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RAPID PUBLICATION

Latency: Another Potential Code for Feature Binding in Striate Cortex

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SUMMARY AND CONCLUSIONS

1. We recorded the responses of 37 striate cortical complex cells in fixating monkeys while presenting a set of oriented stimuli that varied in contrast.

2. The two response parameters of strength and latency can be interpreted as a code: the strength defines the stimulus form (here the orientation), and the latency is more a function of the stimulus contrast.

3. Synchronization based on latency could make a strong contribution to the process of organizing the neural responses to different objects, i.e., binding.

INTRODUCTION

Neurons send messages to other neurons by the use of the rate at which they generate action potentials, which is often referred to as the strength of the response. However, there is increasing evidence that the variation of the firing rate over time can also be used to transmit information independently of strength (Richmond et al. 1987), although how this temporal modulation of the firing rate should be interpreted is not clear. We find that for striate cortical complex cells the response strength is primarily driven by the orientation of a stimulus. On the other hand, the response latency, although related to both orientation and contrast, is more strongly a function of the stimulus contrast.

If the neuronal responses to an edge defined by one contrast all started at one time, and the neuronal responses to another edge defined by a different level of contrast started at a different time, then this could be a very strong signal to the rest of the nervous system about which parts of the visual scene should be processed together. It has been suggested that low-frequency oscillations of spike firing contribute to binding the responses of visual system neurons that are responding to different parts of a single object into a single percept (Eckhorn et al. 1988; Gray and Singer 1989). Combining these results with ours, we now raise a more general possibility: the response strength encodes information about the localized features in a scene, whereas temporal variation carries information that is used to help solve the binding problem.

METHODS

We anesthetized two rhesus monkeys with halothane and prepared them for single-unit recording by implanting a recording chamber over striate cortex and a coil of stainless steel wire under Tenon's capsule of one eye to monitor eye position with the use of the magnetic field/search coil technique (Judge et al. 1980). The monkeys were rewarded with juice when they maintained fixation within ±0.3° of a fixation spot. The optimal combination of position, orientation, and width was found for black and white bars. A neuron was classified as complex if its responses to black and white bars were approximately equal, and the responses remained strong as the optimal width bar was translated across the excitatory region of the receptive field. Only oriented neurons, where the maximal response was at least twice the minimal response for at least one level of contrast, were studied here. It makes no sense to study the interaction between orientation and contrast in neurons that are insensitive to orientation.

We carried out the experiments using a standard set of stimuli. For each of 12 orientations (0–180° in 15° increments) there were four white (contrasts: 78%, 34%, 10%, and 5%) and four black (contrasts: 94%, 48%, 19%, and 9%) bars. Contrast was defined as $(max - min)/(max + min)$, where *max* and *min* are the maximum and minimum luminances, respectively. The bars were 1.75° long and 0.15° wide, longer than the maximum extent of the largest receptive field and narrower than the minimum extent of the smallest. The luminance of the background was 1.94 cd/m^2. The stimuli were presented on a video monitor running at 60 Hz. The luminance of each gray level used was checked at the specific position on the screen at which stimuli were presented with a Minolta CS-100 spot photometer. Video timing and synchronization was checked by taping a photocell to the video screen and feeding the electrical output into the data acquisition system. The stimuli were presented in random order for 200 ms each on the receptive fields of the neurons ≥10 times each.

The shortest latency seen under these conditions was 34 ms, so we calculated the average number of spikes between 30 and 200 ms after the stimulus appeared. The individual spikes were convolved with a Gaussian waveform (σ = 5 ms) and averaged over all trials (Heller et al. 1995). The time when the response waveform was at half peak defined the latency. If half peak was not at least twice the spontaneous activity during the 50 ms preceding stimulus onset, the latency was left undefined. This method of quantifying latency was chosen both to avoid the extreme variability of trying to quantify the latency for very weak responses and to avoid the logical paradox of trying to define a latency for responses that were statistically indistinguishable from zero.

We believe that these cells were located in the supragranular layers because they were all found within 700 μm of the cortical surface, and were superficial to a layer with units that were spontaneously active in the dark, a characteristic of layer 4c (Lund et al. 1976; Poggio et al. 1977). All of the receptive fields were ~5° away from the fixation spot, and ranged from 1.5 × 0.9° to 0.8 × 0.6° in extent.

RESULTS

We recorded 37 complex cells from two monkeys. All of the cells displayed significant orientation tuning, with the ratio of the strongest to the weakest responses at the highest contrast varying from 2.2 to 47.2 (12.8 ± 0.04, mean ± SE). For all of the cells, decreasing the stimulus contrast at the optimal orientation caused large increases in response latencies, with only modest effects on the response strength (Fig. 1, *top 4 rows*), whereas holding the contrast fixed and moving away from the optimal orientation caused the response strength to decrease while leaving the response latency almost unchanged

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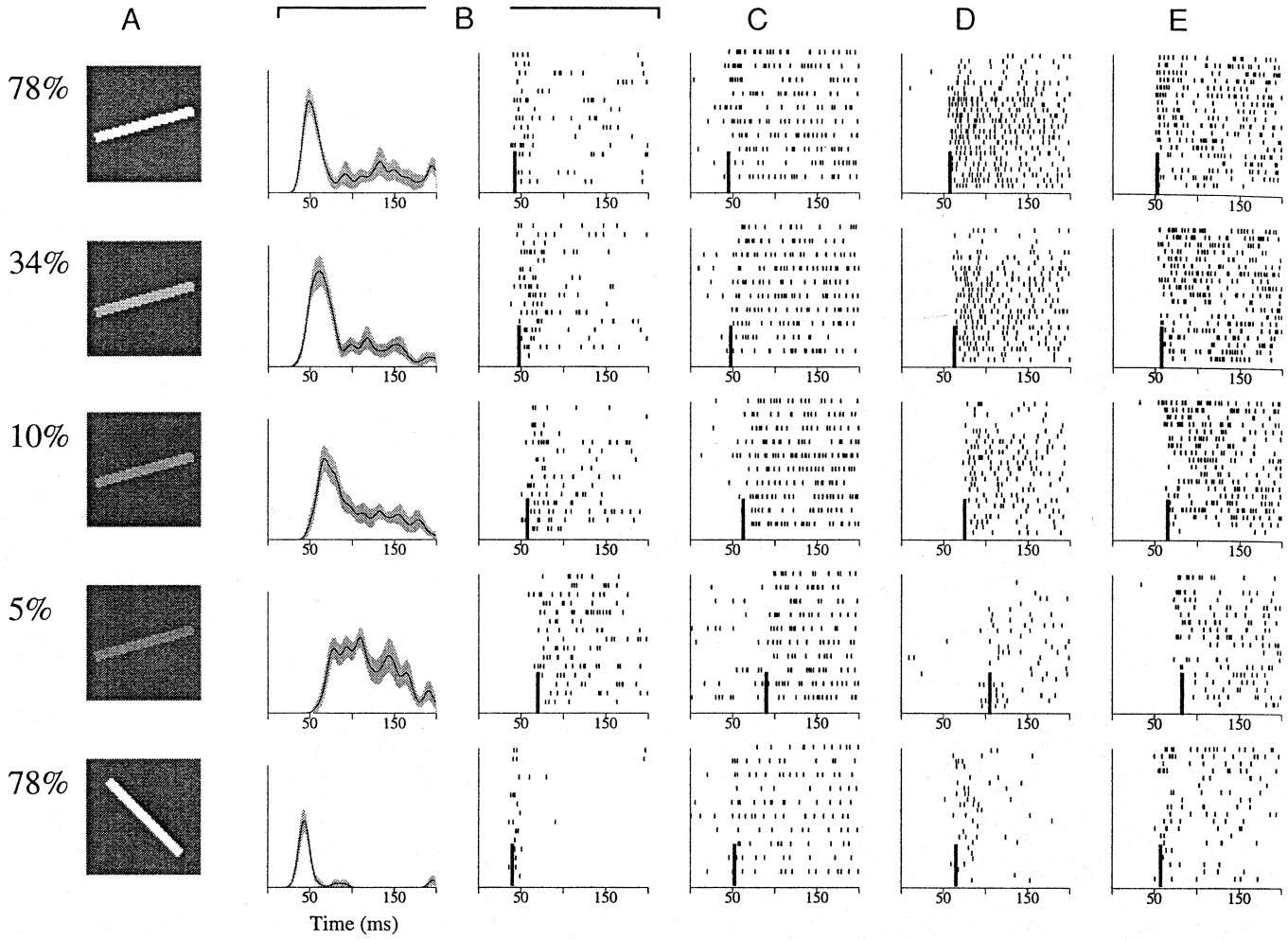

FIG. 1. Example data from 4 neurons. *Top 4 rows*: data taken at the optimal orientation for the white bars at 4 levels of contrast (see *far left*). *Bottom row*: data at the highest contrast (same as the *top row*), for a nonoptimal orientation. *A*: representations of the specific stimuli for the responses of the neuron shown in *B*. Responses in *B* are shown both as rasters, in which each dot is a single action potential and succeeding lines are different trials, and as spike-density waveforms (see text), in which the mean ± SE is represented as the shaded gray area. The responses of the neurons illustrated in *C–E* are shown as rasters only. Lowering the stimulus contrast increases the latency, generally by 30–40 ms. Thick vertical lines: point at which response onset was assigned. Changing the orientation with the contrast fixed decreases the response strength without affecting the latency nearly as much as reducing the contrast does (compare *top* and *bottom rows*).

(Fig. 1, *bottom row*). A two-way analysis of variance (ANOVA) without replication was performed on a neuron-by-neuron basis, with the factors being the stimulus orientation and contrast (Fig. 2). The ANOVA shows that the response strength is related almost entirely to orientation, and the latency, although related to both orientation and contrast, is related more closely to contrast.

When the whole range of orientations and visible contrasts is studied (Fig. 3, *A* and *B*), the response strength changes as a function of stimulus orientation, and is affected by changes in stimulus contrast only at the lowest contrasts, and then only to a small degree. At high contrast, latency varies little even as the response strength goes from maximum to near zero. As contrast is lowered at the optimal orientation, the average latency increases by 39.4 ± 2.3 (SE) ms. The response strength is only weakly affected across most of the range of contrast, falling to a mean of 88 ± 0.05% of peak at 19% contrast and 69 ± 0.07% of peak at 5.1% contrast. This rough specialization of strength for orientation and latency for contrast holds until the stimulus contrast is so low that the stimulus is barely visible (<10% contrast). When the orientation is far from the optimal one, the latency shows a strong dependence on both contrast and orientation. There was no significant correlation between the degree of orientation tuning, as defined by the ratio of the maximum over the minimum response at the highest contrast, and the degree of latency shift ($r^2 = 0.04$).

Although the ANOVA models these data well, the shapes of the orientation tuning curves suggest that the data can be roughly fit by any number of unimodal functions, e.g., cosine or Gaussian, and the data for latency can be fit by a slightly curved surface (Fig. 3, *C* and *D*). The analytical relationships

$$\text{Magnitude} = a_1 \cos(\theta) + a_2 \log_{10} \alpha + a_3 \quad (1)$$

$$\text{Latency} = b_1(2 - \log_{10} \alpha) \cos(\theta) - b_2 \log_{10} \alpha + b_3 \quad (2)$$

where magnitude is the response strength in spikes per sec-

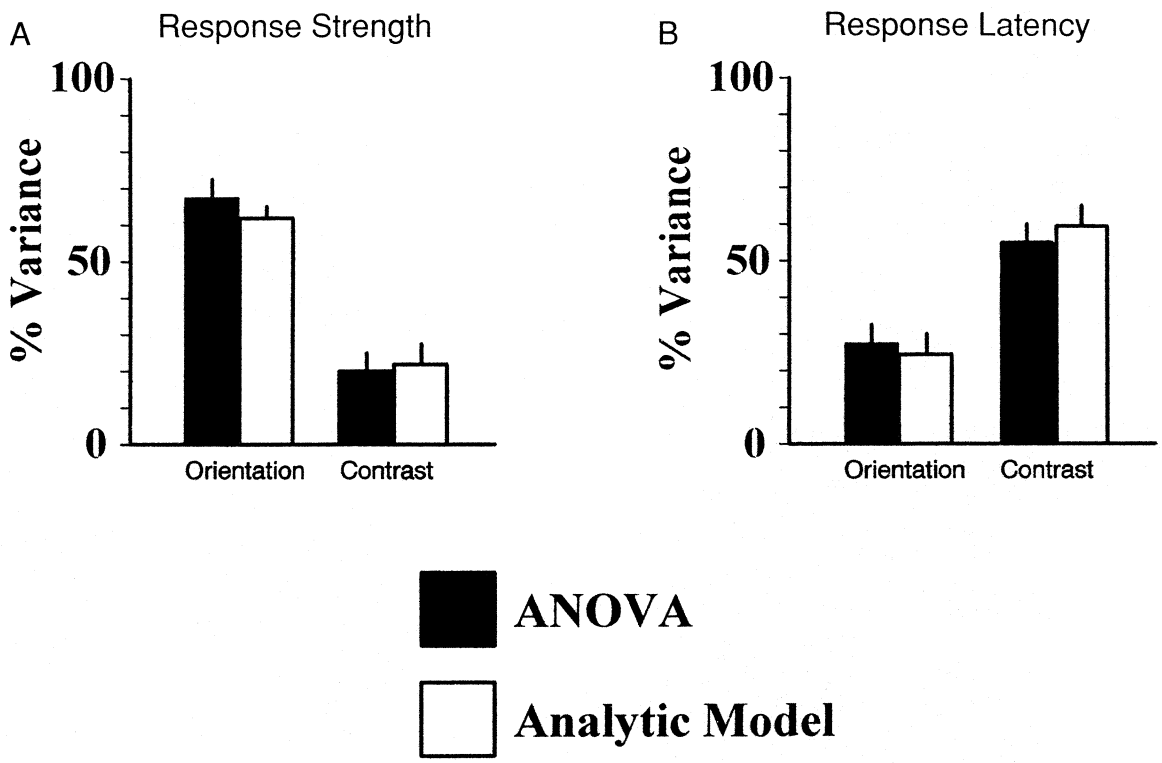

FIG. 2. Summary of 2-way analysis of variance (ANOVA) averaged across neurons. *A*: amount of variance in the response strength accounted for by orientation and contrast. *B*: same plot for the response latency. Filled bars: results for the ANOVA. Open bars: same operation for a simplified analytical model (see text, *Eqs. 1* and *2*). Error bars: mean ± SE. ANOVA shows that much of the variance for both the response magnitude and latency can be accounted for by contrast and orientation. However, the large number of degrees of freedom in this model (23) makes its interpretation difficult. The analytical model on average accounts for the same amount of variance with the use of only 3 parameters (orientation, contrast, and a constant). Thus *Eqs. 1* and *2* allow accurate predictions of the response latencies and magnitudes given the orientation and contrast, or by rearranging the parameters, the orientation and contrast can be decoded from the response given the latency and magnitude.

ond, θ is the orientation angle normalized to go from 0 to 2π, α is the contrast in percent, and latency is the response latency in ms, account for the variance of the magnitude and latency as well as the ANOVA, as shown in Fig. 2. The term in the latency that depends on the orientation had to be weighted by contrast. Modeling the orientation sensitivity with the cosine function was chosen for convenience. For the example shown in Fig. 3, *A* and *B*, $a_1 = 31.1$, $a_2 = 0.13$, $a_3 = 3.84$, $b_1 = 18.9$, $b_2 = 31.8$, and $b_3 = 103.3$, and these fit surfaces (Fig. 3, *C* and *D*) accounted for 76% of the variance in the magnitude and 86% of the latency for this example. The mean values of the nonconstant parameters for all neurons are: $a_1 = 15.2 \pm 1.9$, $a_2 = 1.6 \pm 1.3$, $b_1 = 21.4 \pm 4.0$, and $b_2 = 37 \pm 2.9$. a_1 And a_2 were essentially uncorrelated ($r^2 = 0.05$), as were b_1 and b_2, ($r^2 = 0.03$).

DISCUSSION

The independence of latency and response strength as contrast and orientation were varied was unexpected. The strongest effect on response strength was related to stimulus orientation, whereas the strongest effect on latency was related to contrast. The independence of these effects does not say that response strength is not influenced by contrast; rather, the influence is in general small until the contrast is low (on average the response strength had fallen to 69% of peak when the contrast was reduced from 94% to 5.1% at the optimal orientation). This relation between contrast and response strength is similar to that found by others, such as Skottun et al. (1987), who found that reducing the contrast from 100% to 10% reduced the response strength to 70% of peak, and Sclar and Freeman (1982), who showed data in which reducing the contrast from 80% to 7% only cut the response magnitude by approximately one third. Tolhurst and Dean (1987), studying simple cells, also found cases in which there was a clear breakpoint at ~10% contrast, although their use of a limited range of contrast makes direct comparisons to the work here difficult.

Not every neuron had a contrast-response strength function that exactly matched the population average: some neurons had response strengths that were relatively unaffected by contrast across the entire range (Fig. 3), whereas others showed declines in response strength at the lower contrasts (Fig. 1, *D* and *E*). The variable nature of the relationship between contrast and response strength between different neurons has been described before (Albrecht and Hamilton 1982).

A recent paper on simple cells in the visual cortex of both monkey and cat (Albrecht 1995) found that the neuronal responses to drifting sinewave gratings were delayed by ~45 ms as contrast was lowered to a level near threshold, and that this change was not systematically related to the magnitude of the response. Another recent study of V1 simple cells found that, as contrast was reduced, the responses to drifting sinewave gratings again were delayed by 50 ms

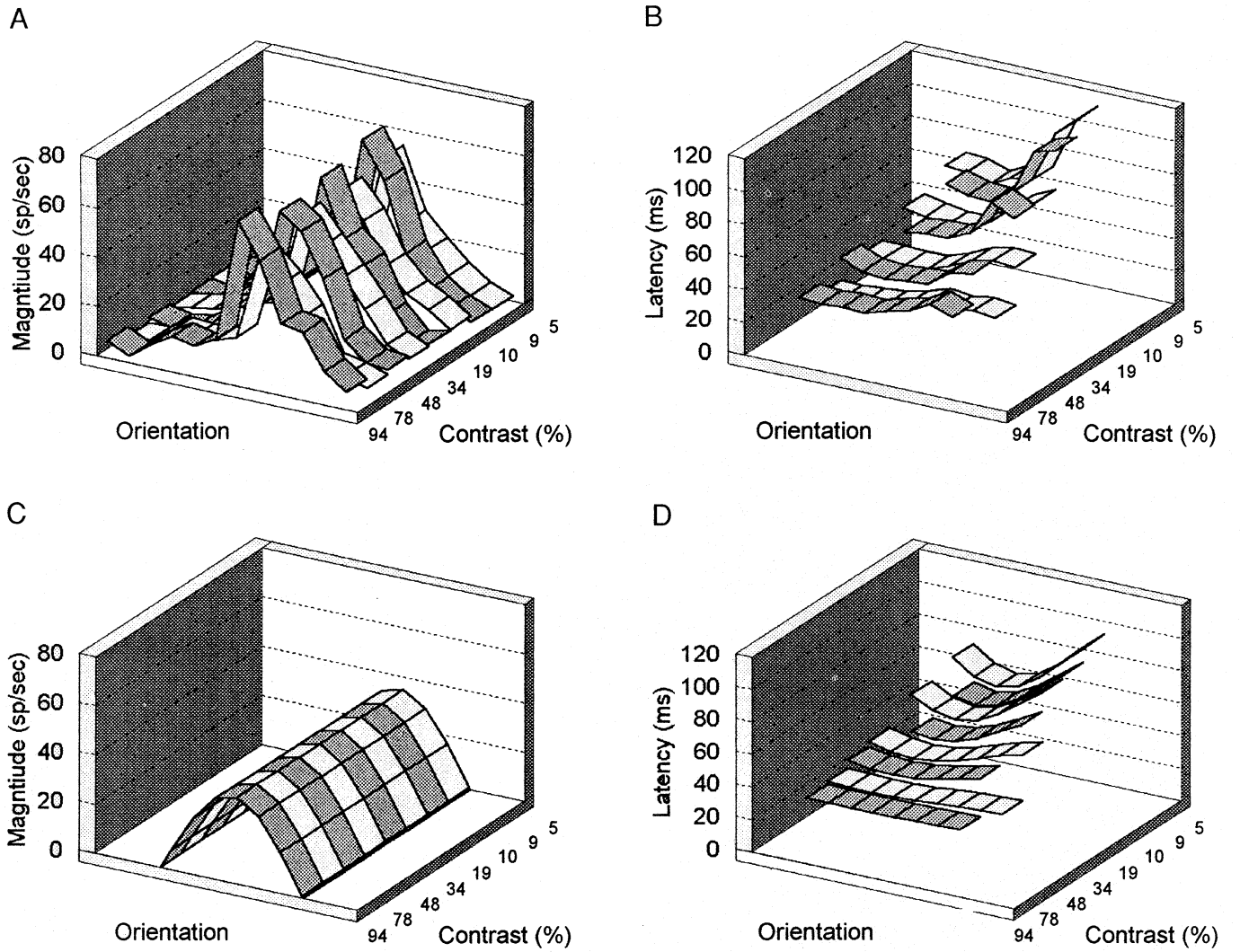

FIG. 3. *A*: response strength as a function of stimulus orientation and contrast for data from the same neuron used for Fig. 1*B*. White surfaces: data from white bars. Darker surfaces: data from black bars. The response strength is strongly affected by changes in orientation, whereas the tuning is only weakly related to changes in contrast over a broad range. *B*: response latency as a function of orientation and contrast. At high contrasts response latency is weakly affected by changes in stimulus orientation, although as shown in *A*, the same changes in orientation had strong effects on the response strength. As contrast decreases, latency increases substantially at all orientations. At and near the optimal orientation, the same changes in contrast had little effect on the response strength. At low contrasts and orientations far removed from the optimal one, latency and response strength do covary. *C* and *D*: surface plots of the fit of *Eqs. 1* and *2*.

(Carandini and Heeger 1994). Although changes in phase to a drifting stimulus cannot necessarily be translated exactly to changes in latency to a flashed stimulus, the results of both of these studies appear to be in accord with the results presented here.

Celebrini et al. (1993) measured the latencies of striate cortical cells to stationary gratings of different orientations and a single contrast. Their study showed some dependency of latency on orientation, as does ours. However, Celebrini et al. did not simultaneously vary stimulus contrast, so there is no way to tell whether or not the effect of orientation on latency is weaker than the effect of contrast. Thus, although Celebrini et al. came to a different interpretation than we did about of the role of latency, there is really no conflict between their results and ours.

As we have shown, the segregation of contrast and orientation by the use of response latency and response strength is not perfect. Nonetheless, the nervous system could make use of latency and strength together, in effect solving the problem of two equations in two unknowns (*Eqs. 1* and *2*), to eliminate the problem of less than perfect correspondence between strength and orientation, and latency and contrast.

It has been proposed that one method the nervous system could use to organize information about a visual scene would be for neurons that are responding to the same object to have responses that oscillate in phase (Eckhorn et al. 1988; Gray and Singer 1989). The results of this study suggest another possible mechanism for using the timing of a response for segregating stimuli. If the responses of the neurons to an edge of one contrast were delayed relative to the responses to an edge of a different contrast, this delay could be used by the rest of the nervous system to signal that these neurons are responding to different edges. Clearly such a simple mechanism cannot account for the ability of the ner-

vous system to treat objects that are made up of multiple edges of different contrasts as a coherent whole. Yet a simple mechanism that could group together the responses of neurons that are stimulated by a single edge could be the first stage of a more sophisticated mechanism that has more general abilities. The mechanism based on latency does not preclude the further use of other relationships, such as coherent oscillations (Eckhorn et al. 1988; Gray and Singer 1989), but rather raises the intriguing possibility that time relationships carry the information needed to solve the binding issue.

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