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Dynamics of the orientation tuning of postsynaptic potentials in the cat visual cortex

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Abstract

We evaluated the dynamic aspects of the orientation tuning of the input to cat visual cortical neurons by analyzing the postsynaptic potentials (PSPs) evoked by flashing bars of light. The PSPs were recorded using *in vivo* whole-cell technique, and we analyzed the orientation tuning during subsequent temporal windows after stimulus onset and offset. Our results show that the amplitudes of the postsynaptic potential are reliably tuned to orientation and matching that of the spike responses only during certain temporal windows. During the first 100 ms after stimulus presentation, orientation tuning of the membrane potential underwent regular changes. Within particular intervals, orientation tuning of the input was much sharper than that estimated according to the whole response. In most cells, optimal orientation was usually stable over the whole period. In several cells which had a second hump of EPSPs in the response, this second hump was tuned to the same orientation as the first one, but always showed sharper tuning. Estimation of the integration time revealed sufficient delay between the appearance of EPSPs and spikes, to let inhibition influence spike generation. These results show that orientation selectivity of the input to cortical cells is a dynamic function, and also indicate the possibility of temporal coding in the visual system.

Keywords: Cat visual cortex, *In vivo* whole-cell recording, Orientation selectivity, Temporal coding

Introduction

Single cells in the primary visual cortex are presumed to operate as feature detectors, for instance as detectors of the orientation of the contours of objects. The main coding principle in such a system would be a positional code, when cell firing signals the presence of an object with particular properties within the receptive field. Introduction of the temporal parameters of the response as an additional variable would allow a significant increase of the capacity of the coding system. There are indeed indications for the possibility of exploiting a spatio-temporal coding process from studies of the temporal organization of the spatial response profiles of cells. It has been shown that receptive-field structure (Palmer & Davis, 1981; Shevelev et al., 1982, 1992) and orientation selectivity (Shevelev & Sharaev, 1981; Best et al., 1989; Shevelev et al., 1993; Celebrini et al., 1993) of visual cortical neurons are not fixed and stable over time, but undergo regular and consistent changes during the development of the response, in the range of tens of milliseconds. These reports on the dynamics of orientation tuning and receptive-field structure were based on evaluations of extracellularly recorded spike responses, which are a measure of the output of the cell. Any spatio-temporal organization of the response occurring at the level of the membrane potential prior to reaching the action potential threshold cannot be tapped by extracellular recordings.

In the present study, we have investigated the dynamic properties of the orientation tuning of the inputs to visual cortical neurons. We recorded visually evoked postsynaptic potentials using an *in vivo* whole-cell technique (Pei et al., 1991*a*) and applied to these responses a temporal slice analysis (Shevelev & Sharaev, 1981). We analyzed the orientation tuning during subsequent temporal windows after stimulus onset and offset. Our results show that the amplitudes of the postsynaptic potential is reliably tuned to orientation and matching that of the spike responses only transiently. During most of the early 100 ms after stimulus presentation, orientation tuning of the membrane potential underwent regular changes.

These results have important implications for the neuronal mechanism of orientation selectivity as well as for spatio-temporal coding of sensory information. A brief account of these dynamic changes was included in our earlier paper on the receptive-field structure of postsynaptic potentials (Pei et al., 1994).

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Methods

Experimental procedures were the same as previously described (Pei et al., 1991*a*; Volgushev et al., 1993; Pei et al., 1994). Experiments were done on adult cats (2.0–4.5 kg) bred in the animal house of the Max-Planck-Institute for Biophysical Chemistry. Anesthesia was induced with Ketamine hydrochloride i.m. (Ketanest, Parke-Davis, Berlin, 25 mg/kg i.m.) or with Nembutal (Sanofi, Ceva, 35–40 mg/kg i.p.), and maintained with i.v. infusion of 3–4 mg/kg/h pentobarbitone (Nembutal) without nitrous oxide or with 1–2 mg/kg/h Nembutal and a gas mixture of 70% N_2O plus 29.2% O_2 and 0.8% CO_2. Muscle relaxation was induced and maintained with gallamine triethiodide (Flaxedil, Davis & Geck, Pearl River, NY). End-tidal CO_2, body temperature and electrocardiogram were continually monitored. The adequacy of the anesthesia was attested by the stable heart rate and synchronized EEG waves at the doses we used. The general state of the animal, the eyes, and the cortex were in good condition for 2–3 days. Postsynaptic potentials from neurons in the primary visual cortex were recorded using *in vivo* whole-cell technique (Pei et al., 1991, 1994; Volgushev et al., 1991*a*, 1993; Ferster & Jagadeesh, 1992). We used electrodes similar to those used for single-channel recording (Sakmann & Neher, 1983), with a tip diameter of 1–3 μm, pulled with a patch-clamp pipette puller L/M-3P-A (David Kopf Instruments, Tujunja, CA). Their resistance was 2–7 MΩ when filled with a conventional patch pipette solution (Edwards et al., 1989): 130 mM K-gluconate; 5 mM NaCl; 10 mM EGTA; 10 mM HEPES; 1 mM ATP; 1 mM $CaCl_2$; and 2 mM $MgCl_2$; pH 7.4 (KOH). An electrode holder through which positive or negative pressures could be applied (Hamill et al., 1981) was connected to a hydraulic microdrive (David Kopf Instruments, Tujunja, CA) that was mounted on the skull. On gaining access to the interior of a cell, stable recordings could be maintained over several hours with membrane potentials of usually −30 to −60 mV and cell input resistances of 40–200 MΩ. Only occasionally were membrane potentials more negative than −60 mV. These values are generally within the range reported for visual cortical cells *in vivo* by others (Creutzfeldt et al., 1974; Douglas et al., 1991; Ferster & Jagadeesh, 1992; Nelson et al., 1994). Further details of the experimental procedure and discussion of our recording situation are published elsewhere (Pei et al., 1991*a*, 1994).

Visual stimuli (light bars) from a projector were presented using a computer (PC 386) on a screen positioned 57 cm in front of the animal, whose eyes were focussed on the screen using appropriate hard contact lenses. Pupils were dilated by atropine and artificial pupils (4 mm in diameter) were used.

To minimize spurious results due to response variability, stimuli of different orientations and positions on the screen were interleaved in a pseudo-random order. Receptive fields were classified according to conventional criteria (Henry, 1977). This was done first with the aid of a hand-held projector and then the classification was checked during off-line analysis from the data collected with computer-controlled visual stimuli. For testing orientation tuning, the stimulus was centered usually on the ON-excitatory zone.

To evaluate dynamic properties of the input to cortical cells, a modification of the method of temporal slices (Shevelev & Sharaev, 1981) was used. We adapted this method for the analysis of PSPs. Response strength was estimated as the integral area of averaged PSP which differed from the mean resting membrane potential by more than one standard deviation within successive temporal intervals (temporal windows) of a given duration (for example: 30–35 ms, 35–40 ms, 40–45 ms, and so on) usually in steps of 2 to 20 ms. Responses to each orientation presented were processed in this way. The reading made just before presentation of each stimulus was used as the baseline resting potential to calculate the mean resting potential and its standard deviation. These values were calculated across all orientations and repetitions and hence represent mean membrane potential and its variability during the whole period of orientation tuning test. In some cases, spikes were truncated in each single sweep before averaging with the use of a computer algorithm based on the detection of peak-shaped events with a very fast rise and fall. Orientation tuning curves were plotted for each temporal window using the values of response strength obtained from responses to different orientations. Examples of some of these tuning curves are shown in Fig. 1B, where the starting point of the temporal window is marked on the upper left. For those slices in which maximal response for an orientation was at least 10% of the absolute maximum across all slices, the half-width at half-height and the optimal orientation were estimated and plotted against time (Figs. 1C and 1D, respectively). We would refer to this as a "differential" estimation of the dynamics of orientation tuning.

A cumulative ("integral") estimation was obtained using the same procedure, but in this case the duration of the temporal window was sequentially increased by a given step, while its initial point was the same for all the windows (i.e. 30–35 ms; 30–40 ms; 30–45 ms, and so on).

Results

We made intracellular recordings from neurons in the primary visual cortex (area 17) of the cat using the *in vivo* whole-cell recording technique (Pei et al., 1991*a*). Eighteen cells in which significant postsynaptic potentials were evoked by bars flashed in the receptive-field center and at least eight different orientations were tested, were selected for analysis in the present study. Orientation tuning of some of these cells estimated from the whole response and receptive-field profiles of their excitatory and inhibitory regions were evaluated in earlier papers (Volgushev et al., 1993; Pei et al., 1994).

Here we are reporting the detailed dynamic aspects of orientation selectivity of the inputs to visual cortical neurons, evaluated by means of the temporal slices technique.

The orientation tuning of the input a cortical neuron receives was not constant, but was dynamically changing in a regular manner during the development of the response. Orientation tuning width underwent the most pronounced and regular changes. The earliest response was usually a weak response in the optimum orientation. However, very soon, with the rapid development of the EPSP response to all orientations, tuning was seen to be very broad. Thereafter at a certain period from the beginning of the response, which differed between cells anywhere between 5 and 70 ms, the orientation tuning started to get sharper. After another 30–100 ms, responses were usually getting weaker and their orientation tuning could not be evaluated any more. In most cells, optimal orientation was stable over the whole period. Only in some cells (3/18) did it change consistently during the response.

The simple cell in Fig. 1 fired only when optimally oriented stimuli (140 deg) were flashed on the receptive-field center.

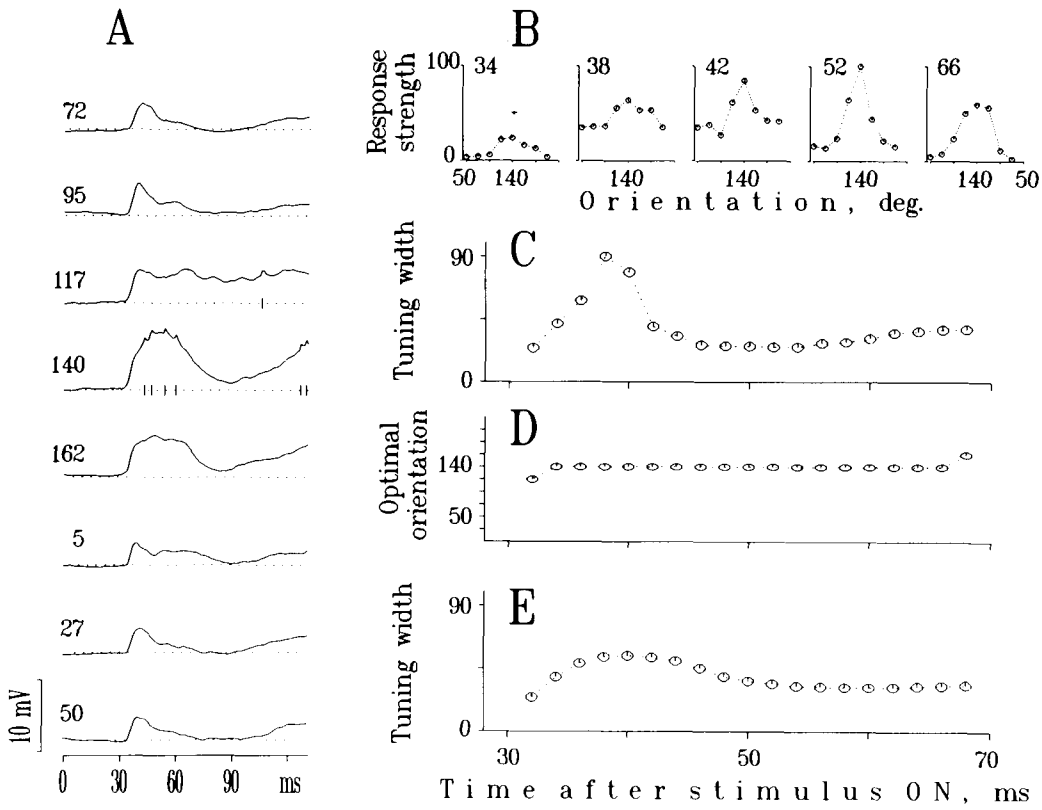

Fig. 1. Dynamics of orientation selectivity of PSPs in a visual cortex cell. A: Averaged postsynaptic potentials ($n = 5$) evoked in the cell by stimuli of different orientations, which were flashed over the receptive-field center. In this and following figures, the dotted line shows mean resting membrane potential (−43 mV for this cell) during the whole orientation tuning test. Short vertical bars at the baseline indicate the occurrence of spikes. Orientation of the stimuli is shown at the beginning of each trace. Time scale starts with stimulus ON. B: Orientation tuning at different temporal windows (slices). Each slice represents orientation tuning of the PSPs within a 2-ms interval, with the starting point marked in the upper left corner (ms from stimulus ON). Strength of responses within a given 2-ms interval was evaluated, normalized over all time intervals and orientations, and plotted against orientation. C: Differential estimation of dynamics of orientation tuning width, measured as the half-width of the tuning curve at half-height. Note the initial increase of the tuning width and its subsequent sharpening. Time scale is common for C–E and starts 30 ms after stimulus onset. D: Optimal orientation for the PSPs at different time intervals. E: Integral (cumulative) estimation of the tuning width. Note the smoother changes in tuning width compared to the differential estimation in C.

Occurrence of spikes is indicated by short vertical bars at the base line. Some spikes appeared during the first EPSP hump at 30–60 ms (Fig. 1A), and many more were generated with the second burst at 120–160 ms (not shown). Only a few spikes were evoked occasionally by stimuli of near optimal orientations. Stimuli of other orientations failed to evoke any spikes. However, pronounced EPSPs were evoked by every orientation (averaged PSPs are shown in Fig. 1A). Responses to the optimal orientation had slightly shorter latency, and therefore just after this latency, tuning of the weak initial response was sharp (Fig. 1B, tuning at 34 ms). But, due to a rapid and nearly equal development of responses to all orientations during the subsequent several milliseconds, orientation tuning of the input widened and selectivity virtually disappeared: half-width of the tuning around 38 ms in Fig. 1B is 90 deg. After that, response to the optimal orientation developed further, leading to spikes, while other responses diminished. This resulted in sharpening of the orientation tuning, which remained sharp during the next 20–40 ms (Fig. 1C). During this period, spikes could be evoked only in a narrow range of orientations. The input to this cell, as estimated from the evoked postsynaptic potentials, was best tuned to orientations around 52 ms after stimulus presentation (Fig. 1B, tuning width at 52 ms: 25 deg). Optimal orientation was stable during the whole period of dynamic changes in tuning width (Fig. 1D). When cumulative estimates of the response strength were used to calculate the orientation tuning within different temporal windows, the dynamics of the input were generally the same, but with smoother and less dramatic changes in tuning width (Fig. 1E).

The dynamics of the orientation tuning of the first-order simple cell in Fig. 2 were similar to those of the cell described above. The orientation tuning width of the input to this cell rapidly became sharper during the development of the response (compare tunings at 30 and 40 ms in Fig. 2B; note that the time scale for A and C differs from Fig. 1). In this cell, inhibition could be distinguished during the sharpening of orientation tuning and this inhibition appeared first at nonoptimal orientations (see tuning of inhibition at 60 ms shown with asterisks in Fig. 2B and the dynamics of inhibition in Fig. 2C). It should be noted here that the inhibition we have plotted is the hyperpolarization that can be detected when the inhibition has overcome the excitation. It is likely that inhibition actually begins much earlier. In

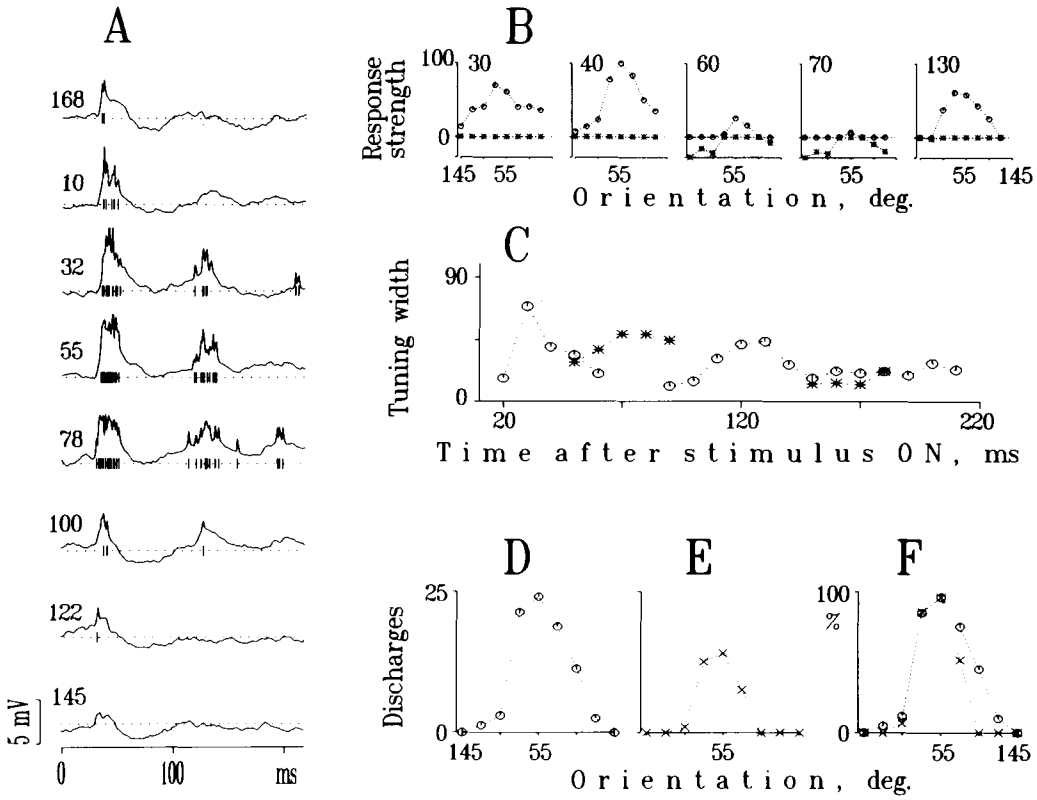

Fig. 2. Dynamics of the orientation tuning of excitatory and inhibitory PSPs in a simple cell. A: Averaged responses ($n = 5$) of the cell to stimuli flashed at different orientations. Mean resting membrane potential was −35 mV. B: Temporal slices of orientation tuning of excitatory (circles) and inhibitory (asterisks) PSPs. Step for slices was 10 ms. C: Dynamics of the orientation tuning width of excitatory (circles) and inhibitory (asterisks) PSPs, differential estimation with a step of 10 ms. Conventions in A–C are as in Fig. 1. The graphs in C are interrupted (for example, around 80 ms for excitation) when the maximal response within a slice was less than 10% of the absolute maximum across all slices. D–F: Orientation tuning of the same cell, estimated as the number of discharges in responses to different orientations. The same responses shown in A were used to count the number of spikes. D: for the first burst (20–70 ms); E: for the second burst (110–160 ms); and F: for the first (circles) and for the second (crosses) bursts, normalized and superimposed. Note sharper tuning of the second burst.

fact, the sharp decline of the membrane potential seen in the non-optimal orientation after the initial depolarization is suggestive of the inhibition starting much earlier than the time when hyperpolarization becomes visible.

Another point to be noted in the case of this cell is a late component in the response around the optimal orientation, which appears as a hump of EPSPs between 100 and 140 ms in Fig. 2A. These late responses were weaker than the early ones, but they were more selective for stimulus orientation (Fig. 2C, see response at 20–50 ms for the early component and 110–130 ms for the late one). Better orientation tuning of the late responses was also evident in spike discharges. Orientation tuning estimated from the number of spikes is broader for the early response components (20–60 ms, Fig. 2D) than for the late components (100–140 ms, Fig. 2E). The difference is obvious in Fig. 2F, where the same curves are normalized and superimposed.

Fig. 3 is an example of the progressive sharpening of orientation tuning of the input to a complex cell with several successive components of response. This complex cell shows at least three humps of EPSPs, separated by troughs, presumably of inhibitory origin, in response to an optimally oriented stimulus (Fig. 3A, 170 deg). During the early component (around 40–70 ms), orientation tuning of the input is very poor (Fig. 3B, tunings at 40, 50, and 60 ms and Fig. 3C). Optimal orientation changes markedly, "scanning" orientations over a wide range from 102–57 deg (Fig. 3D, in the region of 40–70 ms). During the second excitatory component of the response (Fig. 3A, 110–140 ms), orientation tuning of the input was much sharper (Fig. 3B, tuning at 130 ms and Fig. 3C) and optimal orientation was stable (Fig. 3D, region 110–140 ms). However, the second hump of EPSPs is seen clearly also in the responses to orientations near the optimum (Fig. 3A), but during the third excitatory component (Fig. 3A, 200–230 ms) orientation tuning of the input is again very much sharper (Fig. 3B, tuning at 220 ms).

The sharp orientation tuning of the second excitatory component can be seen also in the cumulative estimates. During and immediately after the first component, cumulative estimates show poor orientation tuning (Fig. 3E, 40–100 ms), but this is significantly improved when the second excitatory component of the response appears (Fig. 3E, 110–140 ms).

Up to two or three excitatory components in response to the optimal orientation were observed in four cells. In all of these cases, orientation tuning of the second component was better than that of the first one.

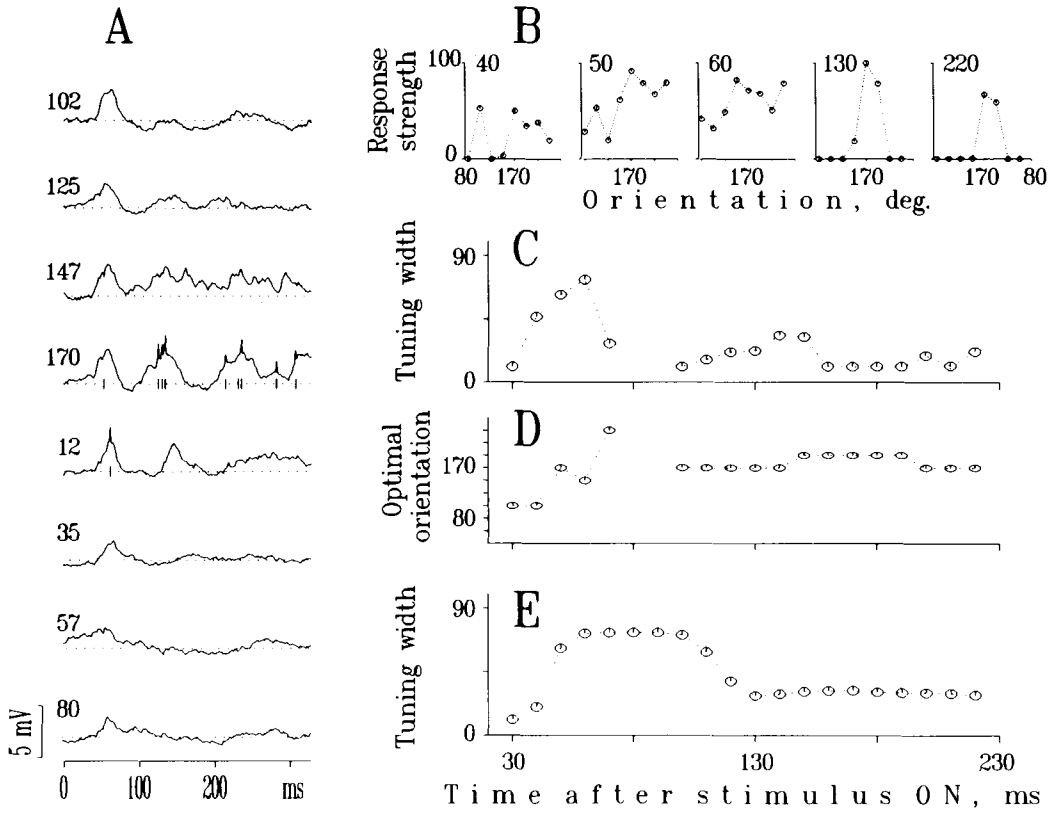

Fig. 3. Dynamics of the orientation selectivity of PSPs in a complex cell with oscillatory responses to stimuli of optimal orientation. A: Averaged responses ($n = 5$) of the cell. Note oscillations of the membrane potential at the optimal orientation (170 deg). Mean resting membrane potential was −30 mV. B: Temporal slices of orientation tuning. Step 10 ms. Note extremely poor orientation tuning of the input to the cell during the first burst (40–60 ms) and sharp tuning during the second (around 130 ms) and third (around 220 ms) waves of the membrane potential. C: Differential estimation of the dynamics of orientation tuning width. D: Dynamics of the optimal orientation. Note dramatic changes of the optimal orientation during the first wave of EPSPs and its stability during the second and the third waves of EPSPs. E: Integral estimation of the dynamics of orientation tuning width. Note that after the second wave of EPSPs orientation tuning got much sharper. Conventions in A–E are the same as in Fig. 1.

An exceptional case with no sharpening of orientation tuning during the response is shown in Fig. 4. This simple cell had a tonic response to orientations in the optimal range (Fig. 4A, orientations 47–92 deg). The width of orientation tuning of the input to this cell increased slowly and progressively during the whole response (Fig. 4C). Fairly similar dynamics was observed with cumulative estimation (Fig. 4E). Preferred orientation alternated between two values (Fig. 4D).

We have compared different estimates of orientation tuning by plotting scatter diagrams. In Fig. 5A, the maximum change in orientation tuning width between the different temporal windows is plotted against the integral estimation of tuning width of the first excitatory phase of response. This is represented by a vertical line for each cell, connecting the sharpest and broadest values of orientation tuning width. Changes in tuning width ranged from 6–72 deg (mean, 32 deg). In four out of 26 cases (15%), the change in orientation tuning was greater than 45 deg. It can be seen that at some moments during the dynamic changes, the input to a cell could be better tuned than the integral estimation, and at other moments the tuning was worse than the integral estimation: the vertical segment, which represents the dynamic range, crosses the main diagonal of the scatter for most cells (Fig. 5A). For the majority of cells (92%), a temporal slice could be found when orientation tuning was at least 5 deg sharper than the integral estimation; i.e. the vertical segments representing their dynamic range have their lower limits below the main diagonal in Fig. 5A. In many of them (75% of the whole sample), the best tuning was sharper than 30 deg. On the other hand, at some periods during the response, the input to a cell could be very poorly tuned. In many cases (61%), tuning in some slices was at least 5 deg broader than the integral, and in some of them virtually absent: the uppermost points in Fig. 5A correspond to a tuning half-width of 90 deg.

In general, differential estimation gave the same or slightly sharper values of orientation tuning than the cumulative estimation. In Fig. 5B, where differential estimation of tuning width at maximal response is plotted against integral estimation made from the beginning of the response to its peak, most points are located below or close to the main diagonal. Interestingly, in many cells (46%) the sharpest tuning was achieved not at the response peak. In Fig. 5C, differential estimation of tuning width at the peak of the response is plotted against the best tuning achieved during the period of dynamic changes. If the slice with the maximal response also exhibited the sharpest tuning, the corresponding point should lay on the main diagonal. However, this is not generally the case, since the majority of the

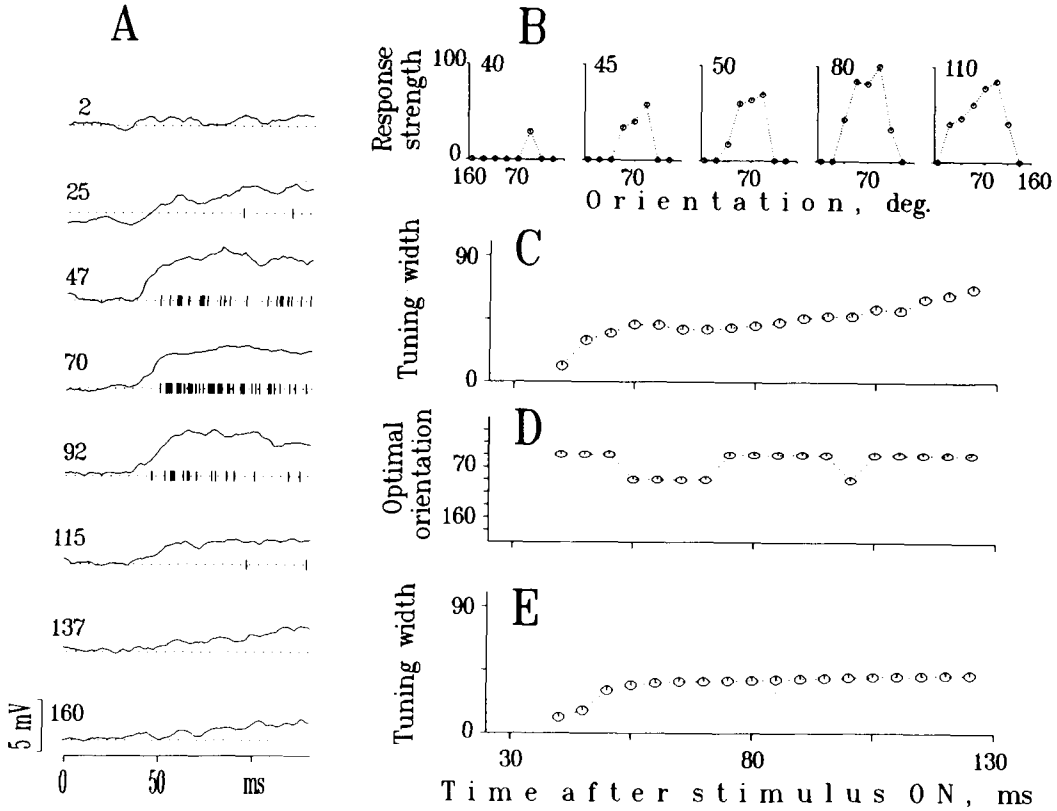

Fig. 4. Dynamics of the orientation selectivity of PSPs in a simple cell with a tonic response. A: Averaged responses ($n = 5$) of the cell. Mean resting membrane potential was −35 mV. B: Temporal slices of orientation tuning. C: Differential estimation of the dynamics of orientation tuning width. Note the gradual increase of tuning width. D: Dynamics of the optimal orientation. E: Integral estimation of the orientation tuning width. Conventions in A–E are the same as in Fig. 1.

points are located above the main diagonal. Most often the best tuning was seen at the end of the burst.

Other temporal aspects of the response that we estimated were the total excitatory phase of the response and the integration time (i.e. the latency from the beginning of the EPSP) required to elicit the first spike in the response. The duration of the excitatory phase in response to flashing bars varied in different cells from 30–100 ms. All of the dynamic changes in

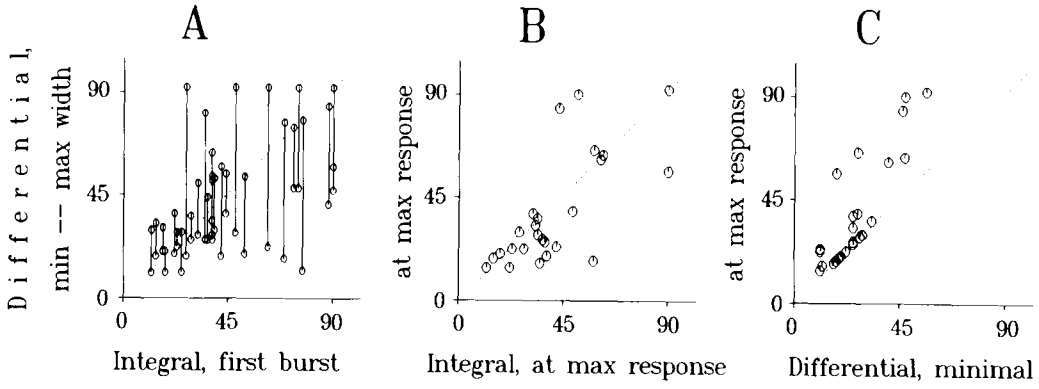

Fig. 5. Comparison of various estimations of orientation tuning width. A: Ranges of the change in orientation tuning width (ordinate), plotted against the integral estimation of tuning width of the first burst of PSPs (abscissa) for each cell. The range is shown as a vertical line, which connects the minimal and maximal values of tuning width. B: Scatter diagram of differential (ordinate) against integral (abscissa) estimations of orientation tuning width in the temporal slice in which maximal response amplitude was observed. C: Scatter diagram of differential estimation of tuning width at maximal response (ordinate, same as in B) against tuning width in a differential slice, which yielded the sharpest tuning. In A–C each point represents the estimate of the orientation tuning of either the ON ($n = 17$) or the OFF ($n = 9$) response. For eight out of the 18 cells in our sample, we recorded orientation tuning of both ON and OFF responses. For all estimations presented in this figure slices with the same temporal window (5 ms) were used. All axes are in degrees.

orientation tuning took place during this period. In four cells, additional excitatory components of response were evident. They appeared within 30–50 ms after the first burst and lasted for 40–70 ms (Figs. 2 and 3). The integration time required for the appearance of the first spike could be estimated only for stimuli of optimal and near-optimal orientations. In responses to optimally oriented stimuli, the first spike appeared 5–12 ms after the beginning of EPSPs (7.6 ms on average). Responses to near-optimal orientations required a longer integration time, namely, 6–15 ms (10.6 ms on average).

Discussion

The main finding of this study was that orientation tuning of the input to visual cortical cells underwent regular dynamic changes during the response. In the majority of cells, after an initial mild widening, the orientation tuning got sharper during the development of the response. Optimal orientation was usually stable over this period, except in three out of the 18 cells. These findings complement previous reports on the dynamics of orientation tuning of the output of cortical cells, estimated from spike responses (Shevelev & Sharaev, 1981; Best et al., 1989; Shevelev et al., 1993; Celebrini et al., 1993).

The initial widening of the orientation tuning was generally short and can be explained by the presence of a mild orientation bias that can be present in the input. This could be either a subcortical bias (Vidyasagar & Urbas, 1982; Soodak, 1987; Shou & Leventhal, 1989) or a small degree of excitatory convergence from a limited number of geniculate fields in a row. Even a mild bias would lead to the response first appearing in one orientation before the others, but with the subsequent rapid development of the response the true nature of the excitatory input could be observed, at least until inhibition begins to play a significant role. Our data indicates that in the majority of first-order cells the excitatory input fields are only slightly elongated (Pei et al., 1994), and the excitatory input during the 5–10 ms after the latency is indeed only broadly tuned to orientation. However, very soon, over the next 20–60 ms, the tuning gets sharper, which we interpret as being partly due to inhibition. Such sharpening has been reported for spike responses of cat cortical cells (Shevelev & Sharaev, 1981; Shevelev et al., 1993). In contrast to the recent work on awake monkeys (Celebrini et al., 1993), we observed sharpening of orientation selectivity after the first spike appeared. This implies that feedback connections, both excitatory and inhibitory, could contribute to the final orientation selectivity of the cell. However, evaluation of the integration time confirms our earlier qualitative observations (Pei et al., 1991*b*), which showed that a delay between the appearance of EPSPs and the generation of the first spikes in the response is long enough to allow feedforward inhibition to participate in the creation of orientation selectivity of the spike response (Celebrini et al., 1993). Given a considerable jitter in response latencies across cortical cells, the early response of many cells can be influenced by disynaptic inputs from the LGN, which can in principle be either excitatory or inhibitory.

We found regular changes in preferred orientation only in a small proportion of investigated cells (three out of 18). This is in contrast to some earlier reports, where such changes in preferred orientation were found in a larger percentage of visual cortical cells (63%, Shevelev et al., 1993). It should be noted here that one cannot make a direct comparison between the dynamics of the input and the output of the cell. Furthermore, the number of stimulus presentations at each orientation was too limited in our study (usually five, and only in some cases, ten) to enable enough spikes to be collected for comparison. Another possible reason for the discrepancy may be differences in the sampling properties of the two types of electrode: for example, our patch electrodes may have a bias for larger cells which may form a subclass with a different ordinal position or differences in stimulus parameters could play a role.

The input a cortical neuron receives does not show an entirely stable orientation tuning. Within certain intervals during the first 100 ms, orientation tuning of the input was much better than that estimated according to the whole response. This implies that there could be some advantages in employing a temporal code. Since input selectivity was better than the average during certain periods of the response, the final selectivity of the cell as an orientation detector could be improved, if particular components of the response could be selectively picked up by the neurons at the next level. It should however be noted here that though changes in orientation tuning of the input to area 17 cells raise the possibility of the visual system using a temporal code, it is the output of these cells and the properties of cells at the next stage that would be decisive in this regard.

In cells which had a second hump of EPSPs in their response, this second hump was tuned to the same orientation as the first one, but always showed sharper tuning. This was true for both the input (EPSP amplitude) and the output (number of spikes in the response) of the cell. Sharper orientation tuning of the second burst of spikes can be seen also in the data of Shevelev and Sharaev (1981, their Fig. 3A). Two questions arise in this connection: how is the sharper tuning of the second excitatory component achieved and what could be its purpose? Most probably, this component is due to the intracortical excitatory feedback (Douglas et al., 1991), or to the stimulus-dependent binding in the LGN by corticofugal feedback (Sillito et al., 1994). In both of these cases, the "recurrent" excitatory input is already tuned to orientation. The fact that the orientation selectivity of this component was not affected by hyperpolarization (see Fig. 2 in Volgushev et al., 1993) supports this view. The existence of a mechanism, which feeds back to the appropriate detectors, perhaps even causing them to oscillate at certain frequencies and thus increasing the persistence of the relevant message, could be advantageous for visual information processing. The fact that these oscillations happened only in responses to the optimal, and near-optimal orientations, suggests that they are due mostly to the properties of the network, rather than to intrinsic properties of the cell membrane.

Evaluation of the integration time revealed a substantial delay between the appearance of EPSPs and the generation of the first spike in the response. This delay was, on average, 7.6 ms for the optimal and even longer (10.6 ms) for near-optimal orientations. It gives enough room for inhibition to develop and affect the generation of spikes, especially in responses to orientations different from the optimal. However, detection of the inhibition a cell receives is complicated by the fact that the inhibition comes after excitation and is interposed on the developing excitatory response. Therefore inhibition is less likely to produce a significant hyperpolarization of the cell membrane relative to the resting potential. This implies that only a strong, well-developed inhibitory process could be detected as a membrane hyperpolarization. Indeed, we often detected inhibition 15–25 ms after the beginning of the excitatory response. If we assume that the development of inhibition requires nearly as much time as that of excitation, it follows that the early "pri-

mary" inhibitory influences arriving with a very short delay after excitation and can be easily masked.

Another role for inhibition which is known from extracellular data and which can be demonstrated on the basis of the evaluation of the dynamic properties of orientation tuning of the input to cortical neurons is to prevent continuous firing and/or to introduce bursts in the response. However, this can be provided by a different inhibitory system, probably of a recurrent nature.

Acknowledgments

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