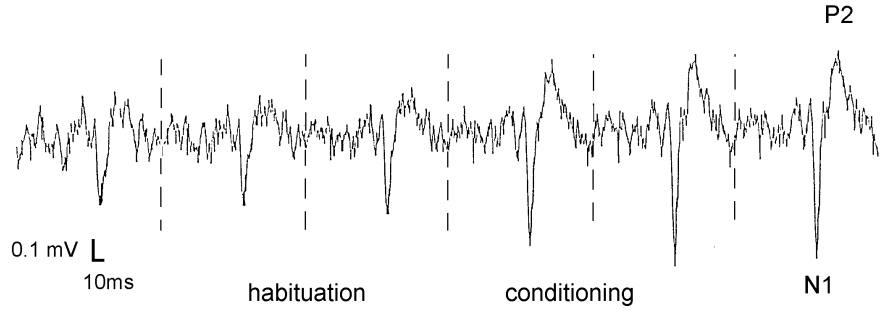

Fig. 1 Averaged, evoked potentials (EP) obtained by stimulation of principal vibrissa in rat R38. To limit individual variability, each EP has been averaged from three consecutive EPs (the current, proceeding, and following). *N1, P2* Negative and positive main EP components measured in this experiment. Note the increase of both of these components with conditioning (three last responses). Positivity is upwards. *Calibration bars* to the left

Excitation of barrel cortex evoked by conditioning stimulus

To reveal the dynamics of sensory processing in the barrel cortex of the conscious rat we recorded evoked potentials (EPs) caused by stimulation of single vibrissa during a classical conditioning procedure (Musiał et al. 1998a). The animals were accustomed to resting in a hammock with their heads fixed by means of a restraining apparatus. Following a few days of habituation, we implanted 2–3 electrodes in both (or one) barrel cortices at the approximate level of layer IV. After recovery from the surgery, rats were placed in the restraining apparatus and, before each experimental session, their vibrissa were glued to the piezoelectric device used for stimulation. The principal vibrissa was selected by choosing the whisker whose stimulation evoked the greatest amplitude of response. A few days of habituation was allowed for the rat to become accustomed to a restrained whisker. The responses were evoked by a 3-ms deflection of the principal whisker at different interstimuli intervals (20–40 s). Each evoked potential (Fig. 1) consisted of two easily recognizable main components: N1, with a peak latency of about 10 ms, and P2, at about 20–25 ms. By recording the EPs to stimulation of all vibrissae in the barrel field, we have mapped the activation fields for both of these components. N1 had a smaller field diameter with a steeper weighing function than P2, which is evident in most of the barrel field (Kublik and Musiał 1997; Wróbel et al. 1997). The distribution of excitation, latency, and polarity of these two main components allowed us to attribute main origins either from the barrel corresponding to the principal whisker (N1) or from the surrounding barrel cortex (P2).

After stabilization of the background responses (see below and Figs. 1 and 4), a mild electric shock for the unconditional reinforcing stimulus (US) was applied to the rat's ear, delayed 200 ms to each vibrissa stimulus (CS). Immediately after the first US, the amplitude of the negative N1 component of the EP on the conditioned side of the cortex grew in relation to the same component of control potentials (Fig. 1) and those evoked by stimulation of symmetrical, contralateral vibrissa (compare Fig. 1 in Musiał et al. 1998a). This enhancement ceased eventually after 2–3 days of conditioning despite continuous reinforcement. We have proposed that such a declining effect might correspond to active habituation of unavoidable aversive stimuli (Musiał et al. 1998a).

We do not know the cellular mechanisms underlying the observed relative enhancement of EP amplitude on the conditioned side of the cortex (Musiał et al 1998a). It is probable that this enhancement originated from more cells being excited in the barrel column by the facilitatory action of neuromodulatory inputs activated by aversive stimulation (see Sara and Segal 1991; McCormick 1992; Steriade et al. 1993; Woody and Gruen 1993). Some possible recruiting effects will be discussed in detail below. We tried to reach a more global insight into these mechanisms by studying the DC level of the local field potential (LFP) measured with the same microelectrode as used for the EP recordings. The preliminary results indicated that the enhancement of the N1 component was preceded by a positive DC shift of LFP level measured at layer IV (not shown). This effect may be partially due to the cholinergic or noradrenergic blockage of Ca-dependent K^+ currents (Steriade 1984; Steriade et al. 1993; Woody and Gruen 1993). Whatever the mechanism, the larger amplitude potentials evoked by sensory stimuli seem to parallel an enhanced activation of the barrel cortex evoked, in our experiments, by the conditioning procedure.

Subcomponents of the evoked potential

The detailed analysis of single evoked potentials recorded during the experiments on awake animals revealed that, besides the two main components (N1 and P2), in the overall EP waveform one can recognize several small ripples of underlying synchronous activity. For the purpose of revealing the possible complexity of the EP source, we adapted principal component analysis (PCA) by considering consecutive EP traces as variables and voltage measurements at chosen time points as case values (Musiał et al. 1998a and below). This method allowed two subcomponents to be discerned in N1, which seemed to start with the same latency (about 5 ms poststimulus), but peaked at different times (in Fig. 2A: 7 and 11 ms).

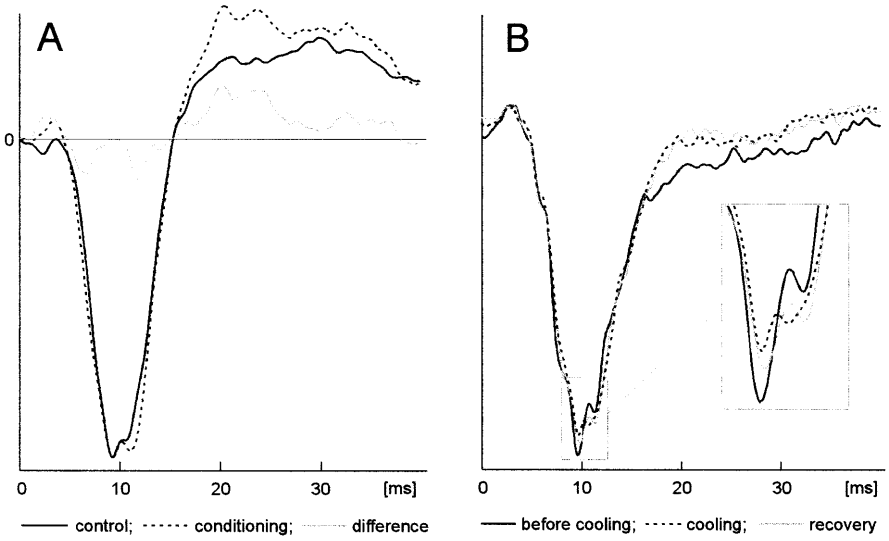

Fig. 2 **A** Averaged potentials (EPs) φ evoked by 23 stimuli to the principal whisker before (*continuous line*) and after (*dashed line*) unconditional reinforcing-stimulus (US) introduction in rat R33. The difference between the two EPs (*gray line*) indicates the relative changes of the subcomponents in the two behavioral situations. **B** Averaged EPs obtained before (*continuous line*) during (*dashed line*), and after cooling (*gray line*) of the cortical surface of the urethane anesthetized rat. EP drawn by the *dashed line* was obtained over 15 s immediately after cooling and, for the *gray line*, during the next 30 s. Note the decrease of the first and the simultaneous increase of the second subcomponent of the N1 after cooling

The onset and time difference (4 ms) between the peaks of the two subcomponents are similar to those found previously by Di et al. (1990) in ketamine anesthetized rats. These authors have analyzed the potentials evoked at different cortical depths and, by means of current-source analysis, have attributed the first and second components to excitation of supragranular and infragranular pyramidal cells, respectively. Since both of these pyramidal cell classes receive the afferent excitation on apical dendrites extending perpendicularly to cortical surface, they therefore form natural dipoles easily detected by microelectrodes. The possible contribution made by stellate and multipolar nonpyramidal cells were found to be attenuated in EPs and were eliminated in CSD analysis. The timing of the two subcomponents obtained in our experiments is congruent with the above model (Di et al. 1990) and also with extracellular unitary recordings from supra- and infragranular cells by Armstrong-James at al. (1992). We would therefore presume that the first subcomponent was produced by postsynaptic excitation of the proximal or basal dendrites of supragranular cells, evoked either directly by thalamo-cortical fibers or by interneuronal relay in granular layer (for a review, see Keller 1995). This subcomponent will be accordingly called N1s. The second subcomponent will be called N1i and is attributed to postsynaptic activation of infragranular cells exerted by the combined action of thalamic and intracolumnar fibers, including collaterals from supragranular pyramidal neurones. Notice that these inputs include mono-, di-, and trisynaptic components (Keller 1995; Paxinos 1995). Such a compound nature agrees with a short-onset latency and late peak response of N1i. The magnitude of this subcomponent depends in part on firing of supragranular cells, which feed in the apical dendrites of layer-V pyramidal cells. The N1i increase does not necessarily mean, however, that infragranular pyramidal cells would fire spikes as their progenitors, since the wave amplitude, as measured experimentally, presumably reflects mainly postsynaptic potentials.

To locate the origin of N1 subcomponents, we briefly cooled the surface of the barrel cortex of urethane anesthetized rats in order to lower the activity of neuronal elements in its superficial layers (Kublik et al. 1997a). The consecutive records obtained during such experiments are shown in Fig. 2B. Cooling exclusively decreased the N1s amplitude, proving that the suppressed neuronal elements are more superficially located than those of the N1i. In fact, the amplitude of this later subcomponent increased at the same time, which suggests reduced activity of inhibitory interneurons in the superficial layers (Szentagothai 1983; Keller 1995). The specific decrease of N1s was reversible within only 15 s after cooling, and no evident, overall EEG change was observed in a meantime. We conclude that the pyramidal cells contributing to N1s are more superficially located then those of N1i.

In accordance with the postulated attribution of N1s to supragranular-layer activity, this subcomponent was also found to be associated by principal component analysis with the P2 wave. As proposed above, P2 represents the response of the surrounding barrel field and may arise from activation of cortico-cortical connections originating in the superficial layers of the principal whisker column (Keller 1995).

Despite their direct sensory input, the firing of infragranular pyramids in awake animals most probably depends upon combined activation from many different sources. This differs from the situation where synchronized firing of all involved cells is evoked at short latency by electrical stimulation of ascending pathway. Such stimuli delivered to the ventral posterior medial nucleus (VPm) in anaesthetized rats trigger spikes in layer-V cells

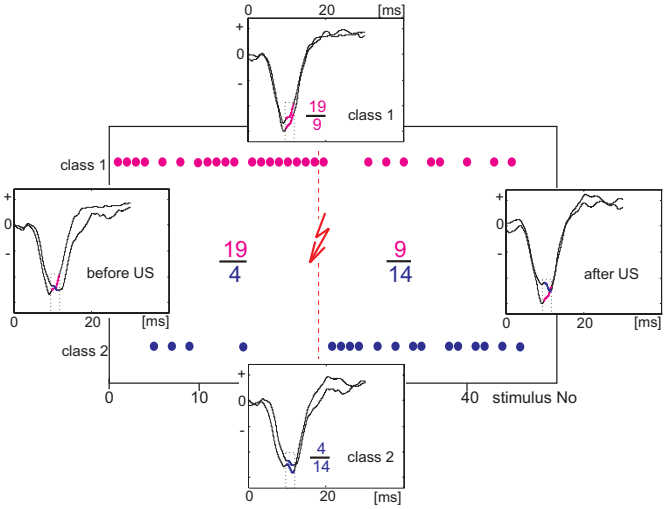

Fig. 3 The relative incidence of the two classes of evoked potentials (EPs), *class 1* and *class 2*, during the first 46 stimuli in a session when the electric shock stimulus (US) was introduced for rat R33. The classes were differentiated by maximal slope differences (see text). The EPs from two classes were averaged separately for responses before and after the 23th trial, from which on the vibrissa stimulation was continuously paired with unconditional stimulus (US) (*inserts* at the left and right of the figure). *Broken arrow* points to the 24th trial, which was the first reinforced with aversive stimulus. Each class-1 response was marked by a *gray dot* in the *upper row*, and all EPs of this class were summed within CS-alone and CS+US periods (19 and 9 occurrences); the class-2 responses are marked by *black dots* (4 and 14). The class-1/class-2 responses from the two periods are compared within the *upper/lower insert*, respectively

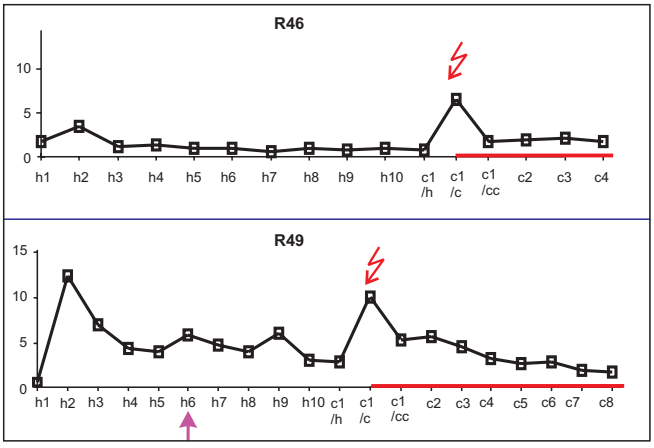

Fig. 4 Dynamic changes of the relative incidence of the two EP classes (differing by the course of both N1 and P2 components) during a conditioning experiment in two rats. Each panel shows the class-2/class-1 ratio averaged daily during the entire experiment. Ninety responses were recorded and classified in each session. *h1–h10* consecutive daily habituation sessions, *c1/h* first part (30 responses) of the first conditioning session, *c1/c* and *c1/cc* second (30 responses) and third (30 responses) part of the same session with each vibrissa stimulation (CS) reinforced by a unconditional stimulus (US), *c2–c8* daily conditioning sessions, all CS responses in these sessions were continuously reinforced by pairing with US (*thicker abscissa line*), *straight arrow* session during which the ear clips were attached for the first time in rat R49, *broken arrows* the beginning of the US application

before layer III is excited via a disynaptic route (Castro-Alamancos and Connors 1996). With electrical stimulation of the lateral geniculate nucleus, the latency difference between di- and trisynaptically activated cells of the cat's visual cortex column were found to be about 1.4 ms (Ferster and Lindström 1983). The longer, 4-ms delay between excitation of supra- and infragranular layers as obtained in our experiments might result from spatiotemporal summation of afferent excitation and subsequent relay along the columnar stream. Additionally, some recurrent mechanisms based on excitatory intracortical loops might contribute to this delay as well (Ferster and Lindström 1983; Douglas et al. 1995; Gray and McCormick 1996).

Transient changes of cortical excitability during contextual manipulations

In order to uncover changes in intracortical activity associated with conditioning, we classified consecutive potentials according to the contribution of their subcomponents to the integral of the whole waveform. This approach clustered all EPs into two clearly differentiated classes. The classification changed negligibly with the length of the time window in which the search for maximal difference between classes was performed. Figure 3 presents results of such a classification of EPs recorded from the awake rat during a session in which the unconditioning stimulus was first introduced. The two classes were differentiated within the 2.5-ms time window, as indicated in the Fig. 3 by broken lines. The time point of the maximal slope change was at around 10 ms after stimulus, just at the top of the N1 wave. Separate averages within each class were then calculated before and after introduction of the US (see inserts at the upper and lower parts of Fig. 3). The second class differed from the first by the presence of an enhanced second subcomponent N1i. Figure 3 illustrates the increase of amplitude of both EP classes (see above) and an even more dramatic change of their relative incidence after beginning of the reinforcement (Wróbel et al. 1995). During the control period (23 nonreinforced stimuli), the class-2 EP was recorded only four times, which increased to fourteen times within the comparable period immediately following the introduction of the conditioning procedure (23 CS-US trials). This pattern was consistently found in the entire group of five animals, proving that conditioning specifically enhances the N1i subcomponent of EPs in all animals. After subtracting N1 waves of the two averaged EPs, before and after US introduction, it was found that the N1s subcomponent also grew slightly after introduction of US (Fig. 2A). We therefore conclude that conditioning enhances excitability of both supra- and infragranular neurons.

The other change accompanying the US introduction was the prominent increase of the P2 component of the re-

corded evoked potentials (see left and right inserts in Fig. 3). It is worth noting that increases in P2 seem to be independent of the presence of a clearly discernable N1i. This finding additionally supports our previous observation that P2 is better associated with the N1s subcomponent.

To follow the dynamics of the relative incidence of EP classes during the entire experimental session, we classified these potentials within a longer time window, encompassing both N1 and P2 waves. With such a classification, we calculated the ratios of the derived classes in all experimental sessions (Kublik et al. 1997b; Wróbel et al. 1997). Figure 4 illustrates these relations for the most apparent data obtained for two animals. It is clear that the ratio of a relative incidence of the two classes was influenced not only by the application of the conditioning stimuli, but also by other sensory stimulation. First of all, gluing of the principal vibrissa to the stimulator produced an arousing situation, because it prevented the possibility of voluntary whisker movements. This initial stimulus was accompanied by an increase in the number of class-2 EPs (compare session h2 in the results presented in Fig. 4), which gradually ceased, in parallel with the putative habituation process, within 2–4 days in most rats. Clipping of the electrode that delivered the US to the rat's ear was another stimulus enhancing the relative incidence of class-2 EPs (Fig. 4, straight arrow). Such an intervention evoked a transient increase in the current EP classes ratio, which similarly habituated within 1–3 days. In one animal (R46), the results of which are presented in top drawing in Fig. 4, the electrode clipped to the ear was mounted in the beginning of experiment and, therefore, no additional increase of the EPs' ratio was observed during the habituation period. Similar changes were observed in the remaining three animals. The dynamics of the observed parameter depended, however, on the value of US (with weak reinforcing current, the same effects were smaller or started with a delay).

Sensory gating at the cortical level

In this paper, we have presented first evidence for the serial relay of excitation, carrying the sensory information through the column of primary sensory cortex of awake animals. The hypothesis proposing such dynamics in barrel column was put forward by Armstrong-James and colleagues (1992) on the basis of single-cell latency measurements within different layers of anesthetized rats. Since our data were obtained with awake animals, we were additionally able to show that such a relay is influenced by contextual sensory experience. We therefore hypothesize that nonspecific, arousing stimuli enhance the excitability of pyramidal cells in supra- and infragranular layers, allowing their previously habituated response to be transmitted outside the barrel column for further comparison and elaboration.

Figure 5 combines our results and hypothesis about gating of the sensory information within barrel cortex. We assume that the two main components obtained by PCA from the potentials evoked in the barrel cortex by vibrissa stimulation reflect sinks caused by excitation of pyramidal cells in supra- and infragranular layers. The time courses of these components are shown in the upper part of Fig. 5. Although many cells of each group receive direct thalamo-cortical input, the infragranular cells reach peak of excitation after a further 4-ms delay because they sum excitation from additional sources, including supragranular pyramidal cells.

The monosynaptic EP wave was originally differentiated from polysynaptic inputs in the primary visual cortex of cats by Ferster and Lindström (1983). For such a separation, one needs the synchronized volley evoked by electrical stimulation and electrodes of higher impedance. Current-source density analysis of high resolution is also capable of disclosing the first synaptic relay in cortex (Tenke et al. 1993). Looking for insight on natural information processing, we decided to fix low-impedance electrodes at cortical depths where all columnar sinks could be easily recorded. Such electrodes limited our resolution to highly polar pyramidal neurons (Di at al. 1990), but, fortunately, these are placed in crucial positions for the intra- and intercolumnar flow of sensory information (Ferster and Lindström 1983; Armstrong-James et al. 1992). The original proposal of sequential information processing (Hubel and Wiesel 1962) in the sensory cortex, as specified in our model, starts with the postsynaptic excitatory responses directly or indirectly at proximal dendrites of small pyramidal neurons of the upper cortical laminae, exactly as proposed by others (Ferster and Lindström 1982; Kulics and Cauller 1986; Di et al. 1990). Kulics and Cauller (1986) proposed that the second subcomponent of N1 (the two subcomponents in monkey S1 having 12- and 20-ms latencies) is from excitation of more superficially located pyramidal cells. We have chosen the interpretation of Di and colleagues (1990), not only because they performed their analysis on the same animal, but also because our data on cooled superficial cortical layers supported their interpretation.

When the context of continuously repeated and therefore habituated vibrissa stimulation changes with the introduction of aversive US, the EP-response amplitudes in the barrel cortex grow (Fig. 1). This increase is most probably due to the modulatory action of cholinergic and noradrenergic pathways, which change the mode of activity of the cells in barrel column (McCormick 1992), as well as due to the activation received by these cells from other cortical areas (Armstrong-James 1995). Among other mechanisms, we propose that the amplification gain is changed in the output cells of the barrel column: pyramidal cells located in supra- an infragranular layers. The excitation within both of these cell groups increases, the latter being supplemented by collaterals of pyramids in layer II and III. Direct thalamic input, together with enhanced excitation from supragranular neurons, further increase the postsynaptic activity of infragranular pyramidal cells (as observed by larger N1i subcomponent) and may better bring them to firing level (Fig. 5, lower part).

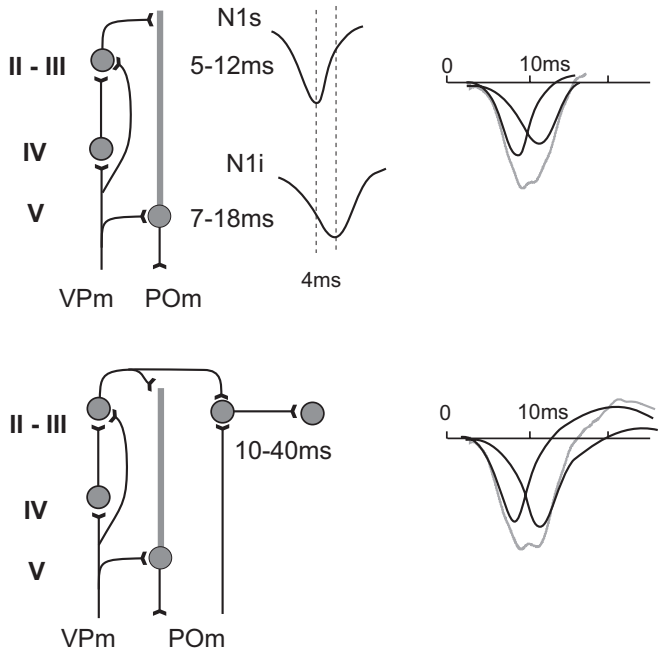

Fig. 5 The gating hypothesis describes the flow of sensory information through the barrel column. *Top* The supragranular cells in *layers II/III* receive thalamic excitation monosynaptically or via granular cells in *layer IV*. The corresponding subcomponent N1s of an evoked potential (EP) reflects the postsynaptic activation delivered to these pyramidal cells from both inputs. Infragranular cells in *layer V* receive fibers from collaterals of thalamic afferents as well as those of supragranular pyramidal cells (via apical dendrites in upper layers, marked *gray*). The corresponding subcomponent N1i therefore combines mono- and polysynaptically transmitted sensory input. The delay between the peaks of the two subcomponents was typically 4 ms. *Bottom* The arousing aversive stimuli changed the excitability of all cortical cells. The supragranular pyramids amplify their action exerted on pyramidal neurons in layer V and septal neurons between barrels. Infragranular neurons transmit their excitation to cells in the medial region of posterior thalamic group (POm), which in turn feedbacks activation to intercolumnar cells, thus opening the gate to surrounding cortical columns. *VPm* Ventral posterior medial nucleus

The activation of pyramids in layer Vb may prime the cells intercalated between cortical columns via the cortico-thalamo-cortical loop through POm cells (Diamond et al. 1992b). Such an action may in turn open an intracolumnar gate for the sensory information to be transmitted to other cortical areas. The POm cells integrate excitation from many neighboring whiskers and, accordingly, are more activated when more whiskers are stimulated simultaneously (Diamond et al. 1992a). Opening the gate to the surrounding barrels activates the neighboring neuronal elements, which is manifested in our recordings by means of an enhanced P2 wave (Fig. 5, lower part; compare also Figs.1 and 2). The P2 component was not noticed in anesthetized rats by Di and colleagues (1990). On the contrary, in awake, behaving monkeys a similar component has been shown to correlate with sensory discrimination performance (Cauller and Kulics 1991). The corresponding cortical current was recorded in the latter study over broad regions of postcentral gyrus, suggesting its widespread propagation. This result is very similar to that observed for the large activation field of the P2 component (Di and Barth 1993; Kublik and Musiał 1997; Wróbel et al. 1997).

Note that excitation of the surrounding barrels requires simultaneous coactivation of barrel cortex and POm in the proposed model. Thus, both general contextual arousal and excitation of neighboring somatosensory inputs open the gate for information from a single whisker to be transmitted for further comparison and elaboration. In agreement with this, the class-2 responses appeared with higher probability when the DC level measured prior to stimulation was more positive.

One may argue whether the responses of the restrained vibrissae in our experimental setup are physiological, since they are deprived of natural movement. We assumed that, although restraining may change the relative sensibility of a whisker, its sensitivity to natural stimuli is still preserved, as proven by the consequent habituation to sustained stimuli and increased responsiveness to new sensory inputs (Fig. 4).

Transient enhancement of cell responses in supra–and infragranular layers in corresponding cortical columns was observed 24 h after behavioral "pairing" of only two remaining, nontrimmed whiskers during normal whisking behavior (Diamond et al. 1994). The same procedure, prolonged for 3–30 days, resulted in a more persistent plasticity exhibited by barrel cells (Diamond et al. 1993; Armstrong-James et al. 1994). Our results are in accordance with the finding of transient change in the excitability of pyramidal cells. More prolonged, plastic changes of intracolumnar connectivity could then be formed within layer IV (Siucińska and Kossut 1996), which could not be recorded in our experiment since these cells lack apical dendrites and contribute much less to the evoked potentials.

The observed modification of EPs was immediate and started with the first US reinforcement, but in most cases ceased in the next-day session (Musiał et al. 1998a). Similarly, a rapid development of single-cell receptive-field plasticity was observed during classical conditioning in guinea-pig auditory cortex (Edeline et al. 1993). These authors argued that, together with specificity and endurance, such a rapid course of acquisition satisfies all criteria for processes involved in the formation of associative memory. Plastic changes of connection strength were observed during pairing of activity between intracolumnar neurons of monkey auditory cortex in a behaviorally meaningful situation (Ahissar et al. 1992). These changes were independent of the general level of neuronal excitability. Since the EP enhancement found in our experiment is specific to the stimulated hemisphere, it is not a generalized, non-specific response (such as arousal), but also represents a valid mechanism of plasticity (Musiał et al. 1998a). The dynamics of gating mechanism within sensory cortex can, however, be sufficiently explained in nonplastic terms.

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