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Research Note

Intra-cortical Inhibition Prevents Simple Cells from Responding to Textured Visual Patterns

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Summary. Evidence is presented that simple cells in the cat striate cortex (area 17) fail to respond to two dimensional random patterns but respond vigorously to one dimensional patterns with identical power at the preferred orientation of the cell. Further observations suggest that complex cells inhibit simple cells so as to permit them to respond selectively to one-dimensional stimuli. Implications for the role of this inhibition in visual analysis are discussed.

Key words: Visual cortex – Simple cells – Complex cells – Random visual patterns – Orientation tuning – Intracortical inhibition

It is known that, whereas complex cells respond well to two dimentional textured patterns, simple cells do not (Hammond and MacKay 1975, 1977; Orban 1975; Hoffmann and von Seelen 1978). Here we confirm and extend these observations by showing that simple cells, unresponsive to a two-dimensional textured patterns, respond well to a one-dimensional pattern which is, in a Fourier sense, contained within the two-dimensional pattern. We furnish evidence that each simple cell is prevented from responding to the one-dimensional component of two-dimensional patterns by intra-cortical inhibition from cells tuned to orientations outside the selectivity band of the simple cell. The function of this inhibition may be to permit simple cells to respond selectively to one-dimensional structures, such as the contours of visual objects.

We have studied 70 simple and 56 complex cells, recorded from 19 adult cats. Under halothane anaesthesia, an endotracheal tube and venous cannula were inserted, and a small piece of skull and dura overlying cortical area 17 were removed. The cat was then immobilized with Pavulon (injected intra-venously) and artificially ventilated with 70% N_2O and 30%. O_2. EEG, body temperature, and heart rate were continuously monitored, and when judged necessary, the anaesthetic was supplemented with halothane. After dilating the pupils with atropine, optically neutral contact lenses with 4 mm pupils were applied to both eyes and refraction corrected with additional lenses if necessary. Action potentials were recorded from single units with glass micropipettes and analysed on line by a Digital PDP-11/03 laboratory computer. On isolating a unit, we determined its preferred orientation and classified it as simple or complex, using the standard hand plotting technique and classification procedure of Hubel and Wiesel (1962). Hypercomplex, or end stopped, cells were rejected. The visual stimuli were oriented appropriately and positioned to fill the receptive field of the preferred eye, the other eye being occluded. Figure 1A illustrates the two-dimensional (2-D) and the one-dimensional (1-D) textured patterns used as visual stimuli. Both patterns were generated on an oscilloscope face under the control of a PDP-11/03 computer. The 2-D pattern comprised 800 randomly positioned spots of light caused to drift in the direction orthogonal to the cell's orientation preference by periodic displacement of all the points every frame. The 1-D patterns was constructed from the 2-D pattern by "vertical smearing": it comprised 800 randomly positioned parallel lines, produced by replacing the computer driven Y-input with a fast (3 MHz) triangular-wave raster, and the unblanking pulse Z-input with a DC voltage adjusted so that the mean luminance, and hence the horizontal power spectrum, was the same for both patterns. (Equality of the two spectra was also confirmed by photometric measurement of the light distributions of the patterns.) Contrast was varied by a system of crossed

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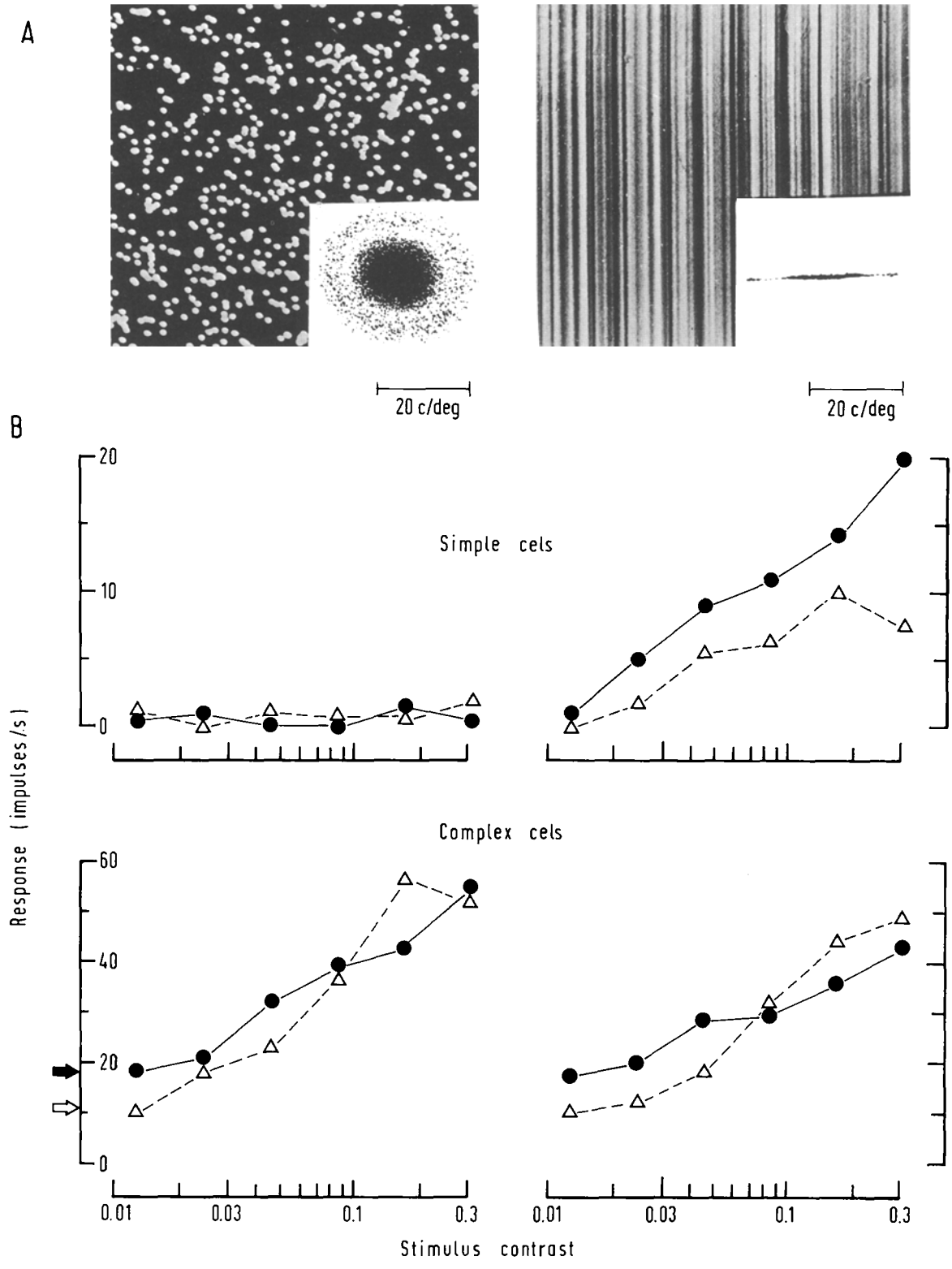

Fig. 1. A Example of the two-dimensional (left) and one-dimensional (right) random visual patterns. The insets show the Fourier transforms of the two stimuli (obtained by optical means). Note that whereas the two dimensional pattern has energy at all orientations, the one dimensional pattern has energy only within a narrow band of orientation, but at this orientation the energy of the two patterns is identical. **B** Response of two representative simple (upper) and two representative complex (lower) cells to 2-D (left) and 1-D (right) random patterns as a function of pattern contrast (defined as the ratio between standard deviation and the mean of luminance distribution). The arrows indicate the spontaneous activity of the complex cells. The stimuli drifted orthogonally to the cells' preferred orientation at a velocity chosen to elicit maximum response for the 1-D pattern (although the effect held at all velocities to which the cell responded). To avoid any systematic bias of non-station ariness, measurement to 1-D and 2-D stimulation were alternated

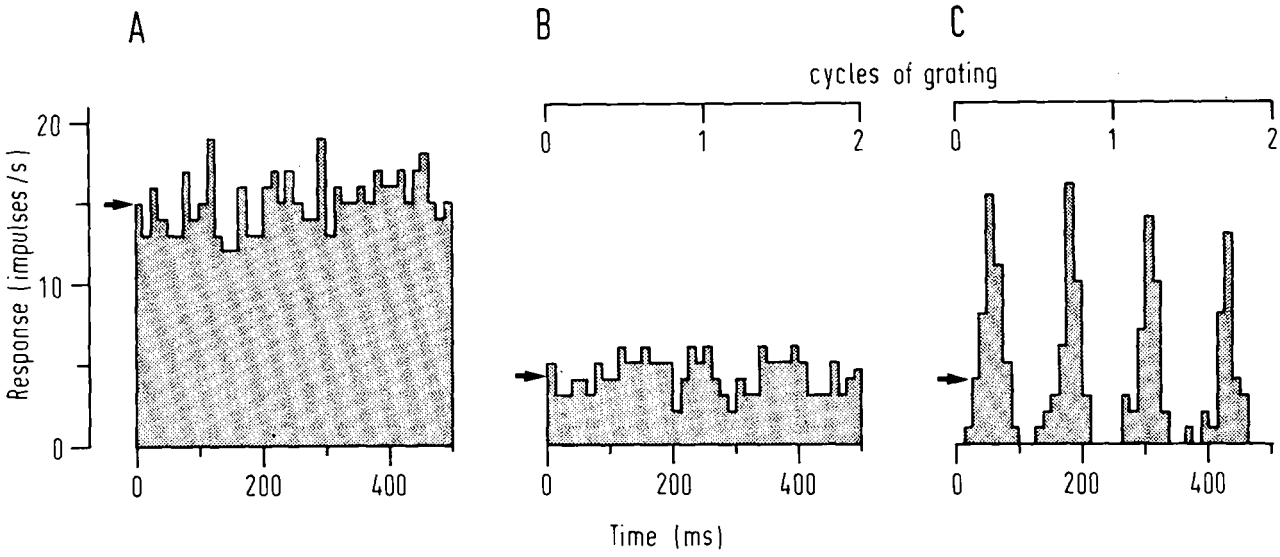

Fig. 2A–C. Effect of non-optimal oriented stimuli on the response of a representative simple cell. Using a beam-splitting prism to superimpose optically two oscilloscope faces, the cell was stimulated simultaneously with two patterns: a 1-D random pattern of preferred orientation (to elicit a response) and a sinusoidal grating oriented orthogonally to the noise. The three PSTHs show the cell response to a random pattern superimposed on: **A** A blank field of matched luminance; **B** an orthogonal sinusoidal grating of 0.5 cycles/deg (the optimal spatial frequency of the cell) and 50% contrast, caused to drift at 4 Hz (8 deg/s); **C** the same grating as **B**, but caused to alternate in counterphase at 4 Hz. Each record is a 500 ms (two cycles of grating) response histogram, synchronized to the modulation of the grating. The arrows indicate the mean response (sum 100, binwidth 12.5 ms)

and rotating polaroids, which selectively mixed the random patterns with a blank field of matched mean luminance (10 cd/m^2), optically superimposed on the noise by means of a beam-splitting prism.

Figure 1B reports representative results of simple and complex cell responses to stimulation by the random patterns. In agreement with previous observations (Hammond and MacKay 1975, 1977; Orban 1975; Hoffmann and von Seelen 1978), all complex cells responded to 2-D patterns, while the simple cells remained virtually silent. However, both simple and complex cells responded well to 1-D random pattern. While 2-D patterns of maximum contrast failed to elicit a response from simple cells, comparable 1-D patterns of 1/10 this contrast evoked a measurable response.

This result is surprising since the 1-D pattern has no greater contrast modulation in one dimension than the 2-D pattern from which it derives, and is, in effect, contained within the 2-D pattern (see inset of Fig. 1A). Or, to express the same concept another way, the power spectra of the lengthwise integral of the two patterns is identical (as one pattern was constructed by integrating and smearing the other). As simple cells integrate spatially along their long axes when lines are used as stimuli (Hubel and Wiesel 1962; Henry et al. 1974), the question is what prevents the integration of 2-D textured patterns?

Many investigators (Benevento et al. 1972; Bishop et al. 1973; Blakemore and Tobin 1972; Watkins and Berkley 1974; Creutzfeldt et al. 1974; Sillito 1975; Tsumoto et al. 1979; Sillito et al. 1980) have suggested that cortical cells differing in orientational tuning inhibit one other. As the 2-D patterns contain energy at all orientations (see Fig. 1A), it is conceivable that they will stimulate a large pool of cells of different orientational tuning, and that these cells will in turn inhibit the simple cell. Here, with a relatively simple technique, we measure directly the magnitude of "cross orientational inhibition" and show that it is sufficiently powerful in simple cells to provide a plausible mechanism to prevent them from responding to textured patterns.

Using two cathode ray oscilloscopes, we simultaneously stimulated simple and complex cells with two one-dimensional patterns: optimally oriented one-dimensional noise to elicit a response and a non-optimally oriented sinusoidal grating to inhibit it. The use of noise patterns together with gratings avoided phase problems. Figure 2 summarizes some results obtained from a typical simple cell. Comparison of the average discharge of records a and b clearly shows that the grating at non-preferred orientations greatly reduced the cell firing rate. The inhibition was of comparable strength when the sinusoid was rotated to any orientation to which the cell itself did not respond, and was very broadly tuned for spatial frequency, implying that it arises not from a single cell, but from a pool of cells of various orientation and size preferences. The response of

complex cells was also attenuated in a similar manner, but typically to a much lesser extent.

Note also the patterning of the discharge records of Fig. 2. While an orthogonal drifting grating produces a uniform, unmodulated depression in the discharge rate (record b), an orthogonal counter-phase alternating grating not only depresses the mean firing rate, but also causes the response to modulate at twice the temporal frequency of the stimulus (record c). Second harmonic modulation to counter-phase alternating gratings and failure to modulate to drifting gratings, here observed in the pattern of inhibition of simple cells, is characteristic of the pattern of excitation of complex (but not simple) cortical cells (Maffei and Fiorentini 1973; Movshon et al. 1978). This result is consistent with previous suggestions (Singer et al. 1975; Creutzfeldt et al. 1975; Hammond and MacKay 1978; Lennie 1980) that the inhibition arises principally from complex cells. Thus we propose that simple cells fail to respond to 2-D random patterns because these patterns, which contain energy at all orientations and spatial frequencies, excite not only the simple cell but also a pool of complex cells whose combined inhibitory drive annuls the excitatory geniculate drive, and hence silences the cells.

What can these result tell us about the role of simple and complex cells in the analysis of visual information? An idea which has recently gained much popularity is that visual cortical cells, particularly simple cells (with their narrow orientation and spatial frequency tuning), serve to perform a two-dimensional analysis of the visual scene, somewhat akin to a Fourier analysis in two dimensions (Ginsburg 1977; De Valois and De Valois 1980). However, any theory of this sort relies on the implicit assumption that cortical cells integrate spatially along their long axis, an assumption we have shown to be invalid (at least for cat simple cells). Such a non-linearity would severely hamper not only a Fourier analysis, but any form of global two-dimensional pattern analysis. However, it should be noted that inhibition from non-preferred orientations, a clear impediment to two-dimensional analysis, would not necessarilly impede a local one-dimensional analysis (Robson 1975; Maffei et al. 1979). Furthermore, it could serve to render simple cells selectively sensitive to visual contours, by suppressing spurious responses to textured patterns. Indeed, Hoffmann and von Seelen (1978) have shown that simple cells respond reliably to a bar embedded in visual noise at much lower signal-to-noise ratios than complex cells.

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