European Journal of Neuroscience, Vol. 12, pp. 257–263, 2000

Comparison of the selectivity of postsynaptic potentials and spike responses in cat visual cortex

Maxim Volgushev,[1,2] Joachim Pernberg[1] and Ulf T. Eysel[1]
[1]Ruhr-University Bochum, Department of Neurophysiology, D-44801 Bochum, Germany
[2]Institute of Higher Nervous Activity and Neurophysiology RAS, 117865 Moscow, Russia

Keywords: direction selectivity, orientation selectivity, postsynaptic potentials, spike generation, tip of the iceberg effect

Abstract

Intracellular recordings were made from neurons in the cat visual cortex (area 17) to compare the orientation and direction selectivities of the output of a cell with those of the input the cell receives. The input to a cell was estimated from the PSPs (postsynaptic potentials) evoked by visual stimulation, and the output estimated from the number of spikes generated during the same responses. For the whole sample, selectivity of the output of cells was significantly higher than selectivity of their input. Upon PSP to spike transformation, the selectivity index was, on average, doubled. However, the degree of the selectivity improvement in individual cells was very different, varying from cases in which highly selective output was created from a poorly selective input and thus selectivity was greatly improved, to little or no improvement in other neurons. The improvement of selectivity was not correlated with resting membrane potential, threshold for action potential generation, background discharge rate or amplitude of optimal PSP response. Further, no systematic difference was found between simple and complex cells in the input–output relations, indicating that the 'tip of the iceberg' effect on shaping the response selectivity was cell specific, but not cell type specific. This supports the notion that multiple mechanisms are responsible for generation of the response selectivity, and that the contribution of any particular mechanism may vary from one cell to the other. The heterogeneity of the input–output relations in visual cortical cells could indicate different functions of cells in the cortical network; some cells are creating selectivity *de novo*, the function of other neurons probably being repetition and amplification of the selected signal and arrangement of the output of a whole column.

Introduction

The major sensory input to the visual cortex comes from the lateral geniculate nucleus, where the cells are unselective or only biased to the orientation and direction of movement of visual stimuli. However, the output of the cortical cells is highly selective for both these parameters. The mechanisms of orientation and direction selectivity of visual cortical cells have been intensively studied over the last decades. Although the bulk of experimental data indicates that multiple cooperative mechanisms are responsible for creation of the response selectivity of cortical neurons, the details remain a matter of debate (see reviews Henry *et al*., 1994; Vidyasagar *et al*., 1996; Sompolinsky & Shapley, 1997; but also see Reid & Alonso, 1996). Three questions are important for understanding the mechanisms of creation of the final selectivity of spike responses: how strong are excitation and inhibition activated by the different stimuli; how are the PSPs summated; and how are the PSP responses transformed into spikes? Intracellular studies were aimed mostly at the former two questions (Creutzfeldt *et al*., 1974; Ferster, 1986; Douglas & Martin, 1991; Douglas *et al*., 1991; Ferster & Jagadeesh, 1992; Volgushev *et al*., 1993; 1996; Nelson *et al*., 1994; Pei *et al*., 1994; Jagadeesh *et al*., 1997; Borg-Graham *et al*., 1998; Hirsch *et al*., 1998), the third issue receiving little attention so far. However, the postsynaptic potential (PSP)-to-spike transformation might play an important role in establishing the sharp final tuning by restricting the spike responses only to the range of the highest PSP responses – a 'tip of the iceberg' effect. In the present study we examined directly the contribution of this effect and made intracellular recordings from cat visual neurons *in vivo*. Both the amplitude of the membrane potential changes and the number of spikes were estimated from the same recordings of responses of a cortical cell to visual stimuli. This allowed for a direct comparison of selectivity of the PSP and spike responses, and thus for a quantification of the 'tip of the iceberg' effect on orientation tuning and direction selectivity. We demonstrate that a significant improvement of the selectivity of spike responses over that of PSP responses does occur in some, but not all, cortical neurons. Some of the results have been presented in abstract form (Pernberg *et al*., 1998).

Correspondence: Dr M. Volgushev, Ruhr-University Bochum, Dept of Neurophysiology, MA 4/149, D-44801 Bochum, Germany.
E-mail: maxim@neurop.ruhr-uni-bochum.de

Received 26 February 1999, revised 28 September 1999, accepted 5 October 1999

Materials and methods

Surgery and animal maintenance were similar to that described in detail earlier (Volgushev *et al*., 1996). Briefly, adult cats (3.0–4.5 kg) were anaesthetized with ketamine hydrochloride (Ketanest, Parke-Davis GmbH, Germany, 1.2 mL, i.m.) and Rompun (Bayer, Germany, 0.3 mL, i.m.). Surgery was started after stable anaesthesia with complete analgesia was achieved. Sometimes this required additional doses of the anaesthetic. After tracheal and arterial cannulations, the animal was placed in a stereotaxic frame, the skull was exposed and a craniotomy (5 mm diameter) was performed over area 17 of the visual cortex centred at P4/L3 (Horsley-Clark). A brass cylinder (diameter 20 mm) was cemented over the opening. The hydraulically driven microelectrode holder (Narishige Instruments, Japan) was mounted

directly onto the skull with screws and dental cement. All wound edges and pressure points were treated with a local anaesthetic (Xylocaine, Astra GmbH, Germany), repeatedly every 5–8 h. Muscle relaxation with alcuronium chloride (Alloferin, ICN Pharmaceuticals, Germany) and artificial respiration were started either at this point, or earlier during the surgery, to avoid respiratory depression due to additional doses of the anaesthetic. Thereafter, adequate anaesthesia was maintained by a gas mixture of $N_2O : O_2$ (70 : 30) and 0.2–0.4% halothane (Eurim-Pharm, Germany). Heart rate, blood pressure and EEG were continuously monitored, and every 2–3 h adequacy of the anaesthesia was additionally attested by the absence of changes while applying noxious stimuli. Fluid replacement was achieved by the intra-arterial administration of 6 mL of Ringer's solution containing 1.25% glucose, per hour. Paralysis was maintained by i.a. infusion of alcuronium chloride (0.15 mg/kg/h) in Ringer's solution. End-tidal CO_2 was adjusted to 3.5–4.3%; body temperature was maintained at ~37–38 °C. The experiments lasted usually for 2–4 days. At the end of the experiment, animals were killed with an overdose of anaesthetics. The methods used in this study were in accordance with the guidelines published in the European Communities Council Directive (86/609/EEC, 1986) and were approved by a regional animal welfare committee (Arnsberg, Germany).

Intracellular recordings from neurons in the visual cortex were made with sharp electrodes filled with 2.5 M potassium acetate or 1 M potassium acetate and 1% biocytin (Sigma-Aldrich GmbH, Germany). Electrode resistance was 70–120 MΩ. After amplification (Axoclamp 2, Axon Instruments, USA) and low-pass filtering at 3–5 kHz, the data were digitized at 10 kHz and fed into a computer (Spike-2, Cambridge Electronic Design, UK; PC-586). Visual stimuli (moving or flashing bars) were generated on the screen of another computer using subroutines of the Vision Works stimulation system (Cambridge Research Systems, New Hampshire, USA). Parameters of visual stimulation, sequence of stimuli (randomized) and communication to the data acquisition computer were controlled by software written by one of us (J.P.). The screen was positioned 57 cm in front of the animal and was focused on the retina using appropriate lenses. Background illumination was 2.37 cd/m^2. Luminance of the dark and light stimuli was 0.02 and 12.8 cd/m^2, respectively. Stimuli were presented monocularly to the dominant eye.

The data were processed using the Spike-2 software and our own programs. The response amplitude was estimated as PSP integral or spike frequency within a 100–500-ms window positioned over the response peak. For calculation of the PSP integral, mean responses obtained by averaging five individual traces were used. The response strength was then calculated as the integral area between the averaged response curve and the resting membrane potential. For any particular cell the width and location of the measuring window was the same for PSP and spike responses. In some cases, spikes were removed by software from individual traces before averaging for calculation of PSP responses (Volgushev *et al.*, 1996). The computer algorithm searched for the spikes, then removed them from the beginning to the end, and linearly interpolated the continuous signal from the membrane potential before and after the spike. However, because the spike subtraction changed averaged PSP amplitudes by less than 5% and did not significantly influence the estimations of tuning width or selectivity indices, in most cases we used data without spike subtraction. A selectivity index (k) was calculated as the ratio of the difference between responses to optimal and non-optimal orientations (or optimal and null directions) divided by their sum:

$$k = (\text{optimal} - \text{non-optimal})/(\text{optimal} + \text{non-optimal}).$$

The selectivity index can vary from 0 to 1, whereby an index of 1 corresponds to the maximal selectivity. The tuning width was calculated as half width of the tuning curve at half maximal response. Receptive fields were classified as simple or complex according to conventional criteria (Orban, 1984). The data are presented as mean ± SEM. For statistical evaluation of the data, *t*-test and non-parametric Mann–Whitney tests were used.

Results

The results presented here are based on the analysis of the data obtained from 15 cells. The main criteria for selecting these cells from a sample of 64 neurons recorded intracellularly in the primary visual cortex of the cat were the following: similarity of the stimulating conditions (background illumination and stimulus contrast); availability of the membrane potential traces recorded during presentation of stimuli for at least eight different orientations; and clear PSP and spike responses to at least some of these stimuli. In addition to the responses of these cells to moving stimuli, also the data on the receptive field structure, as studied with small stationary flashing stimuli presented at different positions, were available for most of these cells. On the basis of these data the receptive field type of all but two cells could be identified unambiguously as simple or

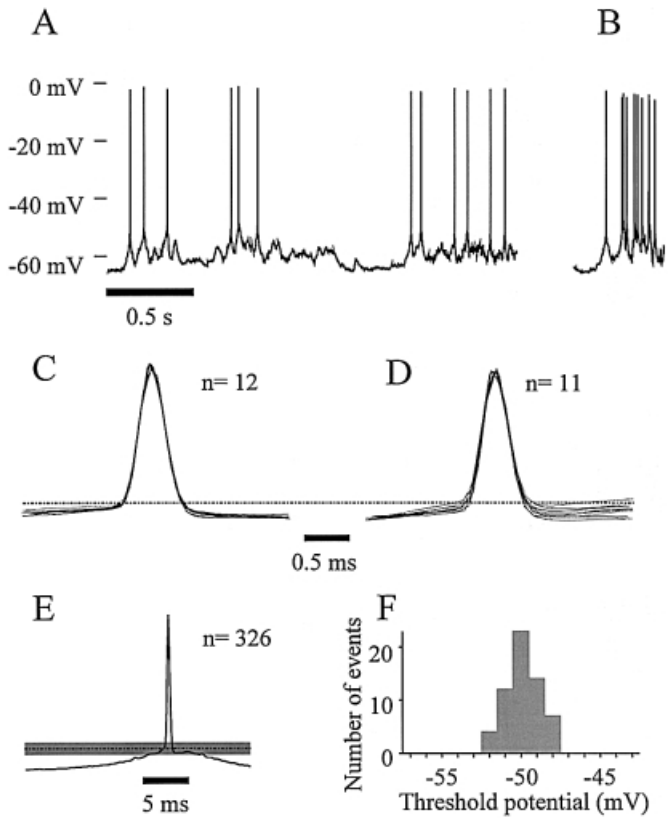

FIG. 1. Stability of the spike shape and activation threshold during background activity and visual stimulation. (A–E) Sample intracellular recording of spontaneous activity (A) and evoked response (B) of a visual cortical neuron. Superposition of individual spontaneous (C) and evoked (D) spikes, and an averaged shape of the action potential (E). Note the stability of the activation threshold (dashed line in C–E; –49 mV), and the amplitude and shape of the individual spikes. Grey bar shows the threshold region for spike generation during background activity. (F) Distribution of the threshold potential for spike generation during background activity of the same cell. Amplitude scaling is the same in A–E.

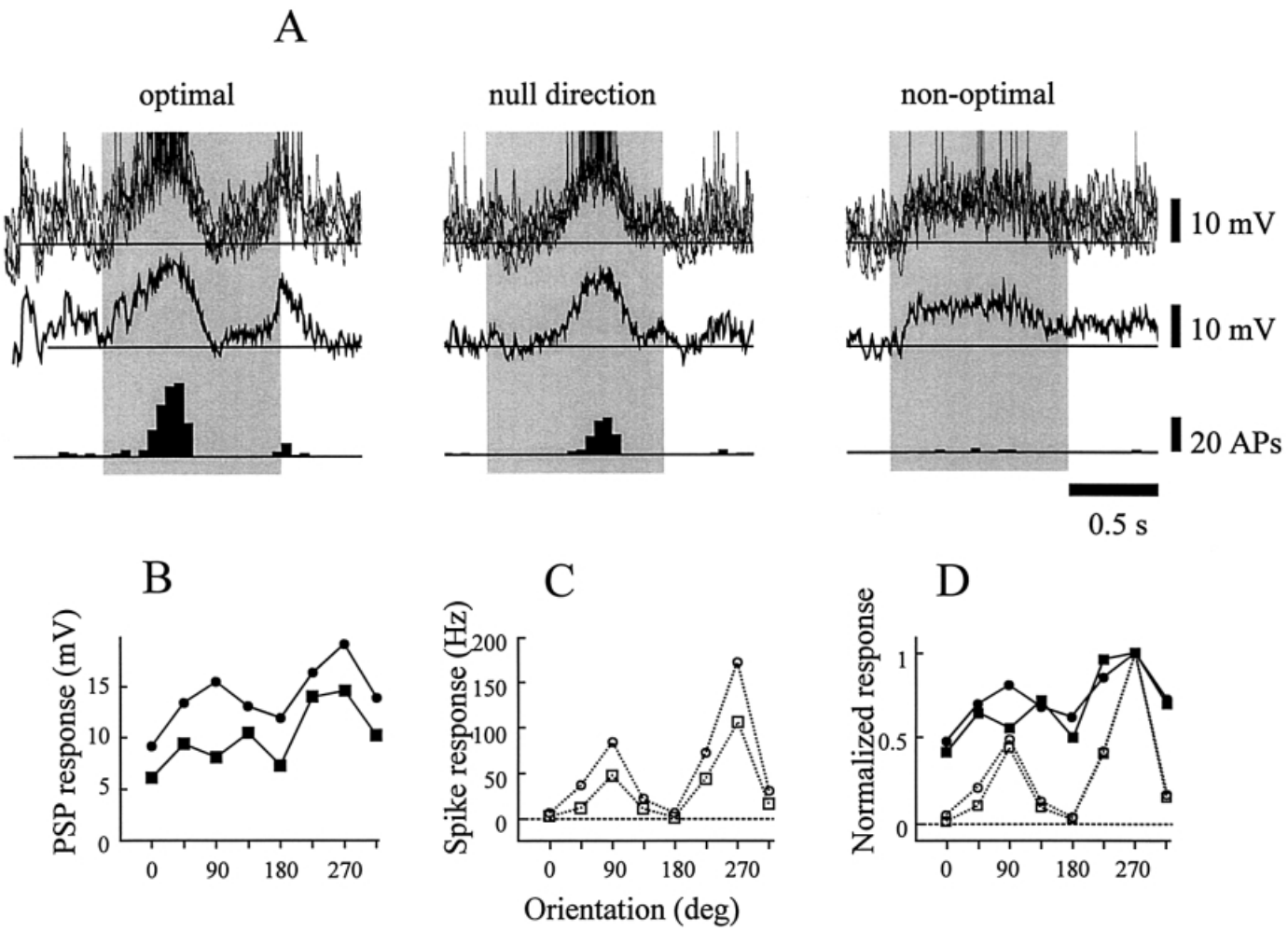

FIG. 2. Dependence of PSP and spike responses in a simple cell on the direction of the movement and orientation of the stimulus. (A) Responses evoked in the simple cell by a bar of optimal orientation moving in the preferred (optimal) direction, null direction, and by a non-optimally orientated bar. From top to bottom, superposition of five individual responses (spikes truncated); averaged ($n = 5$) PSP responses; and spike responses. In this and the following figures the spikes were filtered out from the individual traces before averaging the PSP responses. The shaded area indicates the period of bar movement. The resting membrane potential (horizontal line) equals –68 mV. (B) Dependence of the amplitude of PSP response on the stimulus orientation. The amplitude was measured in 100 ms (circles) or 500 ms (squares) window over the peak. (C) Dependence of the spike frequency during the response on stimulus orientation. Circles and squares – spike responses measured in the same windows as in B. (D) Comparison of the dependence of PSP (filled symbols, continuous lines) and spike responses (open symbols, dotted lines) on stimulus orientation. The same data as in B and C, but normalized to the maximal response.

complex. During interstimulus intervals the recorded cells had a stable membrane potential (mean -63 ± 2.6 mV, $n = 15$), a stable shape of the action potentials, and there was no systematic change of the spike activation threshold. This indicated that the spike generating mechanism was not disturbed (Fig. 1A–E). During the interstimulus intervals the threshold potential for spike generation in a cell illustrated in Fig. 1 was narrowly distributed around the mean of -49.9 ± 0.14 mV (Fig. 1F). In other cells in our sample, spike generation thresholds were in the range from –61 mV to –43 mV (mean -52 ± 1.5 mV, $n = 15$), being on average 10.7 ± 1.6 mV (range 4–22 mV) more positive than the resting membrane potential. The amplitude of the action potentials was 55 ± 3.2 mV. In some cells, the spikes were followed by a pronounced afterhyperpolarization (not shown).

Orientation and direction selectivities were determined from the responses evoked with moving bars. The simple cell in Fig. 2 responded with a strong depolarization when a bar of optimal orientation swept across the receptive field in the preferred direction. After reaching a peak amplitude of ~18 mV, the depolarization declined rapidly (Fig. 2A, optimal). Numerous action potentials were generated at the top of the depolarization and these action potentials formed the peak of the spike histogram (Fig. 2A, bottom). Moving the bar in the opposite direction (Fig. 2A, null direction) also led to a pronounced depolarization of the cell membrane, with a peak amplitude of ~15–16 mV. The shape of PSP responses evoked by the stimuli moving in the null direction was slightly different from the shape of the optimal response, indicating a possible difference in the temporal structure of the input to the cell. The spike response was significantly weaker: both the total number of spikes and the peak frequency of firing were about half of the values during the optimal response. The direction selectivity of the output of this cell increased significantly compared with the input. The direction selectivity index increased from 0.11 to 0.34. A non-optimally orientated bar led to a prolonged plateau depolarization with an amplitude of ~10 mV (Fig. 2A, non-optimal). The mean plateau amplitude was, however, well below the threshold for spike generation (17 mV from the resting membrane potential in this cell) and only occasional high-amplitude EPSPs could reach the threshold. As a result, the spikes were

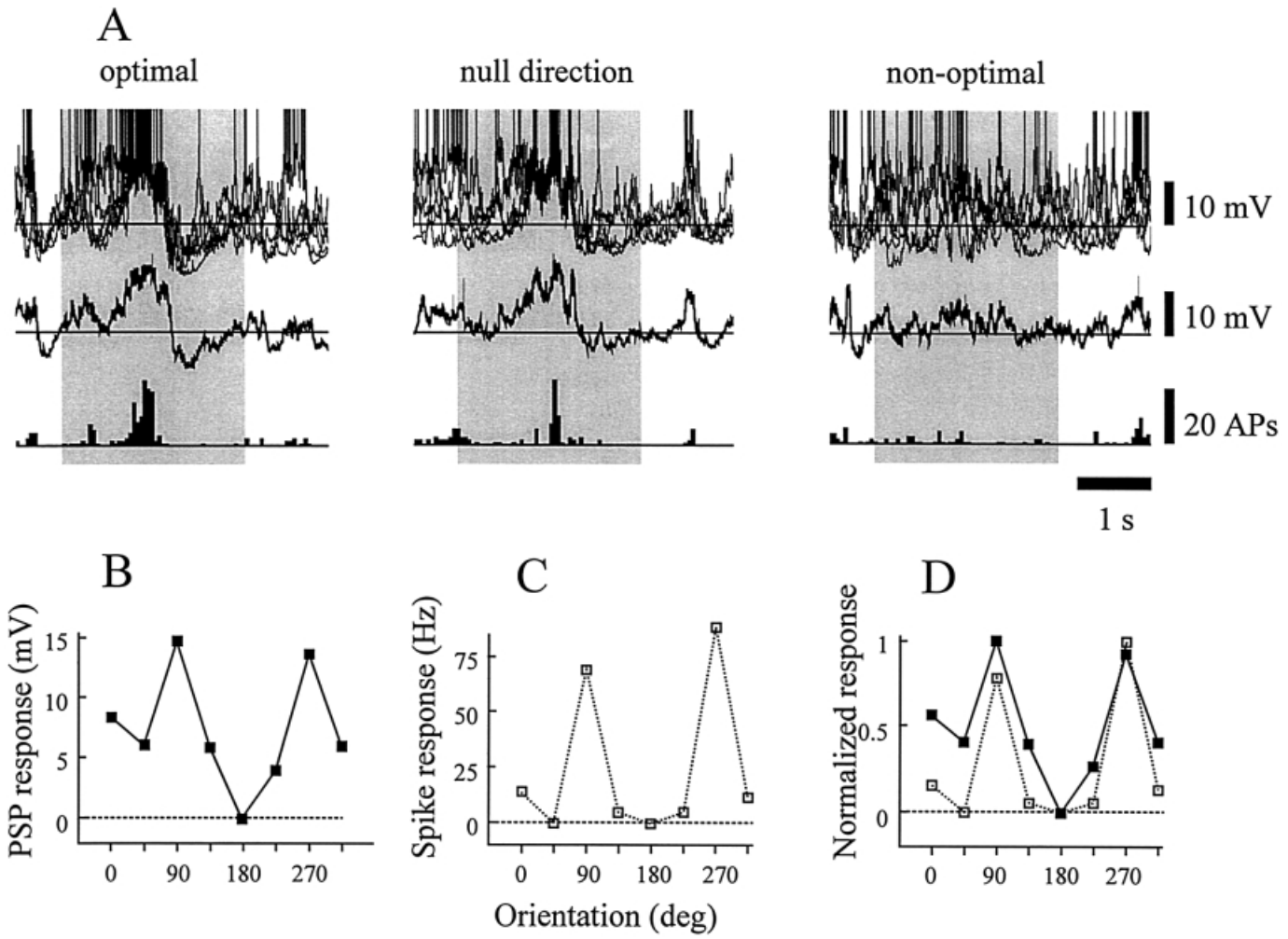

FIG. 3. Dependence of PSP and spike responses in a simple cell on the direction of the movement and orientation of the stimulus. (A) Responses evoked in the simple cell by a bar of optimal orientation moving in the preferred (optimal) direction, null direction, and by a non-optimally orientated bar. The resting membrane potential is –74 mV. (B) Dependence of the amplitude of PSP response on the stimulus orientation. (C) Dependence of the spike frequency during the response on stimulus orientation. (D) Comparison of the dependence of PSP (circles, continuous line) and spike responses (squares, dotted line) on stimulus orientation. The same data as in B and C, but normalized to the maximal response. Other conventions as in Fig. 2.

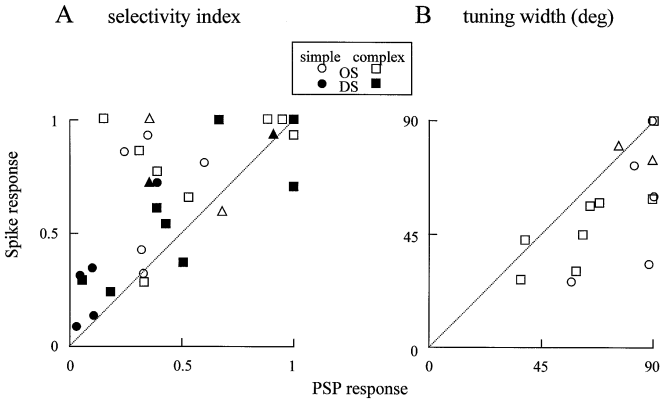

FIG. 4. Comparison of the orientation and direction selectivity indices (A) and orientation tuning width (B) of PSP and spike responses. The values for spike responses (ordinate) are plotted against the values for PSP responses (abscissa). Symbols in A and B: circles, simple cells; squares, complex cells; and triangles, cells with non-identified receptive field type. In A filled symbols indicate direction selectivity indices, and open symbols indicate orientation selectivity indices.

essentially absent in the response to the non-optimal orientation despite a pronounced PSP response. The orientation selectivity index for spike responses was very high and close to 1 (0.94), compared with a low selectivity of PSP responses (0.35). Also, the orientation tuning of the spike responses was much sharper than that of the PSPs, the width of the tuning curve being 33° and 88°, respectively (Fig. 2B–D). Thus, orientation and direction selectivity of the spike output of this cell was significantly improved over a poorly selective input.

Interestingly, changing the width of the measuring window from 100 to 500 ms affected markedly the shape of the tuning curve for the PSPs responses, but had little influence on the tuning of spikes (Fig. 2B–D), indicating a possibility for complex relations between averaged PSP responses and changes of the firing frequency.

A different kind of relation between PSP selectivity and spike responses is exemplified in Fig. 3. In this simple cell an optimal stimulus (270°) evoked a depolarizing PSP response with an amplitude of 12–14 mV. The depolarization developed slowly and after reaching a peak it abruptly declined (Fig. 3A, optimal). After the depolarizing phase the membrane potential was hyperpolarized below the resting level (–74 mV for that cell). The firing frequency increased markedly during the depolarization, leading to a clear peak in the

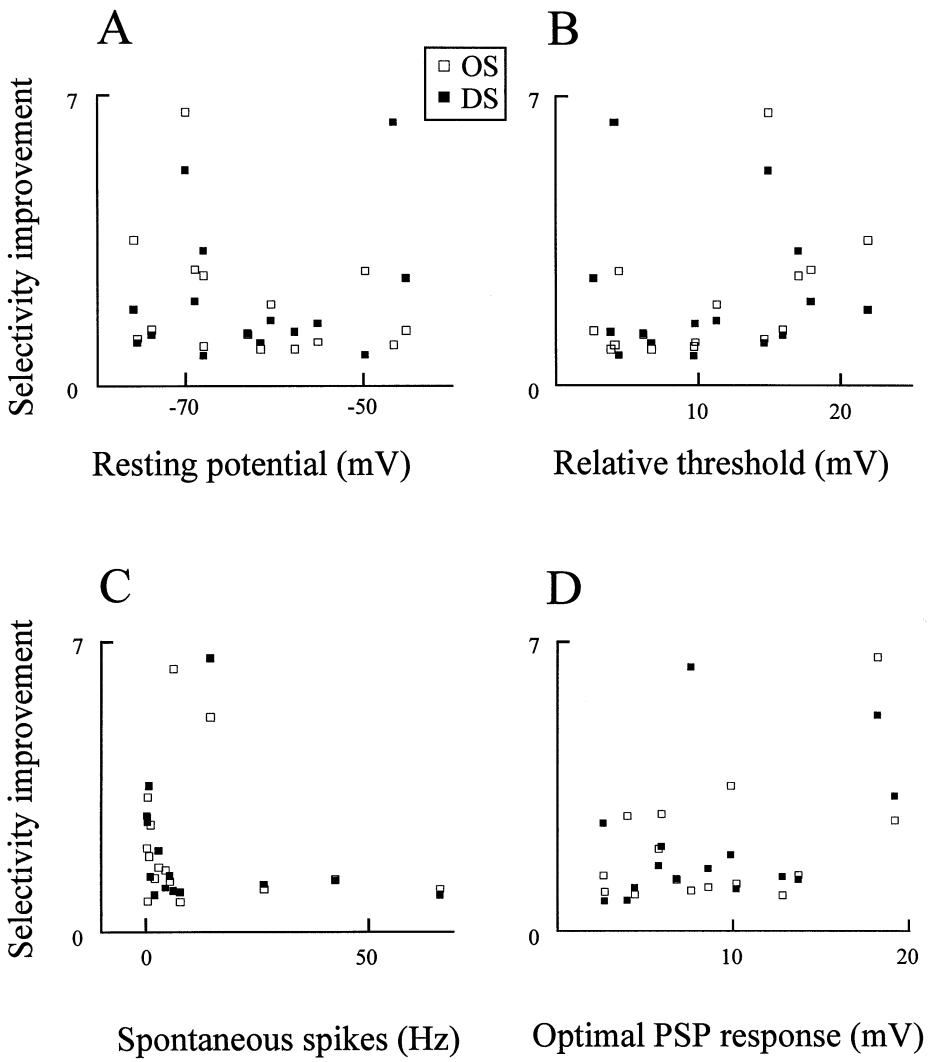

FIG. 5. Relation between improvement of the orientation and direction selectivity upon PSP to spike transformation (ordinate) and the resting membrane potential (abscissa in A), threshold for action potential generation relative to the resting membrane potential (abscissa in B), frequency of spontaneous discharges (abscissa in C) and the amplitude of PSP response to optimal stimulation (abscissa in D). Each point represents data from a single cell. Filled symbols, direction selectivity; open symbols, orientation selectivity. Selectivity improvement was calculated as the ratio between selectivity indices of spike responses over that of PSP responses.

spike histogram. Stimuli moving in the null direction led to the membrane depolarization of ~ 14–15 mV amplitude, but in contrast to the optimal responses, the depolarization phase was interrupted by sharp troughs (Fig. 3A, null direction). Action potentials generated at the top of the depolarizing response formed a peak in the histogram. Stimuli moving in the null direction evoked nearly as large peak spike responses as the optimal stimulus. The peak depolarization, when measured as an integral in a 100-ms window, was in fact even higher in the response to the null direction than in the optimal response. As a result, direction selectivity of this cell was poor, with selectivity indices of 0.04 and 0.1 for the PSP and spike responses, respectively. Stimuli of a non-optimal orientation failed to evoke any appreciable response – neither PSP nor spike (Fig. 3A). As a result, the orientation selectivity indices were equal to 1 for both the PSP and spike responses. The orientation tuning curves were also similar for the PSP and spike responses. The width of the tuning peak around the optimal orientation (270°) was only slightly less for the spike responses than for the PSP responses (25° and 31°, respectively), but sharpening of the spike tuning was substantial around the null direction (from 37° to 17°). Thus, selectivity of the spike responses of the cell in Fig. 3 was not improved significantly compared with the selectivity of the PSP input. The cell received an input which was highly selective for stimulus orientation but poorly selective for direction of movement, and this selectivity, with little change, also emerged in the output of the cell.

The summary data show a general improvement of the selectivity of the output relative to that of the input: an increase of orientation and direction selectivity indices and a decrease of the tuning width. Figure 4A shows the orientation selectivity (open symbols) and direction selectivity (filled symbols) indices for all 15 cells, measured from the PSP responses (abscissa) and spike responses (ordinate). Most of the points are located above the main diagonal, indicating that in most of the cells selectivity of the spike responses was higher. The difference between the selectivity of PSP and spike responses was statistically significant for the whole sample (0.45 versus 0.65, $P < 0.01$, $n = 30$). The spike selectivity was on average about twice as good as the selectivity of PSP responses. The mean ratio between spike selectivity and PSP selectivity was 2.06. In Fig. 4B, which shows the data for orientation tuning width, most of the points are located below the main diagonal, indicating that the tuning curve for spike responses was sharper than the PSP tuning. The difference between the PSP and spike tuning width was significant (72° versus 56°, $P < 0.05$, $n = 15$).

Improvement of the response selectivity upon PSP to spike transformation was, however, very non-homogeneous across the sample, and several tendencies can be noted. Firstly, there is a

tendency for stronger improvement of the orientation selectivity compared with the direction selectivity. Orientation selectivity indices increased significantly from input to output, on average from 0.50 to 0.76 ($n = 15$, $P < 0.01$). Direction selectivity indices increased (from 0.42 to 0.56), too, but this change was not significant. Stronger improvement of the orientation selectivity is also suggested by the fact that in Fig. 4A an averaged distance between the main diagonal and open symbols, which correspond to orientation selectivity, was slightly larger than the distance to closed symbols (0.19 and 0.09, respectively). Secondly, cells differ markedly in their input–output relation. In some cells the selectivity of the output is not improved at all relative to that of the input – these cells are represented by the points at or near the main diagonal in Fig. 4. Interestingly, no or little improvement can occur not only in cells receiving an already selective input, but also in poorly selective cells, as indicated by the points located around the main diagonal, close to its origin. In other cells, a major improvement of the selectivity occurred – the respective points are located far away from the main diagonal. Notably, close to a maximal selectivity of the spike responses can be achieved even in cells receiving only poorly tuned input with PSP selectivity below 0.5. These cells are represented by the points located in the upper left part of Fig. 4A. Thirdly, the degree of the selectivity improvement upon the PSP to spike transition was not correlated with the cell type. In both simple and complex cells, shown in Fig. 4 as circles and squares, respectively, the selectivity of spike responses could be either much higher, or the same as the selectivity of the PSP responses. However, in two simple cells out of five, sharpening of the orientation tuning upon PSP to spike transformation was strongest in our sample (Fig. 4B). Finally, the degree of the selectivity improvement was not correlated with electrophysiological characteristics of the recorded neurons at rest. No significant correlation was found between the selectivity improvement on the one hand, and the resting membrane potential, threshold of action potential generation, frequency of spontaneous spiking or the amplitude of optimal PSP response on the other hand (Fig. 5A–D). Also, no significant correlation was found between the degree of improvement of orientation and of direction selectivity ($P > 0.1$ for all five relations). These data indicate that neither difference of the receptive field type, nor possible differences in the state of depolarization of the recorded cells or diversity of other electrophysiological properties of cortical cells, could account for the various degrees of involvement of the 'tip of the iceberg' effect in sharpening the cells' selectivity.

Discussion

Our data demonstrate that significant improvement of orientation and direction selectivities of the spike responses over that of the PSP responses occurred in some, but not all visual cortical neurons. Restriction of the cells' spiking to a narrow range of the maximal PSP responses – a 'tip of the iceberg' effect – was essential for shaping the selectivity in some cells, but had only a moderate role or did not contribute at all to the selectivity of the other neurons.

The 'tip of the iceberg' effect is considered as an important mechanism of shaping the tuning of cortical cells, however, it has been investigated surprisingly little so far. Jagadeesh *et al.* (1997) mentioned that in simple cells the direction selectivity index of the spike responses was, on average, 2.9 times greater than the index derived from the membrane potential responses. We have observed less selectivity improvement, on average 2.1 times. However, considerable differences in both the recording techniques and the visual stimulation preclude direct comparison and could be a reason for difference in the results. Whole-cell recording changes intracellular milieu, and within a few minutes after rupturing the membrane, concentration of ions equilibrate between the recording electrode and the cell cytoplasm (Pusch & Neher, 1988; Kay, 1992). This could lead to alteration of the equilibrium potentials for the ions which now depend on pipette solution rather than on the 'genuine' ionic concentrations of this cell, and as consequence, to changes of the resting membrane potential and driving forces for excitatory and inhibitory PSPs. All these factors could dramatically influence summation of the PSPs and the relation between PSP and spike responses. Intracellular recordings with sharp electrodes, exploited in our study, are less likely to produce these undesirable alterations of spike generation. The visual stimulation was also different in the two studies. Here we report the data on responses of visual neurons to drifting bars. In the study of Jagadeesh *et al.* (1997) moving sinusoidal gratings were used. Notably, with the use of moving gratings, although rectangular, we have observed a similar degree of selectivity improvement as reported by Jagadeesh *et al.* (1997). In our sample of nine cells, the direction selectivity index of spike responses to the moving gratings was on average 2.85 times higher than the selectivity index of PSP responses (Volgushev, Pernberg & Eysel, unpublished observations).

Upon the PSP-to-spike transition, orientation selectivity improved more than direction selectivity. This could reflect a difference in the mechanisms of orientation and direction selectivities in visual cortical cells, as suggested by some difference in the impairment of these two properties during blockade of inhibition (Sillito, 1977; Vidyasagar & Heide, 1986; Nelson *et al.*, 1994) or inactivation of cortical regions (Wörgötter & Eysel, 1991; Crook *et al.*, 1997). Consider a receptive field consisting of a slightly elongated excitatory and inhibitory zone, located one beside the other. An optimal stimulus enters first the excitatory zone and covers its longer axis, being therefore capable of evoking, at least transiently, the maximal excitatory response not contaminated by inhibition. Responses to a non-optimal orientation are reduced due to the following main reasons. Firstly, a non-optimal stimulus produces excitatory drive of a smaller amplitude, because it covers only the short axis of the excitatory zone. Secondly, because the inhibitory zone is also covered by that stimulus, the inhibition might further reduce the amplitude of the total PSP response. The situation is rather different in the case of an optimally orientated stimulus, which is moving in the null direction. Now the response is reduced because the excitatory zone is activated after the inhibitory, and hence on the background of a continuing inhibitory response. Thus, orientation selectivity depends on the elongation of the excitatory relief, and on the relative strength of the responses evoked from excitatory and inhibitory zones. Direction selectivity depends less on the elongation of the excitatory field, but strongly depends on the time course of the excitatory and inhibitory responses, as well as on the spatial separation of excitatory and inhibitory zones, and therefore on stimulus velocity. Further contributing factors could be a difference in the summation of PSPs along the optimal axis of the receptive field and in the perpendicular direction (Volgushev *et al.*, 1996), and different PSP-to-spike relation during a predominantly excitatory (optimal) response and mixed excitatory and inhibitory (non-optimal or null) responses.

The heterogeneity of the input–output relations revealed in visual neurons allows us to draw the following conjectures regarding the organization of the cortical network. Firstly, various degrees of involvement of the 'tip of the iceberg' effect in shaping the output selectivity lend further support to the notion that multiple mechanisms are responsible for generation of the selectivity of cortical cell responses, and that the contribution of any particular mechanism may vary from one cell to the other (Volgushev *et al.*, 1993; Vidyasagar

et al., 1996). Secondly, our data suggest that involvement of the 'tip of the iceberg' effect in sculpturing the final output selectivity is not cell type specific, as we found no systematic difference between simple and complex cells in that respect. Further, variations between cells in terms of contribution of the 'tip of the iceberg' effect were not due simply to the difference in the functional state of the cell membrane, as there was no correlation between the degree of improvement of orientation and of direction selectivity or between the degree of selectivity improvement and the electrophysiological characteristics of the recorded cells. Thirdly, the wide variance of the input–output relations of cortical cells can be due to and indicative of different roles that the cells may play in cortical information processing. At one end of the spectrum are the cells which perform the major improvement of the selectivity, often creating it from poorly selective input. At the other end are the cells which make little improvement, but rather, 'faithfully' repeat the input, either selective or unselective. Repetition of a highly selective signal can lead to sharpening of the selectivity with time through recurrent excitation (Douglas *et al*., 1991; 1995; Somers *et al*., 1995), increasing the relative contribution of the selective intracortical recurrent excitatory input over a non-selective geniculate input. This could be instrumental for the process of sharpening orientation tuning with the development of the response (Shevelev *et al*., 1993; Volgushev *et al*., 1995), and also for the generation of the output of a whole orientation column. Repetition of a less selective signal might be advantageous too, providing a broadly tuned input for cross-orientation, directional, spatially opponent and recurrent inhibition in cortical networks.

Acknowledgements

We are grateful to Drs Zoltan Kisvarday and Trichur Vidyasagar for their comments. This study is supported by the Deutsche Forschungsgemeinschaft SFB 509 TP A5.

Abbreviation

PSP, postsynaptic potential.

References

Borg-Graham, L.J., Monier, C. & Fregnac, Y. (1998) Visual input evokes transient and strong shunting inhibition in visual cortical neurones. *Nature*, **393**, 369–373.

Creutzfeldt, O.D., Kuhnt, U. & Benevento, L.A. (1974) An intracellular analysis of visual cortical neurones to moving stimuli: responses in a co-operative neuronal network. *Exp. Brain Res.*, **21**, 351–375.

Crook, J.M., Kisvarday, Z.F. & Eysel, U.T. (1997) GABA-induced inactivation of functionally characterized sites in cat striate cortex: effects on orientation tuning and direction selectivity. *Visual Neurosci.*, **14**, 141–158.

Douglas, R.J., Koch, C., Mahowald, M., Martin, K.A.C. & Suarez, H.H. (1995) Recurrent excitation in neocortical circuits. *Science*, **269**, 981–985.

Douglas, R.J. & Martin, K.A.C. (1991) A functional microcircuit for cat visual cortex. *J. Physiol.* (*Lond.*), **440**, 735–769.

Douglas, R.J., Martin, K.A.C. & Whitteridge, D. (1991) An intracellular analysis of the visual responses of neurones in cat visual cortex. *J. Physiol.* (*Lond.*), **440**, 659–696.

Ferster, D. & Jagadeesh, B. (1992) EPSP–IPSP interactions in cat visual cortex studied with *in vivo* whole-cell patch recording. *J. Neurosci.*, **12**, 1262–1274.

Ferster, D. (1986) Orientation selectivity of synaptic potentials in neurones of cat primary visual cortex. *J. Neurosci.*, **6**, 1284–1301.

Hirsch, J.A., Alonso, J.-M., Reid, R.C. & Martinez, L.M. (1998) Synaptic integration in striate cortical simple cells. *J. Neurosci.*, **18**, 9517–9528.

Henry, G.H., Michalski, A., Wimborne, B.M. & McCart, R.J. (1994) The nature and origin of orientation specificity of the visual pathways. *Prog. Neurobiol.*, **43**, 381–437.

Jagadeesh, B., Wheat, H.S., Kontsevich, L.L., Tyler, C.W. & Ferster, D. (1997) Direction selectivity of synaptic potentials in simple cells of the cat visual cortex. *J. Neurophysiol.*, **78**, 2772–2789.

Kay, A.R. (1992) An intracellular medium formulary. *J. Neurosci. Methods*, **44**, 91–100.

Nelson, S., Toth, L., Sheth, B. & Sur, M. (1994) Orientation selectivity of cortical neurones during intracellular blockade of inhibition. *Science*, **265**, 774–777.

Orban, G.A. (1984) *Neuronal Operations in the Visual Cortex*. Springer, Berlin.

Pei, X., Vidyasagar, T.R., Volgushev, M. & Creutzfeldt, O.D. (1994) Receptive field analysis and orientation selectivity of postsynaptic potentials of simple cells in cat visual cortex. *J. Neurosci.*, **14**, 7130–7140.

Pernberg, J., Volgushev, M. & Eysel, U.T. (1998) Comparison of the selectivity of postsynaptic potentials and the spike responses in the cat visual cortex. *Eur. J. Neurosci.,* (Suppl.), **10**, 243.

Pusch, M. & Neher, E. (1988) Rates of diffusional exchange between small cells and a measuring patch pipette. *Pflügers Arch.*, **411**, 204–211.

Reid, R.C. & Alonso, J.-M. (1996) The processing and encoding of information in the visual cortex. *Curr. Opin. Neurobiology*, **6**, 475–480.

Shevelev, I.A., Sharaev, G.A., Lazareva, N.A., Novikova, R.V. & Tikhomirov, A.S. (1993) Dynamics of orientation tuning in the cat striate cortex neurones. *Neuroscience*, **56**, 865–876.

Sillito, A.M. (1977) Inhibitory processes underlying the directional specificity of simple, complex and hypercomplex cells in the cat's visual cortex. *J. Physiol.* (*Lond.*), **271**, 699–720.

Somers, D.C., Nelson, S. & Sur, M. (1995) An emergent model of orientation selectivity in cat visual cortical simple cells. *J. Neurosci.*, **15**, 5448–5465.

Sompolinsky, H. & Shapley, R. (1997) New perspectives on the mechanisms for orientation selectivity. *Curr. Opin. Neurobiol.*, **7**, 514–522.

Vidyasagar, T.R. & Heide, W. (1986) The role of GABA-ergic inhibition in the response properties of neurones in cat visual area 18. *Neuroscience*, **17**, 49–55.

Vidyasagar, T.R., Pei, X. & Volgushev, M. (1996) Multiple mechanisms underlying the orientation selectivity of visual cortical neurones. *Trends Neurosci.*, **19**, 272–277.

Volgushev, M., Pei, X., Vidyasagar, T.R. & Creutzfeldt, O.D. (1993) Excitation and inhibition in orientation selectivity of cat visual cortex neurones revealed by whole-cell recordings *in vivo*. *Visual Neurosci.*, **10**, 1151–1155.

Volgushev, M., Vidyasagar, T.R. & Pei, X. (1995) Dynamics of the orientation tuning of postsynaptic potentials in the cat visual cortex. *Visual Neurosci.*, **12**, 621–628.

Volgushev, M., Vidyasagar, T.R. & Pei, X. (1996) A linear model fails to predict orientation selectivity of cells in the cat visual cortex. *J. Physiol.* (*Lond.*), **496**, 597–606.

Wörgötter, F. & Eysel, U.T. (1991) Topographical aspects of intracortical excitation and inhibition contributing to orientation specificity in area 17 of the cat visual cortex. *Eur. J. Neurosci.*, **3**, 1232–1244.