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Dynamical Representation of Stimuli by Population Activity in the Visual Cortex

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Abstract

The collective representations of stimuli in neuronal populations of cat primary visual cortex were studied. Dynamical neuronal activity distributions of population responses (population representations) were constructed from measured individual cell's responses to foveal stimuli over a defined stimulus parameter space, in our case the 2-dimensional retinal position. We used a set of "composite stimuli" based on combinations of "elementary stimuli" in order to induce and quantitatevly describe cooperative and competitive interactions. In contrast to classical approaches using optimized receptive field centered stimuli the method presented here requires the stimulation of a whole cell ensemble with an identical common stimulus. The constructed activity distribution allows a quantitative investigation of activation dynamics. We found lateral suppressive interactions to be mainly responsible for the observed nonlinear effects.

Introduction

The functional importance of cooperative effects in visual information processing gains increasing interest in both psychophysical and neurophysiological research [1,5,7,12]. Cooperativity leads to essential nonlinear effects in the information processing of sensory stimuli. Classical descriptions of cortical functions in terms of receptive fields appear incomplete in presence of strong cooperative effects [6,9,10]. Moreover, receptive field properties were shown to be highly context dependent [5], to process complex multidimensional tuning properties [11] and complex spatio-temporal transfer characteristics [2,3]. Therefore it is difficult to interprete single cells' responses with respect to their implications for the global behaviour of the neural network.

We propose to analyze nonlinear cooperative phenomena at the level of the dynamics of collective neural activation variables. We transform multineuronal data using a special *population coding* technique that was introduced for the analysis in the motor domain [4,8]. In a sensory domain population coding can be regarded as the projection of many single cells' responses to a common stimulus into a space representing the stimulus parameter of interest. Here we study population responses in cat striate cortex to describe effects of distance dependent interactions of "composite" stimuli. This allows us to compare measured dynamical population representations of these stimuli with representations calculated by superposition of representations of the corresponding single ("elementary") stimuli.

Materials and Methods

1. Electrophysiological Recordings and Visual Stimuli

In the foveal representation in area 17 of 21 anaesthetized cats 186 single units were recorded extracellularly using platinum electrodes. Stimuli were presented on a monitor (120 Hz) at a distance of 114 cm. To all neurons an identical set of flashing stimuli was presented randomly at a fixed foveal position in the visual field (*common stimuli*). These were of two types:
1) *elementary stimuli*, 8 squares (size 0.4 by 0.4°) randomly flashed along a line of 3.2° length, 2) *composite stimuli*, stimuli composed of 2 simultaneously flashed elementary stimuli separated by various distances (0.4°-2.8°), presented for 25 ms, at 0.6Hz, n presented = 32. (Fig. 1A,B). In addition, the location of the receptive fields of each individual cell as quantitatively measured with flashing stimuli (*tuning stimuli*) using the response plane technique (flashing spots of light, 0.40_ - 0.67_ diameter), randomly displayed on a grid, presented for 25 ms, at 1 Hz, presented n = 25. The receptive field (RF) center for each individual cell was defined as the location of the mximum of its smoothed RF-profile (Fig. 2A), which was obtained by mapping the response strength of individual cells onto the positions of the corresponding stimulus grid in visual space.

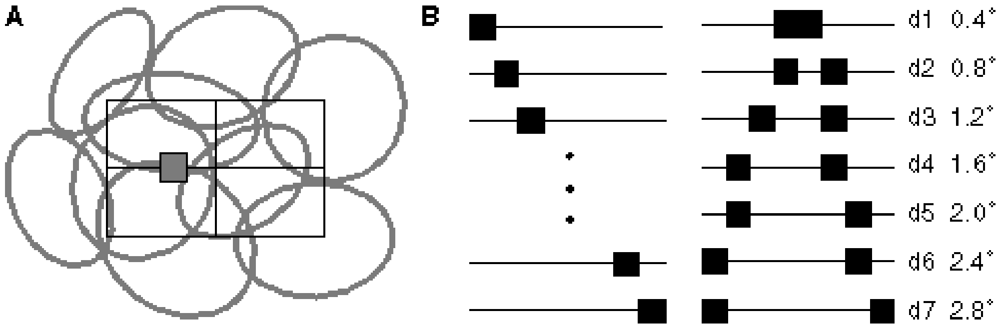

Fig. 1 A: A common stimulus (gray square) is presented within the stimulus grid irrespective of the location of individual receptive fields (gray ellipses); B: Common stimuli are presented along a line of 3.2° length; left – elementary stimuli; right – composite stimuli.

The position of the common stimuli was not changed during the entire recording session, irrespective of the receptive field location of individual neurons (non-RF-centered approach, Fig. 1A). The firing rate of a neuron to a common stimulus was defined as the average response during 32 stimulus repetitions after stimulus onset within a single time window. The individual firing rates of the cells were normalized for their maximum fire rates to all tuning stimuli during any single 10 ms time window, 0 -100 ms after stimulus onset.

2. Construction of population representations

For a given stimulus, the contribution of each cell to the population response is its normalized actual firing rate in parameter space (*x*,*y*) centered at its RF-center location (Fig. 2B). To achieve an interpolated and smooth activity distribution, spatial lowpass filtering was performed by weighting individual firing rates with a gaussian profile.

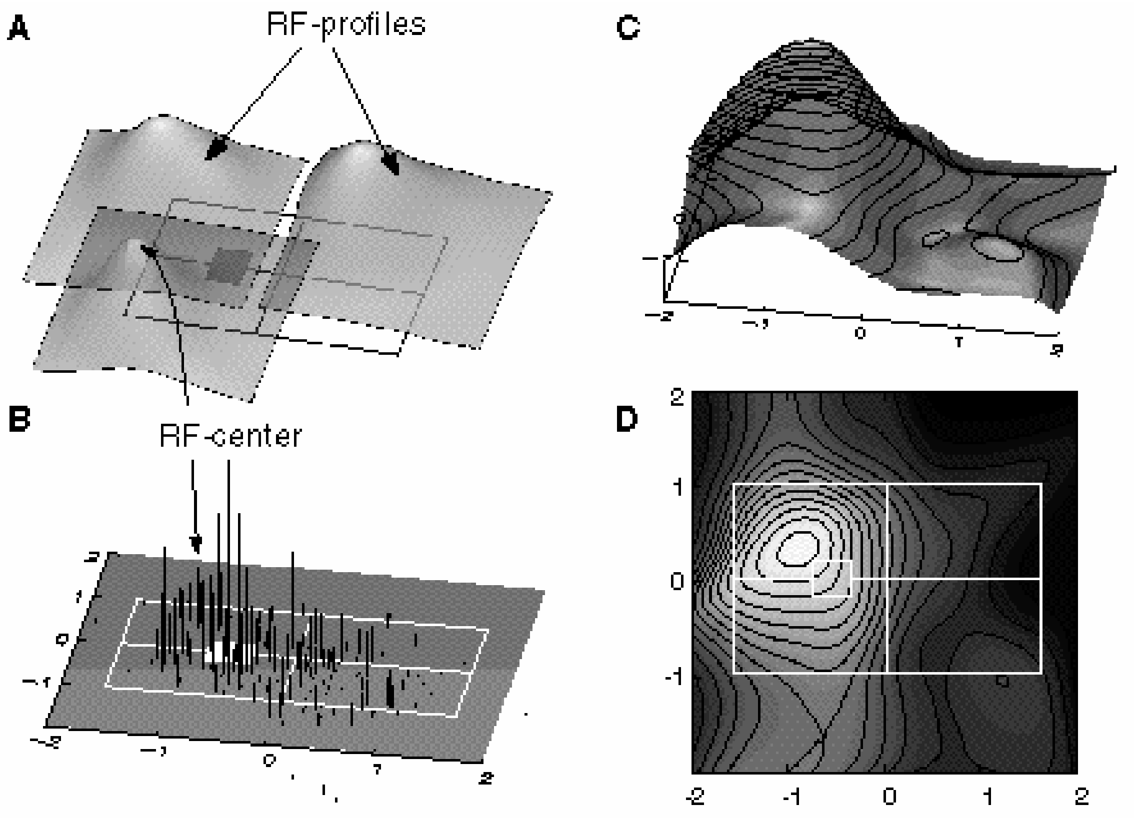

Fig. 2: Construction of a smooth, interpolated neural activity distribution in a visual stimulus space. A: RF-profiles are derived from the single cells' responses to tuning stimuli. RF-centers are defined as the locations of maxima of smoothed individual RF-profiles in the visual space relative to the common stimulus raster. The position of an elementary stimulus is indicated by a gray square within the stimulus raster; B: individual cell responses are normalized for maximum activity and placed in the visual field as delta functions according to their RF-centers (arrow), providing a raw activation distribrution. The height of the lines correspond to the response strength of individual cells to a stimulus (white square); C: the raw distribution is interpolated and corrected for sample density; D: the same data as shown in C, presented graylevel-coded in 2 dimensions. Axes indicate degrees in visual stimulus space

Thus, the contribution of each cell is given as a gaussian profile (sigma = 0.4_ in visual space) in the parameter space (*x,y*) centered at its RF-center location and with a height proportional to its actual firing rate.

To correct for sampling density, the interpolated population activity distribution is divided by a distribution equally constructed from equal individual cell activations of 1. The result is an interpolated population activity distribution taking into account irregularities in the sampling density (Fig. 2C,D).

Results

1. Elementary stimuli - representation of retinal position

a) Within activity distributions based on projections of population responses to elementary stimuli into the visual field we observe areas of raised activity close to elementary stimulus positions. The size of these areas resembles average single cell receptive field sizes (Fig. 3A). The location of maxima of activity distributions displays the actual position of a given stimulus in the visual field with considerable accuracy (mean deviation from 0.14°).

b) Studying the population representations with a "time-slice technique" revealed a gradual and coherent evolution of the activity distributions in time and space (Fig. 4A). This is remarkable in view of the complex spatial-temporal structure of the single cells' receptive fields.

c) The observed accurate reconstruction of each stimulus position is the prerequisite for analyzing interactions of the composite stimuli in terms of parametrical (retinal) space.

2. Composite stimuli

a) Nonlinear interactions were analyzed by comparing the measured population responses to composite stimuli with the calculated linear superposition of the corresponding elementary stimulus representations. The spatial structure of the activity distributions induced by composite stimuli resemble the spatial structure of those for superpositions (Fig. 3B).

b) As the most striking interaction effect we found a stimulus distance dependent suppression of the population response. It was greatest for small distances of stimulus components (Fig. 3B and Fig. 6A).

c) The temporal evolution of activity distributions for representations of composite stimuli differed from those of superimposed representations of elementary stimuli. Dependent on the distance of stimulus components, they reached their maximal activity up to 5ms earlier (Fig. 4B, Fig. 5 and Fig. 6B). This shift in the latency for maximal activity was mainly due to a delayed onset of suppressive interactions (Fig. 5). The latency of maximal suppression correlated with stimulus distance (Fig. 5 and Fig. 6B). The distance-dependent temporal evolution of suppressive and fascilitatory interactions at stimulus positions is summarized in Fig. 6C.

d) We compared activity distributions for composite stimuli and their corresponding superpositions, both normalized for their maxima, and found spatial distortions. The most prominent effects are: (1) a reduction in the size of areas with raised activity, leading to a sharpening of both activity peaks (Fig. 7) and (2) a deepening of the valleys separating the two peaks of the activity distributions.

e) The spatial distortions, like the global suppression described above, appeared with a temporal delay of several milliseconds after the onset of activity. As the onsets of suppression and spatial distortions lye within a time window of 50 to 55ms, we suggest that both interaction effects are mediated by common mechanisms.

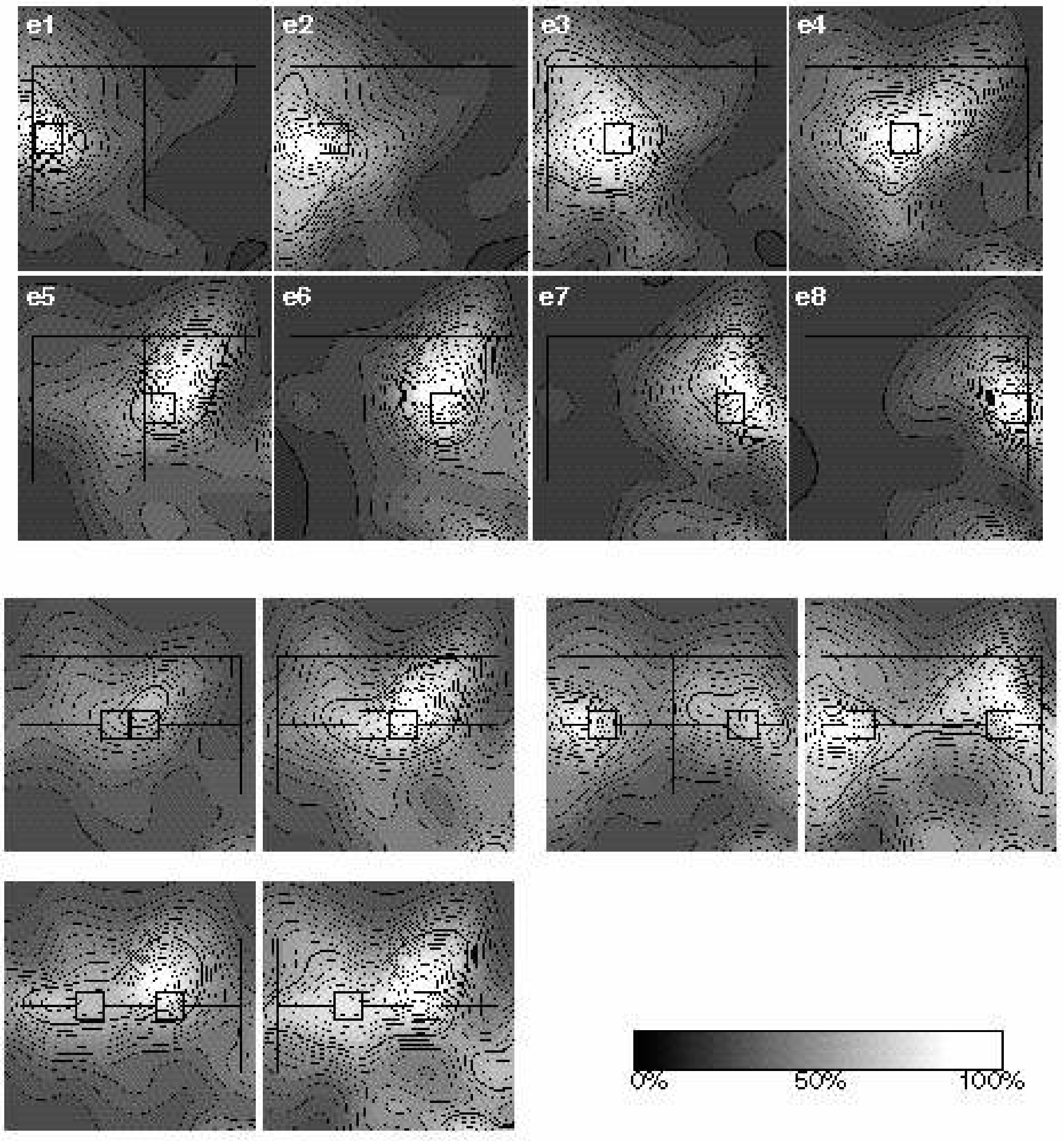

Fig. 3: Static population representations of elementary and composite stimuli, calculated by projecting and interpolating neuronal activities of 186 single units into the visual field. The graylevel-coded activity distributions are based on the summarized responses within 40-70ms after stimulus onset. The displayed visual field area covers 3.6_ by 3.6_. Activity levels are additionaly indicated by equidistant contour lines (5%-steps), with the 50%-contour-line strenghtend; A: activity distributions of elementary stimuli; B: the observed interaction effects are examplified in the comparison of measured activity distributions for four stimulus distances (d1, d3, d5, d7) and the corresponding calculated superpositions (s1, s3, s5, s7), which were obtained by superimposing activity distributions induced by their elementary components.

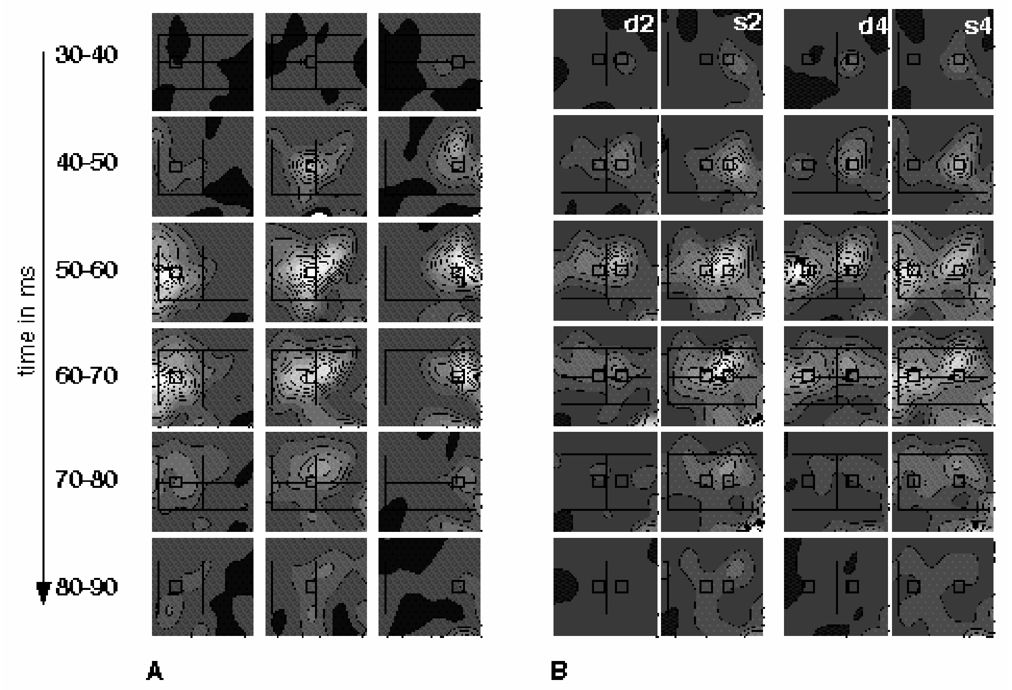

Fig.4: **Dynamic population representations in visual coordinates induced by elementary and composite stimuli; A: spatio-temporal activity distributions induced by elementary stimuli evolve coherently in time; B: comparison of the temporal evolution of the activity distributions induced by two different composite stimuli and their corresponding superpositions.**

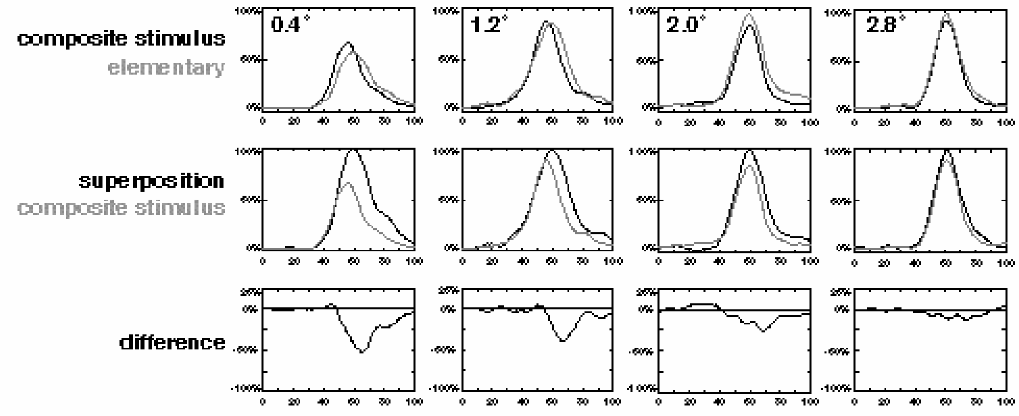

Fig.5: **Temporal evolution of amplitudes of activity distributions at stimulus location in visual space for 4 different distances during the first 100ms after stimulus onset. Upper row: composite stimuli (black) and elementary stimuli (gray); middle row: composite stimuli (gray) and the corresponding superpositions (black); lower row: difference of both curves as an indication for the degree of suppression or fascilitation.**

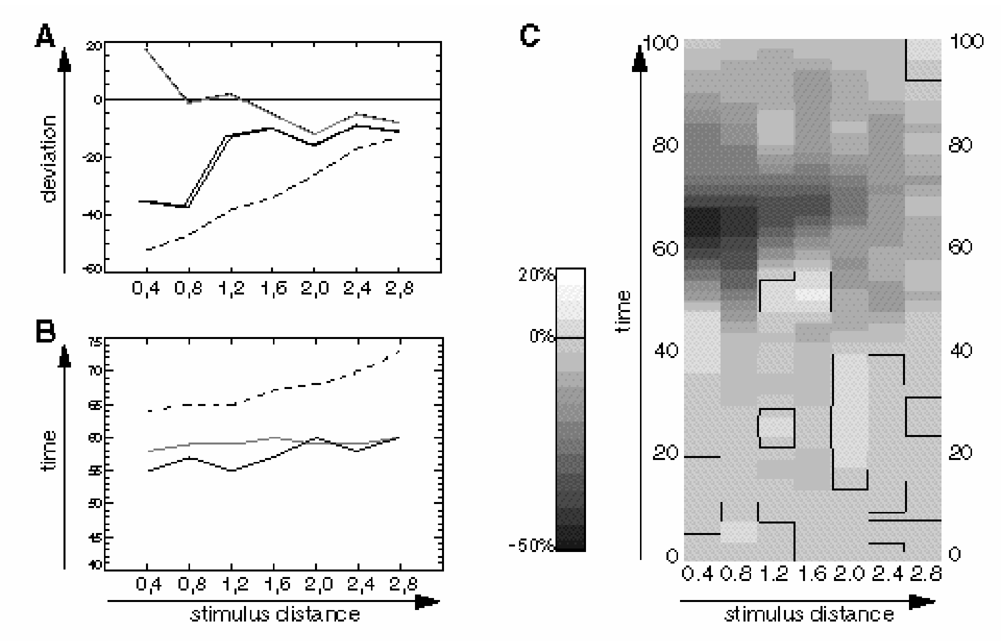

Fig.6: Dependence of various parameters on distance of stimulus components (indicated on x-axis in degree visual angle) at stimulus position; A: 1) percentual deviation of maximal response strength induced by composite stimuli from responses to elementary stimuli (gray) and their superposition (gray) and 2) maximal suppression (dashed) during the first 100ms after stimulus-onset. B: Latency of maximal response for composite stimulus (black line), superposition (gray line), and maximal suppression (dashed line). C: Spatio-temporal "interaction kernel". The temporal evolution of suppression or fascilitation of responses to double stimuli is given as the difference between the response strength

Conclusion

The population coding technique was shown to be an appropriate tool for the analysis of cortical dynamics. The method enables us to construct a collective neural activity distribution (population representation) over a defined parameter space, in our case the retinal spatial coordinates. This population representation is a projection of information distributed across a large number of neurons into a parametrical space defined for abstract variables. Therefore it specifies the meaning of the activity of single cells and their complex tuning properties to the global function in the cortex independently of the constraints of cortical anatomical maps. Even more, the population coding method displays multineuronal data in "psychophysical coordinates" and could be used to directly predict psychophysical observations from the spatio-temporal activity distributions.

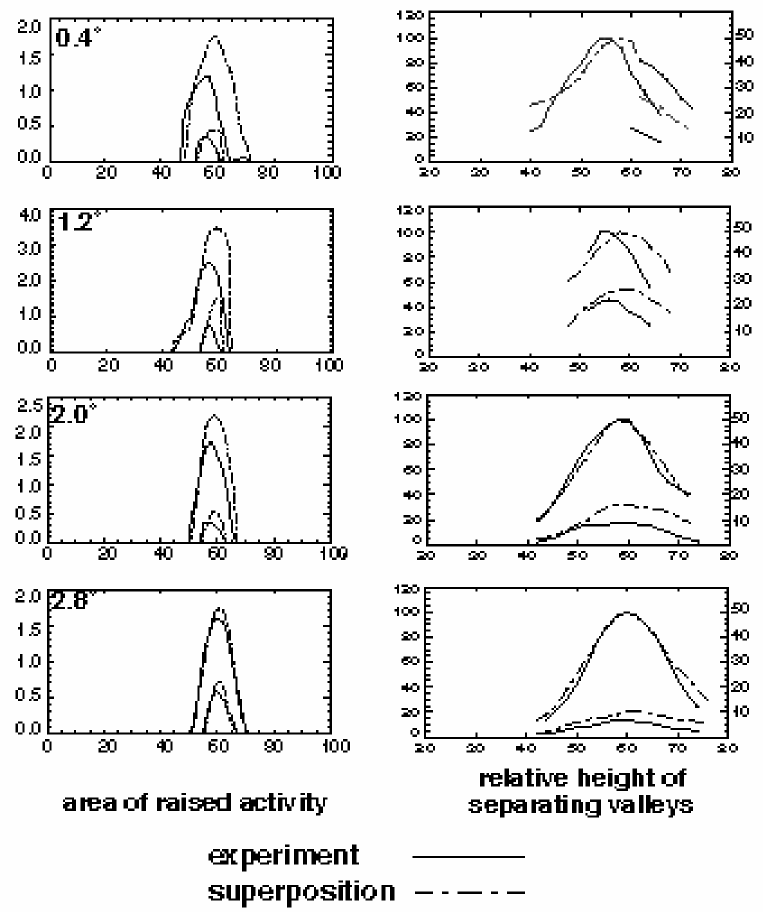

Fig.7: Spatial distortions in activity distributions for composite stimuli (experiment) compared to the corresponding superpositions (superposition) for various distances of stimulus components. The activity distributions were normalized for their maximal amplitudes. Left: Temporal evolution of the size of areas, where the amplitude exceeds 50% of the maximal amplitude (y-axis: size in square degrees). Right: Temporal evolution of the ampitude of the separating valleys between the maxima at stimulus location (left y-axis: height of the maxima at stimulus location; right y-axis: height of the valley minima in percent of the maximal amplitude at stimulus location).

The experimental paradigms have to be adapted to the population coding method. All cells of the sampled ensemble must be stimulated by identical common stimuli independently of the single cells' receptive field properties and locations in the visual field (non RF-centered approach). Stimulus parameters should not be "optimized" in order to achieve high firing rates for individual cells.

Since the population representation is compatible with neural field models, we could demonstrate that a Wilson & Cowan model [14] could accurately predict the deviations in temporal evolution of activity induced by composite stimuli in a recent paper [13]. Here we present additional spatio-temporal effects. The time course of these effects parallels the global suppression, suggesting a common mechanism. To explain the observed spatial distortions (smaller size of activated area, better separation of activity peaks), we propose long-range lateral inhibitory connections and short-range excitatory connections in parametrical coordinates. Since the lateral interactions lead to a sharpening in the spatio-temporal resolution of composite stimuli, one biological function could be a contrast gain via a gain-control mechanism [15]. The fact that the onset of the spatio-temporal interactions is delayed for several milliseconds after the onset of activity in the population representation is a strong indication for the mediation or at least induction of the observed interactions by cortical connectivity.

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