Receptive-Field Maps of Correlated Discharge Between Pairs of Neurons in the Cat's Visual Cortex

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SUMMARY AND CONCLUSIONS

1. To investigate the functional significance of temporally correlated discharge between nearby cells in the visual cortex, we obtained receptive-field maps of correlated discharge for 68 cell pairs in kittens and cats. Discharge from cell pairs was measured by a single extracellular electrode. A reverse correlation procedure was used to relate neural discharge to particular stimuli within a random sequence of briefly flashed bright and dark bars. Binocular receptive fields (BRFs) were mapped by applying reverse correlation to approximately synchronous discharge from two cells. Unicellular receptive fields (URFs) were simultaneously mapped by separately applying reverse correlation to the discharge of each cell.

2. The receptive fields of the two neurons within each pair were initially studied by varying the orientation and spatial frequency of drifting sinusoidal gratings. After these tests a random sequence of appropriately oriented bars was used to evoke discharge suitable for reverse correlation analysis. For most cell pairs, the temporal pattern or strength of correlated discharge produced by such stimulation is different from that observed with stimulation by sinusoidal gratings. This indicates that visually evoked correlated discharge between nearby cells is stimulus dependent.

3. BRFs were classified according to their pattern of spatial sensitivity into three groups that roughly correspond to the single-cell receptive-field types of the lateral geniculate nucleus (LGN; center-surround) and visual cortex (simple and complex). These classifications were compared with the receptive-field types of the single cells within each pair. LGN-type and simple-type BRFs were only seen for pairs in which at least one of the cells was simple. Conversely, complex-type BRFs were only seen for pairs in which at least one of the cells was complex.

4. Because the reverse correlation procedure can be used to characterize the spatiotemporal receptive-field structure of simple cells, we were able to compare both the spatial and temporal properties associated with the URFs and BRFs of simple cell pairs. The spatiotemporal structure of the BRF of a simple-cell pair can largely be predicted on the basis of the two URFs. Although this prediction suggests the possibility that BRFs are stimulus artifacts, a shuffle procedure, in which multiple repetitions of random sequences were presented, verifies the neural origin of BRFs. BRFs emerge from specific neural pathways and are not simply a consequence of uncoupled response preferences.

5. Five measures were derived from the reverse correlation analysis of single-receptive fields: width, duration, optimal spatial and temporal frequency, and optimal velocity. For each single-cell pair, BRFs were compared with the URFs of each cell. BRFs are consistently narrower in width and shorter in duration than URFs. Despite these differences in spatial and temporal extent, BRFs do not consistently differ from URFs with respect to optimal spatial and temporal frequencies, or optimal velocities. Both the mean receptive-field width and the mean duration are significantly smaller for BRFs when compared with the means associated with URFs.

6. The BRF types seen among cell pairs of 4- and 8-wk kittens are the same as those seen in the adult. Therefore the neural circuitry necessary for the establishment of BRFs does not depend on postnatal maturation past the age of 4 wk. Additionally, the median BRF-URF width and duration differences among single-cell pairs are similar at all age groups studied. Finally, the mean BRF width and duration are significantly smaller than the mean URF width and duration for all age groups. Thus the relationship between BRF and URF widths and durations remains essentially unchanged during postnatal development.

7. These findings suggest that correlated discharge between nearby cells could represent visual information with higher spatial and temporal resolution than is possible from the discharge of single cells. The findings provide insight into the manner by which visual information is encoded via patterns of activity distributed among multiple neurons.

INTRODUCTION

Several studies have proposed that receptive fields of single cells are optimized for perceptual tasks such as motion detection (Adelson and Bergen 1985) and stereopsis (Barlow 1972; Ohzawa et al. 1990). In a variety of sensory systems, it has been shown that neurons are systematically organized according to certain receptive-field properties (Kaas 1987). Thus a given stimulus is certain to evoke discharge in multiple cortical neurons. In the visual cortex, for example, nearby cells are likely to have similar orientation preferences, receptive-field locations, and ocular dominances (Hubel and Wiesel, 1962). It is therefore possible that visual information might be encoded via the simultaneous activity of nearby cortical neurons.

Cross-correlation experiments within the visual cortex have demonstrated that nearby cells very often display correlated discharge (Krüger and Aiple 1989; Toyama et al. 1981a,b). They have also demonstrated that correlated activity between cells located on the order of millimeters apart can be evoked by a single stimulus if cells have similar receptive-field properties. This applies to cells within the same area (area 17: Engel et al. 1990; Schwarz and Bolz 1991; Ts'o et al. 1986) and cells in different cortical areas (areas 17 and 18: Nelson et al. 1992; V1 and V2: Bülthier et al. 1992; Roe and Ts'o 1992). Krüger (1990) found that the receptive-field properties of a neuron are correlated with that neuron's tendency to discharge before or after other cortical neurons. Although this research establishes that the existence of correlated discharge depends on the similarity of receptive-field properties, it does not directly address the functional significance of the correlations. Several studies have found stimulus-dependent correlations in the auditory (Aertsen et al. 1989; Espinosa and Gerstein 1988) and visual (Eckhorn et al. 1988; Engel et al. 1991; Ghose et al.
bicellular receptive fields in visual cortex

1991; Schwarz and Bolz 1991; Ts'o et al. 1986) cortex, but the emphasis of most of these experiments has been to infer interactions between specific neurons using cross-correlation analysis rather than to study systematically the stimulus dependence of correlated discharge.

The aforementioned cross-correlation studies have found that correlogram peaks over a millisecond in width are by far the most common pattern of correlated discharge between cells in the visual cortex. For intra-area correlations, peaks up to 10 ms in width are observed; for inter-area correlations, peak widths up to 100 ms are observed. Unfortunately, the interpretation of such broad correlogram peaks is very difficult because they can arise from a variety of different neural circuits (Moore et al. 1970). Broadly correlated discharge could arise from shared common inputs or mutual excitation between the cells under study. Given that such broad correlation peaks are found between cells in the retina (Mastronarde 1983a,b) and the lateral geniculate nucleus (LGN) (Arnett 1975), broadly correlated discharge between cortical cells is likely to reflect neural interactions both within the cortex and among the sources of cortical input (i.e., the retina and LGN) (Mastronarde 1989). Correlated discharge between cortical cells is therefore the by-product of multiple neural pathways. It is not readily apparent how broadly correlated activity can be used to dissect the exact underlying circuitry between nearby neurons in the visual cortex. However, it is possible to infer the functional significance of correlated discharge by using the highly localized stimuli of the reverse correlation technique. This method identifies the set of localized stimuli that is capable of evoking correlated discharge, and it shows how the characteristics of this stimulus ensemble relate to the receptive-field properties of the neurons under study.

In our study the stimulus ensemble associated with the correlated discharge between two cells is termed the bicellular receptive field (BRF). BRFs can be associated with the output of visual filters that are fundamental to perception in the same manner as are the receptive fields of single cells, which are termed unireceptive fields (URFs). BRF analysis might also provide insight into organization hierarchies among neurons. If a higher-order neuron were to receive inputs solely from two input cells, then the URF of that neuron would exactly correspond with the BRF of the two inputs. Although the situation of one neuron's output being determined by only two inputs is simplistic, the suggestion that the activity of relatively small numbers of neurons may account for many perceptual phenomena (Barlow 1972) implies that a small number of cells might participate in perceptually relevant correlated discharge. In this case even the measure of correlated discharge between two neurons, as is the case with BRFs, might provide valuable insight into the potential stimulus dependencies of unobserved higher-order neurons. Indeed, BRFs, which are based on correlated spikes, might be a better measure of stimulus-evoked neuronal output than URFs, which are based on spike counts. Because discharge is likely to result from the simultaneous activation of the inputs to a neuron, correlated discharge between potential inputs is, in principle, a more physiologically relevant measure of neuronal output than spike counts of the same inputs.

In the study described here, a receptive-field mapping technique is applied to the discharge from pairs of nearby neurons within area 17 of anesthetized and paralyzed cats and kittens. BRFs are mapped by combining the cross-correlation and reverse-correlation methods. BRFs are visible between all pairs of simple cells exhibiting correlated discharge, and their spatiotemporal structure can be largely predicted on the basis of the individual cells' receptive fields. Consistent differences exist between BRFs and URFs at all ages studied. These differences suggest that the BRFs associated with the correlated discharge of cells are capable of providing higher resolution information than is available from the receptive fields of the individual cells.

methods

physiological preparation

Twenty-three adult cats, 17 kittens at postnatal day 28, and 4 kittens at postnatal day 56 were studied with the use of standard extracellular recording techniques. The details of the experimental techniques have been described previously (DeAngelis et al. 1993a,b; Ghose and Freeman 1992). Briefly, a craniotomy was performed over the area 17 representation of the area centralis, and the dura was reflected. Animals were paralyzed through a continuous venous infusion of gallamine triethiodide (Flaxedil at 10 mg·kg⁻¹·h⁻¹) mixed with dextrose-supplemented Ringer and artificially respirated with a mixture of N₂O (75%) and O₂ (25%). Anesthesia was supplemented by a continuous infusion of thiamylal sodium (Surital) at 1 mg·kg⁻¹·h⁻¹. Expired CO₂, the electrocardiogram, the electroencephalogram, and body temperature were continuously monitored throughout the experiment. Corners were protected by contact lenses.

Two tungsten-in-glass (Levick 1972) microelectrodes (with a horizontal separation of ~200 μm), encased in a common tube, were positioned over the exposed cortex. The area of the tooth was sealed by agar covered with wax, the two electrodes were advanced at angles A10°, M20°. Electrodes were advanced by a micropositioner until spike waveforms could be clearly isolated from background activity on the basis of amplitude. Because, in our experience, nearby cells are the most likely to display correlated discharge, all cells pairs presented in this study were recorded from the same electrode. Spike waveforms corresponding to the discharge from different neurons were isolated on the basis of amplitude.

histology

For each electrode penetration, two or three electrolytic lesions were made at regular intervals along the track as the electrodes were withdrawn from the cortex. This was done by passing DC current through each electrode (5 μA for 5 s). At the end of each experiment, the animal was given an overdose of pentobarbital sodium (Nembutal) and perfused through the heart with buffered saline (0.9%) followed by Formalin (10%). Blocks of visual cortex were cut in the plane of the electrode tracks, and 40-μm frozen sections were cut and stained with thionin. Lesions were located, and electrode tracks were reconstructed to determine positions of recorded cells. The neurons we studied were located in area 17, and all cortical lamina were represented in the sample.

Visual stimulation

The occurrence of each action potential was recorded by a computer with a resolution of 1 ms. Bar stimuli projected on a tangent screen 57 cm from the cat's eyes were manually moved during electrode advancement to isolate and initially characterize single-
unit activity. A half-silvered beam splitter placed in front of the cat allowed for visual stimulation by either the tangent screen or by two cathode ray tube (CRT) displays. The displays were positioned so that they could be used to independently stimulate each eye from a distance of 57 cm. After cell pairs were isolated, a search program was used in conjunction with these displays to estimate ocular dominance, orientation selectivity, and receptive-field position of the cells. The orientation and spatial frequency of drifting sinusoidal gratings at 50% contrast were initially varied in randomly interleaved sequences to determine the receptive-field types and optimal sensitivities of the cells under study.

After initial characterization by drifting gratings, monocular receptive fields were mapped in detail by the use of the reverse correlation method (Jones and Palmer 1987a). As depicted in Fig. 1, a random sequence of bright and dark bars of optimal orientation is used to evoke neural discharge. Each bar is presented at a point on a grid that is centered on the receptive fields and oriented parallel to the preferred orientations. During any moment, only one bar is present. Each bar is present for a fixed period of time (no more than 48 ms). The background at all times during the stimulus sequence is maintained at mean luminance. Bar dimensions are set according to the particular neurons under study. Bar width is

set according to the optimal spatial frequency as measured by gratings and is typically between 0.25 and 0.5º. If bars of ~1º in length fail to evoke sufficient neural discharge, long bars (usually 10º) are used. When such long bars are used, the aforementioned grid is reduced to a linear array of points. For such cases, a one-dimensional spatial map is constructed in which only those sensitivity variations perpendicular to the preferred orientation are studied.

Spatiotemporal characterization of receptive fields

In the reverse correlation procedure, URF maps are constructed by inferring the causal stimulus for each spike. Spatial maps are constructed by identifying the particular stimulus that preceded each spike by a specified delay. Separate bright and dark bar histograms are accumulated that describe the number of spikes associated with each bar. For simple cells, the linearity of spatial summation (DeAngelis et al. 1993b) allows the construction of a composite receptive-field map by taking the difference between the bright and dark bar histograms. The procedure is performed on-line to verify grid positioning and neural responsiveness. Different random sequences are repeatedly presented until sufficient detail is visible within the on-line histograms. The occurrence of every spike and the position and occurrence of every bar stimulus are stored for subsequent analyses.

The temporal structure of simple-cell receptive fields is studied by constructing composite profiles with different spike-stimulus delays. Although this procedure can be used for any spike-stimulus delay, temporal resolution is fundamentally limited by the duration of each bar flash (usually 48 ms). Typically, analyses are performed for different delays in increments of 20 ms up to the delay at which no spatial features are visible (usually 300 ms for cells from the adult cat). For cells from kittens, this maximal delay is usually around 400–500 ms, and it can be as high as 800 ms (DeAngelis et al. 1993a). For cases in which the bar length was short enough to study the two-dimensional (X-Y) spatial structure of receptive fields, the use of multiple spike-stimulus delays yields a three-dimensional spatiotemporal (X-Y-T) response histogram. Because the stimulus grids are aligned according to optimal orientations, there are never any large variations in Y. This allows us to reduce the three-dimensional (X-Y-T) histogram to two-dimensions (X-T). All spatiotemporal analyses on such three-dimensional histograms were conducted after collapsing the second spatial dimension by summing the histogram values along the Y dimension. For long-bar stimulation, this procedure is unnecessary because the stimulus allows only a one-dimensional (X) spatial characterization.

Simple-cell receptive fields are characterized in frequency space by computing a two-dimensional fast Fourier transform (FFT) of the X-T profile. Optimal spatial and temporal frequencies are computed by two-dimensional cubic-spline interpolation of the points surrounding the largest amplitude FFT bin. Optimal frequencies are only computed for cases in which no more than one peak was present in the quadrant of the X-T spectrum corresponding to the preferred direction selectivity of the cell. Optimal velocity is computed by taking the ratio of the optimal temporal frequency to the optimal spatial frequency. Receptive fields are also quantified according to full-width half-magnitude estimates of their spatiotemporal envelopes. One-dimensional profiles in X and T that contain the peak response point were extracted from the X-T profiles. Separate envelopes were constructed in X and T by summing the square of these one-dimensional profiles with the square of their corresponding Hilbert transforms (DeAngelis et al. 1993a). This procedure was used to eliminate the phase information in the original one-dimensional profiles.
RESULTS

**BRF analysis**

Altogether, we examined 41 cell pairs from adults, 5 from kittens at 8 wk, and 28 from kittens at 4 wk. Because we were interested in examining BRFs between cortical neurons, we did not analyze the six adult cell pairs in which one of the receptive fields seemed to be associated with an LGN fiber. For eight cell pairs, reverse-correlation data were available for both eyes. For these cell pairs the two monocular BRFs were analyzed.

Cross-correlation analysis reveals the distribution of interspike intervals between the discharge of two neurons. Because neural discharge is evoked by visual stimulation in our experiments, one must also account for purely stimulus-dependent increases in correlated discharge. To estimate the effect of stimulus-locked discharge on correlated activity, shuffled cross-correlograms are computed in which the cross-correlation procedure is applied to different trials of the same stimulus (Perkel et al. 1967). To isolate neurally evoked correlation, this shuffled cross-correlogram is subtracted from the original "raw" correlogram. For 19 cell pairs (9 from the adult, 2 from the 8-wk kitten, and 8 from the 6-wk kitten), shuffled correlograms can be constructed for the reverse-correlation stimulus because the same random sequence of bars was presented several times.

Previous studies have shown that correlated discharge can be stimulus dependent in that different stimuli can evoke different patterns of correlated discharge (Engel et al. 1991; Espinosa and Gerstein 1988; Gerstein 1970; Palm et al. 1968). Evidence for the dependence of correlated discharge on the nature of visual stimulation is seen in Fig. 2. Cross-correlograms for two cell pairs (A and B) are shown under stimulation by both the reverse correlation method and drifting sinusoidal gratings of optimal spatial frequency and orientation. For each cell pair and stimulus condition, shuffled cross-correlograms, as well as shuffled-subtracted correlograms, are shown. In neither of these examples does the shuffle-subtracted correlogram correlate with correlated discharge. Cross-correlogram peaks are sometimes only visible with one type of stimulation. The type of visual stimulation can also affect the tightness of neural synchrony, as indicated by the different bandwidths of the correlogram peaks shown in Fig. 2. For all of the 19 cell pairs in which shuffled correlograms can be computed for the reverse-correlation stimulus, the shuffle-subtracted correlograms are different for the two methods of stimulation. Raw correlograms obtained under the two methods of stimulation are similar only for those pairs with direct excitatory connections (n = 11), as inferred by the presence of cross-correlogram peaks on the order of 1 ms in width. Cell pairs exhibiting such "narrow-peak" correlograms are not included in the BRF analyses that follow. All cell pairs used in the following analyses exhibit cross-correlogram peaks of at least 10 ms in width.

For the cell pairs in which we did not present random sequences multiple times, shuffled cross-correlograms cannot be computed. For these cell pairs, discharge from nonidentical trials is cross-correlated to provide an estimate of the correlation expected due to direct stimulus effects. This estimated shuffled correlogram is then subtracted from the raw cross-correlogram. For the 19 cell pairs in which random sequences of bars were presented more than once, genuine shuffled correlograms are constructed and subtracted from the raw cross-correlogram. For the purpose of our analysis, correlated discharge is said to exist between cell pairs that tend to fire within 128 ms of each other (i.e., a peak in the shuffle-subtracted cross-correlogram is apparent between -128 and +128 ms). Although the majority of cross-correlogram peaks are within 10 ms of exact
synchrony (e.g., Fig. 2, A and B), in some cases, the most common interspike interval is as large as 100 ms (e.g., the cell pair shown in Fig. 8).

After cross-correlation analysis, BRFs are mapped by applying the reverse-correlation procedure to spike pairs with interspike intervals that correspond to the cross-correlogram peak. Therefore only spike pairs whose temporal separation is near the most commonly observed interspike interval are used in BRF analysis. The size of the cross-correlation range used in BRF analysis depends on the total number of spike pairs observed during the course of the stimulation. Interspike interval ranges of 8, 16, 32, and 64 ms are used depending on the number of spike pairs around the peak of the cross-correlogram. Reverse correlation associates these spike pairs with a single bar of a certain luminance and position. However, the receptive fields associated with patterns of discharge among multiple neurons can also be constructed with the use of alternative methods of noisilike stimulation (Reid and Shapley 1992; Sakai et al. 1988; Sutter 1992). The extension of our analysis to other methods of receptive-field mapping and multunit recording is detailed in the APPENDIX.

BRFs are constructed according to the smallest interval range that yields visible features after reverse-correlation analysis. In no cases did choosing a range larger than this minimum significantly alter the BRF profile. For the example shown in Fig. 3, the receptive fields of a pair of nearby simple cells are mapped. The reverse-correlation stimulus evoked correlated discharge as evidenced by the broad cross-correlogram peak. (For this experiment a shuffled cross-correlogram cannot be obtained because no random trial sequences are used more than once.) A total of 2,156 spike pairs are contained in the interspike interval range of 16 ms centered on the interval −20 ms in the cross-correlogram. The reverse correlation of spike pairs falling within this range reveals the BRF for the two simple cells. The BRF in this case contains an elongated region of dark sensitivity that spatially corresponds with dark response regions in the two URFs. The correspondence of BRF and URF profiles is addressed further on.

Pathways with different response sensitivities might evoke distinct temporal patterns of correlated discharge in the same pair of cells. For example, two cells might share two distinct inputs, one of which causes cell 1 to fire before cell 2, and the other of which causes cell 1 to fire after cell 2. Therefore broadly correlated discharge between a pair of cells might reflect the temporal superposition of distinguishable functional pathways. This possibility was examined with the use of the reverse-correlation method to map BRFs associated with different interspike intervals. No cell pairs that displayed broadly correlated discharge showed any interspike dependence other than that expected from the single-cell temporal response properties (see Eq. 1 below). In general, different interspike intervals are associated with the same stimulus, as illustrated in Fig. 4, which shows the correlated discharge from an LGN fiber and a simple cell. In Fig. 4, reverse correlation was applied to spike pairs with a variety of interspike intervals. For all interspike intervals examined, the BRF is constant in shape. The data indicate that different interspike intervals cannot be associated with distinguishable functional pathways. Therefore the constancy of BRFs over different interspike intervals for all cell pairs examined allows the use of broad cross-correlogram windows in the BRF mapping procedure.

**BRF Types**

Correlated discharge during stimulation used for reverse correlation was seen in 47 pairs of simple cells, 14 pairs in which one cell was simple and the other complex, and 7 pairs of complex cells. As illustrated in Fig. 5, the spatial structures of BRFs can be classified into three groups: uni-
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FIG. 4. BRFs do not depend on interspike intervals. Here BRF difference plots are shown for a stimulus-spike interval $t$ of 50 ms and a variety of interspike intervals $\Delta$. Spike 1 is a lateral geniculate nucleus (LGN) fiber, and spike 2 is a simple cell. Shaded regions near the center of the cross-correlogram indicate the spike pairs used to construct each of the BRFs. All the BRFs show a sensitivity to bright bars within the same patch of visual space. Although the sensitivity, indicated by the brightness of this patch, varies with $\Delta$, the spatial organization of the BRF does not vary.

modal (U), simple (S), and complex (Cx). These classifications correspond to single-cell receptive-field types in the LGN and cortex. U-type BRFs are unimodal in that they show sensitivity to only one type of luminance (bright or dark). In contrast to circularly symmetrical LGN receptive fields (Hubel and Wiesel 1961), U-type BRFs consist of response regions that are spatially elongated along the angle of preferred orientation. S-type BRFs resemble simple cells in that they consist of alternate elongated regions of bright and dark stimulus sensitivity that are aligned along the direction of preferred orientation. Finally, Cx-type BRFs resemble complex cells and consist of overlapping regions of bright and dark stimulus sensitivity.

Table 1 summarizes the distribution of BRFs according to the receptive-field types of single neurons. Because of limited sample sizes for the kittens groups at 4 and 8 wk of age, the data from all ages have been grouped for this comparison. In four cell pairs from 4-wk kittens, no BRF was visible despite the presence of correlated discharge. These BRFs are labeled as type N (none) in Table 1. Single cells were classified on the basis of their reverse correlation profiles except for eight cell pairs (2 from adults and 6 from 4-wk kittens) in which a BRF was visible but one of the single cell profiles was not resolvable by reverse correlation. In these cases cell class was determined by the degree of response modulation to sinusoidal drifting gratings. We focused on pairs of simple cells because their linearity allows a fairly complete receptive-field characterization by the reverse-correlation procedure (DeAngelis et al. 1993b; Jones and Palmer 1987a). However, our sample did include some complex cells. For example, Cx-type BRFs were only visible when at least one of the cells was complex. Although U-type BRFs were almost never observed when one cell of a pair was complex, this absence might be an artifact of the limited complex cell sample size. The sample size of simple-cell pairs was sufficient to allow for a comparison between

![Diagram of receptive fields](image)

FIG. 5. Visibility of BRFs analyzed according to the method of Fig. 1 depends on the receptive-field properties of the pair of neurons under study. BRFs are commonly visible with pairs of simple cells exhibiting correlated discharge. However, they are only rarely visible with pairs of complex cells. Visible BRFs can be classified according to their spatial organization into three groups that correspond with single-cell receptive-field classes: U, S, and Cx. U resembles a colinear array of LGN cells of the same center type. In the example shown here, we see a line of dark response, which resembles a linear array of off-center LGN cells. S types contain nonoverlapping bright and dark response regions, whereas Cx types discharge when either bright or dark stimuli are flashed throughout their receptive fields. All single-cell receptive fields can be classified into either simple or complex.

<table>
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<th>Table 1. Bicellular receptive-field types</th>
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U, unimodal; S, simple; Cx, complex; N, none.
the two receptive fields limits correlated discharge to very small regions of space (top, Fig. 6).

For pairs of simple cells, the BRF is predicted on the basis of the single-cell receptive fields with the product model described above. Spatiotemporal URFs and BRFs are mapped by using the reverse-correlation procedure with multiple stimulus-spike delays. URF profiles are normalized so as to provide an estimate of the probability of discharge with various stimuli for the two cells ($P_1$ and $P_2$, respectively). An estimated spatiotemporal BRF ($P_\ast$) is predicted by

$$P_\ast(x, t) = P_1(x, t)P_2(x, t - \Delta)$$

where $x$ is position, $t$ is the stimulus-spike interval, and $\Delta$ is the interspike interval. Note that this predicts that the BRF will depend on the interspike interval according to the extent of temporal changes within the URFs. As shown in Fig. 7, the product rule accurately predicts the observed BRF for the same pair of cells shown in Fig. 3. This is the case for all pairs of simple cells. When deviations from the product rule occur, they are most often located at temporal intervals in the BRF before the peak response of the single cells. These deviations are likely to be the result of common inputs. However, the deviations are relatively minor compared with the peak responses seen in the $X\cdot T$ BRF profile.

The correspondence between observed BRFs and the

Relationship between URFs and BRFs for pairs of simple cells

The simplest model of BRF structure is that BRFs arise directly from stimulus-evoked discharge. In such a model, the BRF is exactly predictable on the basis of the overlap of similar response regions in the two single-cell receptive fields. This model is illustrated in Fig. 6, in which the one-dimensional RF profiles of two simple cells are modeled as Gabor functions in the right column. These functions can be used to describe the receptive fields of almost all simple cells (Jones and Palmer 1987b). Cell 1, in the bottom row, has a maximal probability of discharge ($P_1$) when a bright bar is presented at the center of its receptive field. Cell 2, on the other hand, has a maximal probability of discharge ($P_2$) when a bright bar is presented to the right of center or when a dark bar is present to the left of center. If we assume complete independence between the discharges from the neurons, then the probability of correlated discharge with any stimulus is predicted by the product of the probabilities of single-cell discharge (Bayes’ law). In this example, although the receptive-field centers are exactly aligned, the difference in the positions of bright and dark subregions in

FIG. 6. A simple model is shown that predicts the structure of BRFs on the basis of uncellular receptive fields (URFs). Assuming complete independence, one would expect the greatest number of correlated spikes with stimuli that evoke maximal discharge in the 2 cells. Here 1-dimensional Gabor functions represent the spatial profile of sensitivity to bright and dark bar stimulation of 2 single cells. Receptive fields are centered at the same position but differ in their spatial structure (i.e., the relative positions and size of bright and dark subregions). Because receptive-field profiles can be used to predict the probability of discharge, the probability of correlated discharge ($P_\ast$) is the product of firing probabilities for each cell ($P_1 \times P_2$). This is done separately for the bright and dark bar response profiles. The vertical scale of the top row is expanded for visibility.

FIG. 7. Spatiotemporal profiles of the cells shown in Fig. 2 demonstrate that the product rule described in Fig. 6 accurately predicts the BRF. The temporal dimension of receptive fields is examined by varying the spike-stimulus interval $t$ from 0 to 300 ms in steps of 16.7 ms. Top row shows the BRF prediction according to the product of the normalized spike 1 and spike 2 $X\cdot T$ profiles.
product model, which is based on neural independence, suggests that BRFs might be a direct artifact of stimulus-induced discharge. If this is the case, then the receptive-field map of spike pairs within the shuffled cross-correlogram should exactly match the BRF computed with the raw cross-correlogram. To test this possibility, we computed shuffled BRFs for 19 cell pairs. Shuffled BRFs are only possible when the same stimulus sequence is repeated. For these 19 cell pairs, identical random sequences were repeated up to 4 times. Spike trains from different repetitions of the same random sequence are used to construct a shuffle correlogram. A shuffled BRF is constructed by applying the reverse-correlation procedure to those spike pairs corresponding to a certain range of the shuffle cross-correlogram. As shown in Fig. 8, no features are resolvable in the shuffled BRF. This was true for all 19 cell pairs for which shuffled BRFs could be constructed. The lack of any features within shuffled BRFs implies that BRFs are not solely the by-product of stimulus-locked discharge and suggests that observed BRFs do indeed reflect neural interactions. This suggestion is corroborated by the observation that, within the same interspike interval range, there are always more spike pairs in the raw cross-correlogram than in the shuffle cross-correlogram. For the cell pair shown in Fig. 8, for example, 2,001 spike pairs were present in the interspike interval range from 84 to 116 ms of the raw cross-correlogram, whereas only 1,340 spike pairs were present in the same interval range of the shuffled cross-correlogram. In some cases the raw cross-correlogram contains roughly three times the number of spike pairs seen in the shuffle cross-correlogram. This is to be expected given the weakness of the stimulation. Because for any single flashed bar there is relatively low probability of elicited spikes, correlated discharge is unlikely to occur simply on the basis of stimulus-evoked increases in discharge.

Quantitative comparison of URFs and BRFs for simple cells

Because single-unit discharge is often considered to be the output of perceptual filters that are described by receptive-field analysis, it is reasonable to suggest that correlated discharge might also represent the output of perceptually relevant filters. To evaluate this possibility we compared quantitatively the URF and BRF properties of simple-cell pairs so as to ascertain the potential advantages of observing the output of bicipellar, as opposed to unicellular, filters. To determine whether bicipellar differences emerge as the result of postnatal maturation, we compare the results for cell pairs from three age groups in which the spatiotemporal structures of URFs have been studied (DeAngelis et al. 1993a).

Five measures of receptive fields are derived from the data of 51 monocular reverse-correlation runs of simple-cell pairs. Because these measures are derived from both the two URFs and the BRF of a cell pair, each cell pair yields a total of 15 measurements. Figure 9 illustrates these measurements for a pair of adult simple cells of opposite direction selectivity. Two measures describing the spatial and temporal extent of the receptive field are derived from each X-T profile (left column, Fig. 9). As discussed in METHODS, these measurements are made by constructing envelopes in X and T around the peak response within the X-T profile. The remaining three measures describe the location of the peak within the frequency spectrum (right column, Fig. 9) derived from the X-T profile. This location is characterized according to spatial and temporal frequency, as well as velocity (temporal frequency/spatial frequency). For every pair of cells and type of measurement, two sets of comparisons are made. Unicellular properties are compared with each other, and BRFs are compared with the unicellular measures. The 51 BRFs are all based on at least 150 spike pairs within 32 ms of the cross-correlogram peak. Thirteen of the 51 runs were from 13 cell pairs of 4-wk-old kittens, 7 from 7 cell pairs of 8-wk-old kittens, and 31 from 24 cell pairs of adult cats.

Receptive-field size comparisons are seen in Fig. 10. Each simple-cell pair is represented in Fig. 10.A by a line. The horizontal positions of a line’s endpoints correspond to the two URF sizes. The vertical position of each line corresponds to BRF size. The horizontal length of the lines in Fig. 10.A therefore indicates the difference between the two URF values in each cell pair. The clustering of lines to the right of the diagonal indicates that URFs are in general larger than BRFs. The distribution of these URF differences for cell pairs from each age group is shown in Fig. 10.B. The peak of these distributions near zero indicates that receptive-field widths of nearby simple cells are similar at all ages studied. (Similar URF widths are indicated in Fig. 10.A by short or nonexistent horizontal lines between data points.) Although the sample size is small for 4-wk kittens, this group has the largest proportion of URF differences >1°.

If BRF size is always in between the two corresponding URF sizes, then all cell pairs would straddle the diagonal
In Fig. 11. The URF and BRF data are summarized in Fig. 11A. The similarity of URF durations between nearby cells in all age groups is shown in Fig. 11B. For adult and 4-wk kitten cell pairs, BRFs are significantly shorter than corresponding URFs in duration (Fig. 11C). The median URF- BRF duration difference is +24 ms among adult cell pairs ($P < 0.01$) and +26 ms among cell pairs from kittens at 4 wk of age ($P < 0.05$). Among cell pairs from kittens at 8 wk, the median duration difference is also positive (29 ms), but is not significantly nonzero because of the limited sample size. When the cell pairs from all ages are grouped, the median duration difference between URFs and BRFs is significantly nonzero (27 ms, $P < 0.01$).

Of the 51 BRFs from simple-cell pairs, 45 BRF spectra contained a single peak within one quadrant (see Fig. 9, top right). The optimal spatial and temporal frequency data from these spectra are summarized in Figs. 12A and 13A, respectively. Just as with receptive-field width (Fig. 10B) and duration (Fig. 11B), there is a tendency for nearby cells to have similar optimal spatial and temporal frequencies, as shown in Figs. 12B and 13B, respectively. There is no consistent tendency for the optimal biconvex spatial frequency to differ from the optimal spatial frequency seen in URFs in any of the age groups studied (Fig. 12C). The relationship between URFs and BRFs optimal temporal frequencies (Fig. 13) is similar to that seen with respect to optimal spatial frequencies. There is no systematic difference between optimal URF and BRF temporal frequencies at any age group, as shown in Fig. 13C.

Optimal velocity is computed by taking the ratio of the optimal temporal frequency over the optimal spatial frequency for each URF and BRF spectrum. These optimal velocities are summarized in Fig. 14A. As might be expected by the histograms of Figs. 12B and 13B, nearby cells tend to have similar optimal velocities (Fig. 14B). Additionally, as shown in Fig. 14C, no consistent differences are present between the optimal velocities of URFs and BRFs in any age group.

Population comparison of URFs and BRFs

In the previous section we evaluated whether the BRFs of nearby simple-cell pairs consistently differ from the receptive-field characteristics of the individual cells. The findings do not constrain the relationships between the overall populations of BRF and URF properties. For example, the differences in receptive-field widths between URFs and BRFs might only be present among cells with particularly large receptive fields. If this were true, then the entire population of BRF widths might not be any different from the population of URF widths. A comparison of population responses should indicate if there are any differences in the range of parameters that single cells and pairs of cells are capable of signaling.

Figures 15 and 16 show the distribution of URF and BRF widths and durations, respectively. There is considerable overlap in the distribution of URF widths (Fig. 15A) and the distribution of BRF widths (Fig. 15B) at all ages. As shown in Fig. 15C, there is a significant decline in mean URF width from postnatal age 4 wk to postnatal age 8 wk. This is consistent with previous results (DeAngelis et al.
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Receptive Field Width [deg]

FIG. 10. BRFs tend to be smaller than URFs. In the scattergram (A) the widths of URFs are plotted along the ordinate and widths of BRFs along the abscissa. The diagonal line describes equality between URF and BRF width. Cell pairs are linked by horizontal lines. Each cell pair yields 2 connected circles on the scattergram, corresponding to each of the 2 cells of a pair. Cell pairs sharing the same envelope size have overlapping circles with no horizontal line visible. The distribution of horizontal line length describes differences between the cells of a pair (B). A large proportion of cell pairs have URF widths that differ by <0.5°. The relationship between URFs and BRFs is summarized in the histogram in C. Points to the right of the diagonal line of A lie in the positive half of C, whereas points to the left lie in the negative half. The tendency of URF-BRF differences to be >0 in C indicates that the majority of URFs are larger than their corresponding BRFs.

1993a). Additionally, at all ages, the mean BRF widths are smaller than those associated with individual cells (Fig. 15C). Analysis of variance indicates that the relationship between BRF and URF widths does not depend on age. In Fig. 15D, the data on receptive-field widths from all ages are grouped and reveal a statistically significant difference between mean BRF and URF widths (t test, P < 0.01).

The same comparison for the populations of receptive-field durations is made in Fig. 16. Again, there is considerable overlap between the overall populations of URF and BRF durations, as shown in Fig. 16, A and B, respectively. Although Fig. 16C indicates longer durations among cells in 8-wk kittens than among cells in 4-wk kittens, this difference is not statistically significant. Other data from single cells, with a larger sample size, indeed show slightly shorter durations among cells in kittens at 8 wk (DeAngelis et al. 1993a). Just as with receptive-field width, the relationship between receptive-field durations in BRFs and URFs is independent of age. Figure 16D shows a statistically significant difference between unicellular and birecipient BRF durations when data from all ages are grouped together (P < 0.01).

By contrast, a comparison of the populations of optimal spatial and temporal frequencies reveals no difference between URFs and BRFs. Although optimal frequencies do depend on age (DeAngelis et al. 1993a), there is no difference between URFs and BRFs. The population of optimal

Receptive Field Duration [ms.]

FIG. 11. BRFs tend to have shorter durations than URFs (A). Format is the same as that of Fig. 10. The majority of cell pairs have URF durations that are within 50 ms of each other (B). The asymmetry of the distribution of URF-BRF differences around 0 (C) indicates a tendency for the URFs of cell pairs to have longer durations than the BRFs.
velocities does not depend on either the number of cells associated with a receptive field or the age of the animal.

**DISCUSSION**

We have introduced a method for mapping the set of stimuli that tends to evoke correlated discharge between cells. The structure of the BRFs inferred by this analysis does not depend on a choice of spike pairs with particular interspike intervals. The spatial structure of BRFs can be classified into groups analogous to the classes of single-cell receptive fields. Although BRFs between pairs of simple cells resemble those expected between independently firing cells, BRFs in fact arise from neural interactions and are not artifacts of stimulus-induced discharge. The BRF of a pair of simple cells is typically smaller in size and shorter in duration compared with the two simple cells’ receptive fields.

The reverse correlation procedure used to map BRFs is limited in the sense that it reveals a first-order response kernel that completely describes only those receptive fields that are totally linear. Nonlinearities, such as those existing in all complex cells, cannot be characterized by this method. Such nonlinearities might also be present in multi-

**FIG. 12.** Peak spatial frequencies of BRFs are not consistently different from uncellular optimal spatial frequencies. Format is the same as that of Fig. 10. Lines representing cell pairs are symmetrical with respect to the diagonal of A. For most cell pairs, optimal URF spatial frequencies are within 41% (log ratio <0.15) of each other (B). The majority of optimal BRF spatial frequencies are within 25% of the optimal spatial frequencies for the single cells (C).

**FIG. 13.** Peak temporal frequencies of BRFs are not consistently different from uncellular optimal temporal frequencies (A and C). Format is the same as that of Fig. 10. For most cell pairs, optimal URF temporal frequencies are within 33% (log ratio <0.125) of each other (B).
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Velocity [deg/sec]

![Graph A](image1.png)

![Graph B](image2.png)

![Graph C](image3.png)

![Graph D](image4.png)

Cellular receptive fields. Significant nonlinearities might explain the absence of resolvable BRFs between some pairs of complex cells. Indeed, any distributed pattern of discharge in which complex cells participate must contain nonlinearities. The reverse-correlation procedure is also unable to reveal the orientation selectivity of BRFs, because all bars are of the same orientation. This is a particular limitation in light of evidence that correlated discharge is more selective than single-unit discharge with regard to orientation (Ghose et al. 1991). Different methods of receptive-field mapping (e.g., Reid and Shapley 1992; Sakai et al. 1988; Sutter 1992) might overcome some of these limitations.

The application of cross-correlation to other mapping techniques is detailed in the APPENDIX.

One limitation of our study of the stimulus selectivity of multiunit discharge is that we have only recorded from two cells at a time. Given that a single orientation column contains ~100 cells, any single stimulus is likely to evoke correlated discharge among multiple neurons (Mountcastle 1979). Indeed, the nature of "tricellular" and "quadcellular" receptive fields might be very different from that of the URFs and BRFs reported here. Truly multicellular recording could provide insight into how URFs are formed. As mentioned in the INTRODUCTION, multicellular receptive

**Fig. 14.** There is no consistent difference between optimal URF and BRF velocities (A). Format is the same as that of Fig. 10. The majority of cells pairs have single-cell and bicellular optimal velocities within 5 cycles/deg of each other (B and C).

**Fig. 15.** Populations are shown of URF and BRF widths among cell pairs from kittens of 4 and 8 wk of age and adult cats. Distributions of URF and BRF widths are shown in A and B, respectively. Mean URF and BRF widths are plotted vs. age in C, whereas the mean URF and BRF widths over all ages are compared in D. Error bars on C and D indicate the standard errors for these populations. BRFs are smaller than URFs at all ages studied.
fields might correspond to the single-cell receptive fields of higher-order neurons. For example, Hubel and Wiesel (1962) proposed that complex-cell receptive fields arise from the excitatory convergence of overlapping simple cells. If this is the case, then the stimulus selectivity of the correlated discharge over a pool of simple cells should resemble that of a complex cell. This clearly is not the case for pairs of simple cells, because no Cx-type BRFs are observed among such pairs (see Table 1). This suggests that the discharge of complex cells either does not depend on the correlated firing of simple cells or that larger numbers of simple cells are necessary to explain complex-cell receptive-field structure.

A final concern is that correlated discharge may be sensitive to parameters that single-unit discharge is not. In our study, BRFs have only been analyzed with respect to receptive-field properties found in single cells (e.g., size and spatial frequency selectivity). The potential inapplicability of single-unit receptive-field measures can be seen in the U-type BRFs, which, because they are unimodal, have broad spatial frequency tuning. In these cases the BRF field is not well characterized by a single spatial frequency. The possibility of emergent sensitivities is even greater when the activity of larger numbers of neurons is considered. If “higher-order” neurons can be found that are thought to receive convergent input from the pool of neurons under study, then the receptive fields of these higher-order neurons might provide a basis for studying alternate parameters of BRFs.

The difference in correlated discharge during the presentation of gratings and the reverse-correlation stimulus could reflect the intrinsic variability of correlated discharge or an adaptation effect. These possibilities exist because the two stimulation methods were not interleaved: sinusoidal gratings were always presented before reverse-correlation runs. However, we do not believe that variability over time can completely explain the observed differences. First, although cross-correlograms are intrinsically variable, all cross-correlograms compared were accumulated from the responses of between 4 and 50 trials. Second, for cell pairs in which discharge evoked by sinusoidal gratings was measured for periods up to 1 h, we have observed shifts in the magnitude of correlated discharge, but not in the temporal pattern of the correlated discharge (unpublished observations). Temporal effects are unlikely to be responsible for changes in the pattern of correlated discharge seen in Fig. 2. Given the prior reports of stimulus-dependent correlation, together with the data presented here, we believe that the observed differences in the pattern of correlated discharge are a consequence of the radically different nature of the two stimulation methods. Reverse-correlation provides stimulation that is localized in space and time and is broad in the corresponding frequency domains. Sinusoidal gratings, on the other hand, provide stimulation that is localized with respect to spatial and temporal frequency but broad in space and time. Thus reverse-correlation invokes visuotopically localized neural pathways, whereas gratings are likely to activate frequency-specific pathways. Figure 17 plots the receptive fields of hypothetical cells in the domains of position and spatial frequency. Cells with similar receptive-field properties are the most likely to display correlated discharge and are located near one another in these domains. In Fig. 17, regions A and B represent uncellular receptive fields that are near to one another and have similar optimal spatial frequencies. C and D represent the receptive fields of cells that provide input to both A and B. C is nearby to A and B (top) but has a very different optimal spatial frequency (bottom). D, on the other hand, has similar optimal spatial frequency (bottom) but is located far from A and B (top). Because the stimulation used in reverse correlation is spatially localized but broadband in frequency, the correlated discharge between A and B will
activity would be unable to distinguish between the spatial and frequency content of visual stimuli. However, because different patterns of correlated discharge are associated with spatially localized and frequency-localized stimulation, discrimination between the two types of stimuli might be possible on the basis of multunit activity.

The weak dependence of BRF structure on interspike interval suggests that visual information is not encoded by a specific pattern of spikes between two cells, as was suggested by Abeles and Gerstein (1988). Although single neurons in V1 can exhibit stimulus-dependent patterns of discharge (Richmond et al. 1990; Richmond and Optican 1990), the low firing rates of most cells in the visual cortex makes it unlikely that a pair of cells would be able to produce distinctive temporal patterns of correlated discharge within the perceptually relevant time frame of several hundred milliseconds or less. The low number of stimulus-evoked spikes is especially a problem for the theory of stimulus encoding via correlated discharge because relatively few spike pairs share the same interspike interval. For the reverse correlation trials, seldom do >20% of a neuron's spikes fall within 8 ms of another neuron's spikes.

However, even if temporal coding is not present in correlated discharge, it might still exist at the level of single neuron discharge. The reverse-correlation method described in Fig. 1 can be modified to look for temporal coding by single cells (Lestienne and Strehler 1987; Optican and Richmond 1987; Richmond and Optican 1987, 1990; Richmond et al. 1987, 1990), by combining autocorrelation or interspike interval analyses with the reverse-correlation procedure. For example, DeBusk et al. (1992) have provided evidence that 300-Hz bursts of spikes are stimulus dependent. A detailed receptive-field map of such bursts could be constructed by applying the reverse-correlation procedure to only those spikes contained within the first few milliseconds of the autocorrelogram.

The data presented in Figs. 10–14 provide insight into the spatial organization of neurons according to their response properties. Although it has been known for many years that nearby neurons of the visual cortex tend to have similar preferred orientations and receptive-field locations, the B histograms of Figs. 10–14 demonstrate that nearby simple cells are similar with regard to other parameters, including receptive-field size and optimal spatial and temporal frequencies. The spatial organization with respect to these parameters is not as strong as it is with orientation. Although all the nearby cells had preferred orientations within 10° of each other (e.g., Fig. 3), some cell pairs had spatial frequencies that differed by a factor of two. All of these parameters, however, are measurements of overall receptive-field properties and do not describe the relationship of subregions within a receptive field and the overlap between different receptive fields. As can be seen in the examples presented in this paper, the receptive fields of nearby cells are sufficiently varied so as to give rise to a wide spectrum of BRFs. The degree of overlap and the distribution of receptive-field types is therefore a major determinant of multunit receptive fields. Appropriate measures of the subregion organization and the overlap between the receptive fields of nearby cells are subjects of current investigations (DeAngelis et al. 1992; unpublished observations).
The quantitative comparisons of URF and BRF properties suggest the types of visual information that correlated activity is most suited to encode. For example, the smaller spatial extents of BRFs suggest that correlated activity may be able to subserve higher visual acuity than is possible with single-cell discharge (Parker and Hawken 1985). As discussed previously, it is not certain how the stimulus selectivity of multunit activity (i.e., activity from >2 cells) compares with that of bcial and single-cell activity. For example, there is no way of predicting whether tricellular receptive fields tend to be even smaller than BRFs. However, at least for single cells, the product rule of Eq. 1 suggests that the receptive fields associated with higher-order correlated discharge can be predicted on the basis of single-cell receptive fields.

The relationship between URFs and BRFs does not depend on postnatal maturation. Changes seen in single-cell receptive-field properties during postnatal development are paralleled by similar changes among BRFs. For example, BRFs are smaller in width than URFs at all ages studied, whereas BRFs and URFs are similar in optimal frequencies at all ages studied. This suggests that the neural circuitry responsible for the establishment of BRF properties is not dependent on postnatal maturation. Correlated activity among cells with a variety of receptive fields offers the possibility of reducing the ambiguity of single-unit discharge and thereby enhancing discrimination (Sejnowski 1986; von der Malsburg and Schneider 1986; Zohary 1992). This is seen in Fig. 6, in which the second cell responds equally well to different bright and dark stimuli. Thus an ideal observer of spike counts is unable to differentiate the two stimuli. However, the observer of correlated discharge between this cell and the first cell of Fig. 6 is not subject to this ambiguity. An experimental example of the potential of correlated discharge to disambiguate the signals from single cells is seen in Fig. 3. Here, cells of roughly equal sensitivity to bright and dark stimuli fire in synchrony only when a dark bar is present. The ability of correlated activity to underlie perception depends on the stimulus specificity of correlated activity, how discriminable correlated activity is between different responses, and the existence of neural circuitry capable of detecting correlation. The current studies demonstrate the stimulus specificity of correlated discharge between pairs of cells. The discriminability question has been examined with respect to the spike counts (Bradley et al. 1987; Geisler et al. 1991; Tolhurst et al. 1983) and temporal patterns (Geisler et al. 1991) within the stimulus-evoked responses of single cells, but it has not been examined with regard to correlated discharge. Because neurons fire according to summation of numerous inputs, they can be thought of as correlation detectors. In one simulation, the synchronous activation of 25 synapses was 7 times more likely to evoke discharge than was asynchronous activation (Abeles 1991). Indeed, this sensitivity to correlation has led several investigators (Abeles 1991; von der Malsburg and Schneider 1986) to postulate that synchronous activity is the only possible method of transmitting information within the cortex. These considerations, in combination with the receptive-field analyses of our present study, suggest that correlated activity within the visual cortex may play a fundamental role in the representation of visual information.

**APPENDIX**

**Multicellular receptive-field mapping**

The analysis used here to map multicellular receptive fields involves a combination of two correlations. The first is commonly described as cross-correlation and involves the computation of the temporal correlation function between two neurons' responses. If we describe a neuron's response by the function \( R \) then the cross-correlation function \( X \) for two neurons is

\[
X = \frac{\langle R_1(t) R_2(t+\alpha) \rangle}{\sigma_{R_1} \sigma_{R_2}}
\]

where \( \alpha \) is the interval between neural responses \( R_1 \) and \( R_2 \). In the case of extracellular recording, neural responses are described by the occurrences of action potentials. Thus neural response is modeled by a point process in which \( R \) is 1 when a discharge occurs and 0 otherwise. Because spike occurrences are recorded with a finite temporal resolution \( \Delta \), the discrete cross-correlation function (or cross-correlation histogram) involves summation

\[
X = \sum R_1(i\Delta) R_2(i\Delta + \alpha)
\]

where \( i \) is the bin index. In our case the temporal resolution \( \Delta \) is 1.0 ms. As long as the temporal resolution is sufficient to represent the discharge, i.e., all interspike intervals are greater than the temporal resolution, this summation is adequate for computing the correlation function. However, to be fully generalizable to continuous responses (such as intracellular potentials or optically recorded signals), the following correlations will be expressed in terms of temporal integrals. The second correlation involves the correlation of a stimulus sequence \( S \) to a neuron's response. This process is described as reverse correlation. In the case of visual stimulation, \( S \) is a function that describes luminance in space \( x \) and time \( t \). In the reverse correlation of a spike train every spike is correlated with the stimulus that preceded the spike by an interval \( \delta \)

\[
F(x, \delta) = \sum S(x, t - \delta) R(t) dt
\]

If \( S \) does not contain significant spatial or temporal correlations (i.e., \( S \) is a pseudorandom sequence of spatially and temporally limited stimuli), this correlation accurately characterizes the first-order response kernel. For totally linear receptive fields, this first-order kernel is a complete description of the receptive field. The first-order kernel therefore provides an estimate of the receptive field on the basis of the assumption of linearity. To obtain an estimate of the BRF, which describes the stimulus sensitivity of the correlated discharge between two cells, cross-correlation is combined with reverse correlation. For simplicity the first-order reverse correlation is used here

\[
X_F(x, \delta) = \sum S(x, t - \delta) R(t) R(t + \alpha) dt
\]

Because the \( X_F \) function shows little variation over a range of \( \alpha \) on the order of milliseconds (Fig. 3), the signal-to-noise ratio of profiles based on this function can be enhanced by integrating over a range of \( \alpha \)

\[
X_{F,\alpha}(x, \delta) = \int X_F(x, \delta) d\alpha
\]

The correlated discharge profiles presented here are representations of the \( X_{F,\alpha} \) function based on simultaneous extracellular recording from two neurons. The range and resolution of \( \alpha \) and \( \delta \) are parameters of the analysis. The spike-stimulus interval \( \delta \) was varied up to a delay at which no spatial features were present (usually between 200 and 300 ms for adult cells). For the mapping of correlated discharge, the \( \alpha \) "window" was usually 16 ms in width, and it was centered on the value of \( \alpha \) at which the cross-correlation function \( X \) was maximal.
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The Xf profiles presented in this paper are based on recordings from cell pairs. Multicellular receptive fields can also be characterized for many-cell recordings. For example, if simultaneously recording from three neurons, one can compute the first-order kernel of correlated response among the three neurons

$$\text{Xf}(x, y) = \int S(x, t - \beta) R_i(t) R_j(t + \alpha) R_k(t + \beta) \, dt$$

where $\beta$ is the interval between neuron 1 and neuron 3 responses.

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