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Research Note

Spatio-temporal interactions and the spatial phase preferences of visual neurons

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Summary. We recorded single neuron responses in the cat's lateral geniculate nucleus (LGN) and visual cortex to compound stimuli composed of two sinusoidal gratings in a 2:1 frequency ratio. To probe visual receptive field symmetry, we varied the relative spatial phase of the two components and measured the effect on neuronal responses. We expected that on-center LGN neurons would respond best to gratings combined in positive cosine (bright bar) phase, while off-center LGN neurons would respond best to gratings combined in negative cosine (dark bar) phase. When drifting stimuli were used, cells' phase preferences were roughly 90 deg away from the expected values; when stationary, contrast-modulated stimuli were used, phase preferences were as originally predicted. Computer simulations showed that this discrepancy could be explained by taking into account the cells' temporal properties. Thus, tests using drifting stimuli confound the spatial structure of visual neural receptive fields with their temporal response characteristics. A small sample of data from cortical neurons reveals the same confound.

Key words: Lateral geniculate nucleus – Visual cortex – Receptive field – Spatial phase – Cat

A key question in the study of the central visual pathways has been to determine the spatial structure of visual receptive fields (Hubel and Wiesel 1962; Movshon et al. 1978a, b; Field and Tolhurst 1986). A major problem in attempting to measure receptive field profiles directly – for example, by characterizing a spatial line-weighting function – is that the task becomes too time-consuming to encourage an extensive survey of receptive field types. Furthermore, in visual cortex, measurements of complex cell subunits derived from point- or line-weighting function experiments are not even possible, since complex cells respond uniformly to flashed stimuli placed anywhere within the cell's receptive field (Movshon et al. 1978b). We set out to develop a simple method to measure the shape of cortical receptive fields. We measured the sensitivity of visual neurons to the relative spatial phase of two superimposed sinusoidal gratings that drifted across the cells' receptive fields. We reasoned that by identifying the optimal relative spatial phase of the two gratings, we could infer the shape of the underlying receptive field. Because this method does not depend on measurements of sensitivity to *absolute* phase, it could also be applied to the study of complex cells, which are insensitive to absolute spatial phase (Maffei and Fiorentini 1973). We expected that neurons would respond best to patterns whose profiles best matched the receptive field's sensitivity profile. To validate the method, we first applied it to neurons in the lateral geniculate nucleus (LGN), which are known to have even symmetric receptive fields. We expected that on-center cells would respond best when the component sinusoids were in bright bar (positive cosine) phase, while off-center cells would prefer dark bar (negative cosine) phase. The results reveal that this is true only when stationary gratings are used; drifting gratings elicit an altogether different pattern of response. A preliminary account of these results has been presented elsewhere (Levitt et al. 1987).

We recorded extracellular activity of single neurons in the A layers of the lateral geniculate nucleus (LGN) and visual cortex from acutely-prepared adult cats paralyzed with pancuronium bromide and anesthetized with sodium pentobarbital supplemented with N_2O; our methods for neurophysiological recording are detailed elsewhere (Schumer and Movshon 1984a). We presented stimuli on the face of a Hewlett-Packard 1332A display oscilloscope with a P31 phosphor and a mean luminance of 40 cd/m^2. Stimulus presentation was controlled by a PDP11 computer, which also accumulated and analyzed the data. To minimize effects of response variabili-

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ty, stimuli were presented in random order within each block of experimental trials; several repeats of each block were performed. Contrast was held constant within any one series and was generally chosen to be 50%. LGN cells were classified as on- or off-center, and then as X or Y by establishing whether the cell showed a null phase in response to stationary temporally modulated gratings (Enroth-Cugell and Robson 1966), and by the latency of response to electrical stimulation of the optic chiasm. Cortical neurons were classified as simple or complex by the criteria of Hubel and Wiesel (1962). After isolating and classifying a cell, we first measured its spatial frequency response function to determine which frequencies to use in constructing our compound grating stimuli. We selected gratings whose spatial frequencies varied from 0 c/deg (uniform field) to 10 c/deg, a spatial frequency above the resolution limit for all cells encountered. These gratings were drifted across the receptive field at a temporal frequency of 2 Hz. We Fourier analyzed averaged responses and determined the response modulation at the stimulus temporal frequency as a function of spatial frequency. We then constructed compound gratings consisting of a fundamental and a second harmonic in order to perform the phase interaction experiment. We chose sinusoidal gratings in a 2:1 frequency ratio straddling the peak of the response function, to ensure that the cell responded well to each component alone. These two component gratings were then combined in various relative phases and drifted across the cell's receptive field, generally at a rate that drifted the fundamental component at 2 Hz. Relative spatial phase was varied in increments of 45 deg from 0 through 315 deg (see Fig. 1a). To maintain a constant relative spatial phase as the gratings drifted, the temporal frequency of the second harmonic was twice that of the fundamental. The conventional method of measuring the response modulation at the stimulus temporal frequency cannot be used in this case because the stimulus always contained two temporal frequencies. Measuring response modulation at each of the two temporal frequencies would inform us of the magnitude of response to each stimulus component. However, we wanted to determine which phase condition elicited the best overall response from the cell. We therefore measured responses by computing the peak firing rate for each condition within any 32 msec time window; this particular choice of window duration did not importantly influence the results.

Figure 1a shows our stimuli and the receptive field profiles of several hypothetical neurons. A cell having an even symmetric receptive field should respond best to complex gratings whose components are combined

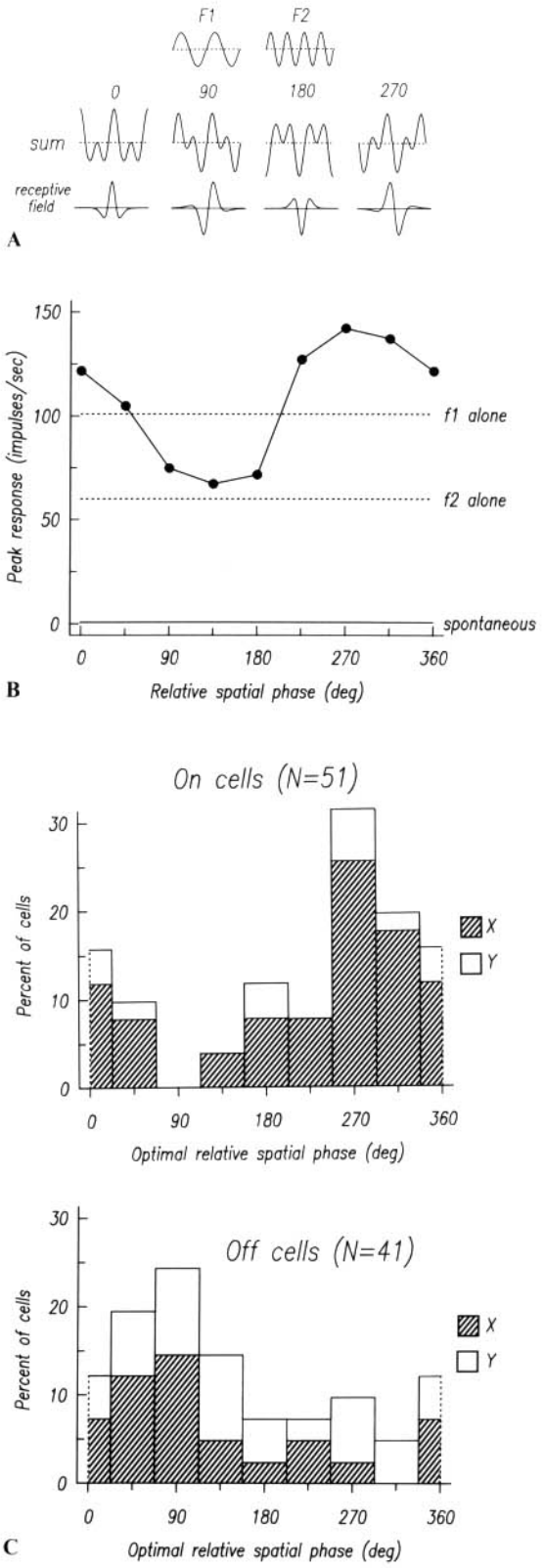


Fig. 1. A Several hypothetical receptive fields together with the compound grating stimuli which should elicit the greatest response from each. The stimulus profiles consist of two sinusoids, one having twice the frequency of the other, combined in various relative phase relations. The two individual components are shown at the top of the figure. Each column, labeled at the top with the relative spatial phase (in deg) of the components, shows the sum of the two individual components and the corresponding "optimal" receptive fields. **B** Response of an on-center LGN cell to drifting compound gratings that differ in the spatial phase offset between the individual component gratings. The response of the cell to each component presented alone, and to a blank screen of the same mean luminance as a measure of spontaneous activity, is also shown. Here the response measure is *peak* response (see text). **C** Histograms showing the distribution of optimal relative spatial phases of LGN cells. On and Off cells are plotted separately, and each graph is further subdivided into X and Y cells

in *cosine* phase, so that the luminance peaks of the components are aligned with the peak of the sensitivity profile (first and third columns). A cell having an odd symmetric receptive field should prefer components combined in *sine* phase, so that the zero-crossings of the components are aligned with the zero-crossing of the sensitivity profile (second and fourth columns). Cells having receptive fields that are neither strictly even nor odd symmetric should prefer components combined in some intermediate phase. The luminance profiles of the composite grating stimuli we used in these experiments are also shown in Fig. 1a. LGN receptive fields are known to be even symmetric, so we predicted that on-center cells would respond best to components combined in positive cosine phase (0 deg relative phase), while off-center cells would respond best to components combined in negative cosine phase (180 deg relative phase).

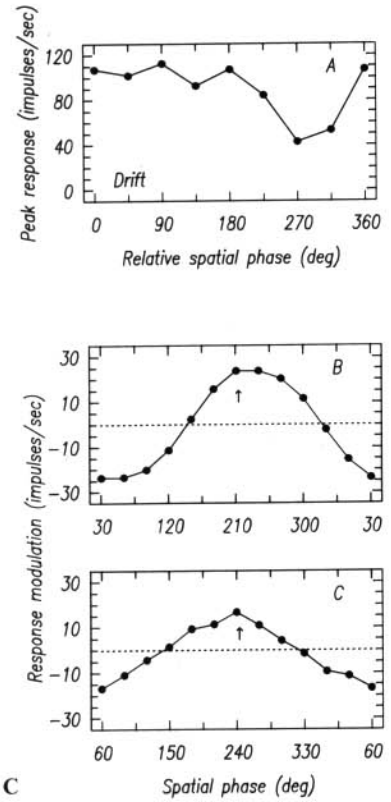
Full quantitative data were obtained for 92 LGN cells recorded from 6 cats; all cells could be unambiguously identified as X or Y. Figure 1b illustrates the way in which an LGN cell's peak response was affected by changing the relative phase of the second harmonic component of the stimulus. The horizontal dashed lines indicate the responses elicited by the two component gratings presented alone. The responses of this cell were clearly affected by the relative phase of the component gratings, but the preferred phase was roughly 270 deg, 90 deg away from the expected value of 0. This behavior was seen consistently in our population of LGN cells. Figure 1c plots the distributions of phase preferences for all the on-center (top) and off-center (bottom) cells we studied. The distributions are rather broad, and are centered around 270 and 90 deg, about 90 deg away from the expected values of 0 for on-center cells and 180 for off-center cells (On cells: mean = 291.3, S.D. = 59.6, $N = 51$; Off cells: mean = 76.9, S.D. = 67.0, $N = 41$). There are no apparent differences between the distributions of X and Y cell preferences.

Despite the variation in phase preferences, these distributions are clearly peaked, and peaked at values different from the expected ones. Confronted by these unexpected data, we sought factors which could have been responsible for the anomalous phase preferences encountered. We initially thought that an imbalance in the strength of the cell's responses to the two grating components might affect spatial phase preferences. However, examination of the data indicated that spatial phase preferences were not systematically related to the strengths of the responses elicited by each of the two components.

To determine the effect of temporal factors on neural phase preferences, we presented some units with the same compound grating stimuli as before, but rather than drifting them across the receptive field, we used stationary stimuli whose contrast was modulated in time either by a sine wave or a square wave. All stimuli were modulated at the same temporal frequency, generally 2–4 Hz. The absolute spatial phase of each component grating was varied independently with respect to an arbitrary point on the display screen. The phase of the lower frequency component (F_1) was shifted in 30 deg increments from 0 through 150 deg, and the phase of the higher frequency component (F_2) was shifted in 30 deg increments from 0 through 330 deg. Since these were phase-reversing gratings, we needed to vary the absolute phase of the F_1 component through only 150 degrees to present all stimulus conditions to the cell. Responses to stimuli in which the absolute phase of F_1 lies in the range 180 deg to 330 deg are simply the inverse of responses to stimuli where the F_1 absolute phase lies between 0 deg and 150 deg, i.e. responses occurred in the second half of the stimulus cycle instead of the first. In this way all relative phase combinations varying in 30 deg steps from 0 to 330 deg were each presented at 12 different absolute positions across the receptive field. From the resulting data matrix, we extracted the response to each *relative* phase condition at each of several *absolute* positions within the receptive field, and determined the overall best response for each relative phase condition. In addition, we measured responses to each component grating alone in order to compare the results of the compound grating experiment with synthesized predictions. These stimuli contain only one temporal frequency, and are therefore immune from the possible complication of our compound stimuli containing more than one temporal frequency.

Figure 2 shows results from another LGN unit. When tested with the drifting stimulus, the off-center cell had its peak response at a relative phase of 90 deg – again 90 deg away from the expected value (Fig. 2a). The remaining panels of Figure 2 illustrate results from the experiment using contrast-modulated stimuli. The *absolute* phase values are given with respect to an arbitrary reference point on the edge of the display screen. We have rotated these plots to put the peak responses in the middle of each, but each component's absolute spatial phase is still measured from the same arbitrary reference point. Figure 2b, c shows the cell's responses to each individual component as a function of absolute spatial phase. Responses varied regularly with spatial phase, as expected. The arrows indicate the spatial phase of each grating that elicited the greatest response – 210 deg for F_1 and 240 deg for F_2. If this cell were simply summing the responses to each component alone, then one would predict that the overall best response elicited from this cell would occur when each component is positioned at its optimum, and the data show this to be true. In Figure 2d we have plotted a perspective view of the surface showing the cell's responses to all compound stimuli. The X and Y axes represent the absolute spatial phase of the two component gratings, and the Z axis represents response magnitude. Figure 2e is a contour plot of the same response surface. When presented with the compound stimuli, this cell's responses were clearly modulated as the phase of F_1 varied, but much less modulation of responses was seen as F_2 varied. Presumably this was due to response saturation; in the presence of F_1 the absolute spatial phase of F_2 was less important in modulating cell response. However, these plots show that the *relative* phase between components did change cell responses.

In these plots, diagonal lines having a slope of 2 indicate stimuli of constant *relative* phase, but successively increasing *absolute* phase. We determined the peak



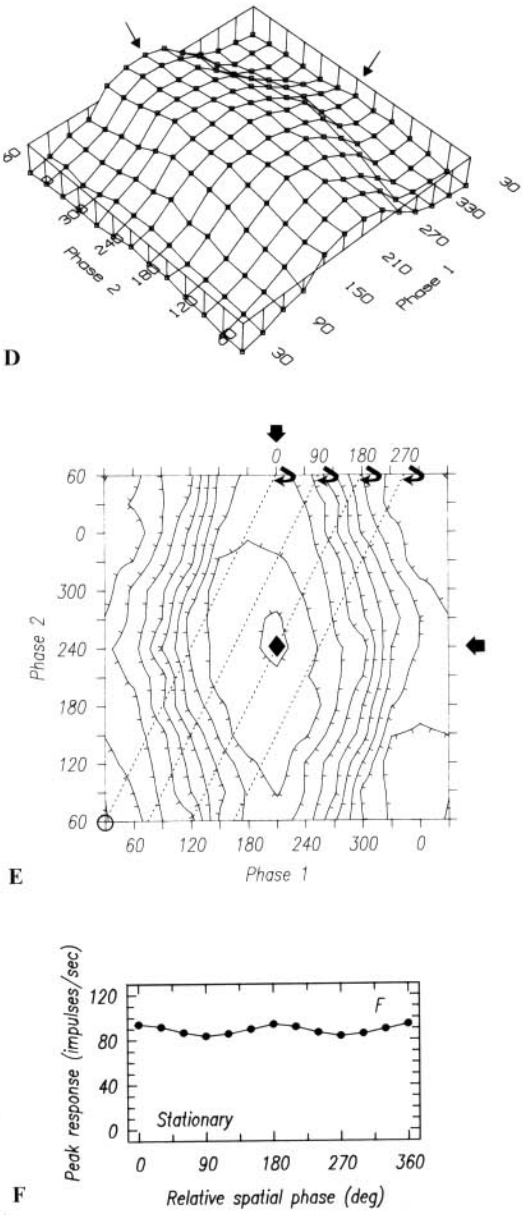


Fig. 2. A Response of an LGN cell to drifting compound gratings as the spatial phase offset between the components was varied. **B, C** Response of this unit to each component presented alone using stationary contrast modulation. Each component was presented at several different *absolute* spatial phases (positions) across the receptive field. We also measured the temporal phase of response; negative responses are those occurring in the second half of the stimulus cycle. Response amplitudes to the 0–180 conditions are the same as to the 180–360 conditions except for a 180 degree shift in the *temporal* phase of response. The arrows indicate the spatial phases at which the best responses occurred. **D** Responses elicited by compound stationary contrast-modulated stimuli. The spatial phase of each component was varied independently so that all relative phase combinations were presented to the cell. The data are presented in a three-dimensional perspective view. The height of the surface above and below the base plane represents response magnitude; the peak modulation was 24 impulses/s. Arrows indicate the optimal phases for each component when presented alone. **E** Is a contour map of the data shown in **D**. Lines denote constant surface height, or iso-response levels, derived from the data shown in **D**. Contour lines are spaced at intervals of 10% of the maximum modulation. Ticks point "downhill" toward lower response levels. The dashed lines having a slope of 2 indicate stimuli of constant *relative* phase, but successively increasing *absolute* phase; the labels at the top show the relative phase for each line. Since the periodicity of F_2 is twice that of F_1, F_2 must be shifted 60 deg in absolute phase when F_1 is shifted 30 deg in order to maintain a constant relative phase offset between them. Bold arrows indicate the optimal absolute phases for each component. **F** Shows the peak response for each relative spatial phase condition from the contrast-modulation experiment. We determined the peak response for each relative phase condition by picking the maximum response along each diagonal line in the stimulus matrix shown in **D, E** and then finding the peak firing rate within a 32 ms time window for that stimulus condition

response for each relative phase condition by picking the maximum response along each diagonal line in the matrix and then determining the peak firing rate in that stimulus conditions as before. We then plotted this peak response for each relative phase condition in Figure 2f. The cell's responses as a function of relative phase match our expectations about the spatial organization of the receptive field. The stimuli at cosine phase (0 and 180 degrees relative phase) elicited the best responses, while the stimuli at sine phase (90 and 270 degrees relative phase) elicited the smallest. These figures show that the best response is indeed produced when each of the two components is positioned at its own optimal phase, again indicated by the arrows. Furthermore, it is apparent that the largest responses – denoted by the open circle and the diamond in Fig. 2e – correspond to the 0 and 180 degree relative phase conditions, which is what we had originally predicted for even symmetric LGN cells.

Thus, identical stimuli that differ only in their tempo-

ral characteristics can elicit different responses and therefore lead to different conclusions when inferring the spatial organization of receptive fields. It is clear that when drifting stimuli are used, the *spatial* organization of the receptive field becomes confounded with the *temporal* character of the stimulus. To explore the nature of this confound, we used computer simulations from the *SIMPLE* model of Schumer and Movshon (1984b). *SIMPLE* was designed to model simple cortical cells responses, so we made parameter changes appropriate to the measured spatial and temporal characteristics of LGN cells.

The *SIMPLE* model neurons gives responses determined by the independent convolution of the stimulus with spatial and temporal filters that simulate measured receptive field properties.The model is linear throughout, except for a threshold nonlinearity that rectifies responses. The line-weighting function is modeled as a difference-of-Gaussians function, and the temporal response of the cell is modeled using a formulation taken from Bergen (1979). The model calculates responses as follows. At each instant of the stimulus presentation cycle, the sum is taken across space of the cross-product of the spatial stimulus and the spatial receptive field. This is the spatially integrated response of the modelled cell as a function of *time*. This temporal function is then convolved with the temporal impulse response function of the cell. The result of this operation is subjected to a threshold to eliminate all values less than some specified value. This then is the final response of the simulated cell, which reflects the product of separate and independent spatial and temporal filters.

We first simulated the responses of cells with even symmetric receptive fields and rather transient temporal responses, typical of most LGN cells. These simulations also produced phase preferences that were shifted 90 deg away from the expected values. Further simulations demonstrated that the optimal relative spatial phase shifted as the temporal response properties of the cell were altered. The optimal relative phase of simulated on-center cells approached our originally predicted value of 0 degrees as the temporal response of the model cell was made more sustained (low-pass temporal filtering). The optimal relative phase approached a value 90 degrees away from that as the temporal response was made more transient (band-pass temporal filtering). However, in simulations of contrast-modulation experiments, we found that the phase preference was independent of the temporal response properties when stationary stimuli were used, in agreement with our experimental data (as in Fig. 2). Therefore, when drifting stimuli are used, the measured phase preference depends both on the spatial structure of the receptive field and on the temporal characteristics of the cell's response.

When we made similar measurements in cortical neurons, we obtained similar results. In 5 of the 6 neurons for which we measured phase preferences with both drifting and stationary stimuli, the optimal relative phase varied depending on whether drifting or stationary stimuli were used. This suggests that cortical neurons are subject to the same confound as LGN neurons. Previous investigators (Henry and Bishop 1972; Schiller et al. 1976) have also shown the dependence of spatial receptive field maps on the temporal nature of the stimuli used. This spatiotemporal confound, whose origin and consequences we have explicitly demonstrated, and which earlier work implicitly suggested, is untreated in other recent work. Pollen et al. (1988) also utilized compound grating patterns as a probe of receptive field symmetry in simple cells. They claimed that in all 9 simple cells from which they recorded, the optimal relative phase condition could be predicted by merely examining the cell's line-weighting function. However, their claim that simply inspecting the receptive field profile permits them to predict the component phase offset leading to the greatest peak response should be taken with caution, as apparently no attempt was made to correct for the effects of temporal frequency. The results of Gaska et al. (1987) concerning the spatial structure of the constituent subfields of complex cells are similarly suspect. Because the *temporal* response characteristics of neurons contribute importantly to their preference for *spatial* phase when drifting gratings are used, we conclude that this type of method is not sufficient, when applied alone, for measuring the spatial structure of visual receptive fields.

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