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Time course of perceptual discrimination and single neuron reliability

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Time Course of Perceptual Discrimination and Single Neuron Reliability

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Abstract. The reliability of identification of a visual target increases with time available for inspection of the stimulus. We suggest that the neural basis of this improvement is the existence of a mechanism for integrating a noisy firing rate over some period, leading to a reduction in mean firing rate variance with available processing time. We have determined the experimental time course of the improvement in reliability in a parallel search task where the available inspection time is limited by the presentation of a mask at various times after a brief stimulus. We compare the resulting psychometric functions with the predictions of a model based on Signal Detection Theory. The model is based on the assumption that the reliability of the observer's response is limited by the variability of the responses of individual neurons. The reliability of the discrimination between two stimuli at the neuronal level is then directly related to the ratio of the difference between their integrated mean responses (over many trials) to the response standard deviation. This reliability increases with inspection time. To demonstrate application of the model to electrophysiological data, "neurometric functions" are derived from the firing rates of a monkey *V*1 cortical neuron. The data were obtained while the animal was active in a discrimination task. The results correspond qualitatively to our observed human psychometric functions.

1 Introduction

One of the central goals of sensory neurophysiologists is to understand the neural basis of perception. Barlow (1972) has suggested that this problem should be dealt with at the level of the responses of the single neuron. A number of attempts to match visual performance with neural function at this level have been made recently (for example see Tolhurst et al. 1983; Bradley et al. 1987; Skottun et al. 1987; Barlow et al. 1987; Newsome et al. 1989). One of the main topics in this domain is the study of psychophysical reliability and its possible neural basis.

Psychophysical reliability in visual stimulus discrimination has been shown to depend on task difficulty. The stimulus contrast (Skottun et al. 1987), the available processing time (the stimulus onset asynchrony, Julesz 1981), and the degree to which the target differs from surrounding distractors (Bergen and Julesz 1983a) contribute to this difficulty.

Discrimination reliability may be assumed to be limited by neuronal response variability, and a number of authors have examined this relation using Signal Detection Theory. Tolhurst et al. (1983) have shown that the probability that a neuron fire a criterion number of impulses grows monotonically with the visual stimulus contrast and that neural "psychometric functions" can be compared to psychophysical responses of humans. Skottun et al. (1987) showed that some cortical cells exhibit the psychophysically observed saturation of discrimination ability at quite low contrast. Barlow et al. (1987) demonstrated that monkey cortical neurons exhibit a threshold for contrast discrimination at about the same level as that observed psychophysically in man. Tolhurst (1989, using an information theory approach) found that a typical cortical neuron can convey less than one bit of contrast information in 0.5 s. Bradley et al. (1987) assessed the minimum orientation and spatial frequency differences that elicit a criterion level of discrimination between two stimuli and found that the selectivity of the best cells was comparable to the psychophysical thresholds.

Psychophysical studies by Julesz and collaborators (Julesz 1981; Bergen and Julesz 1983b) have shown the importance of available processing time for target detection in pop-out experiments. However, the neural basis for the development of psychophysical reliability as a function of available processing time (the temporal psychometric function) has not been explored. We now present a neural model for this function.

The general model posits a continuous flow of noisy information in response to each of the two stimuli to be discriminated, for a limited time. Under certain mild constraints, any mechanism for information integration and comparison will lead to a decision reliability which increases monotonically with available processing time to a saturated value, similar to the form of the temporal psychometric functions. In this sense, the qualitative predictions of the model are exceedingly robust and general.

In order to make the model explicit and quantitative, we suppose the information to be carried by noisy response firing rates in a single neuron (or a group of neurons acting together). We suggest that the psychophysical decision is based on the integration of the firing rates over the available processing time. We make certain further explicit assumptions for ease and transparency of calculation, but the generalization of the model presents no problems, nor would the qualitative predictions be affected.

The dependence of reliability on integration time could be measured for either of the two modes of early visual processing of multi-element stimuli – parallel or serial – or for an isolated element. We have chosen initially to work on the parallel mode. We shall begin by describing the application of Signal Detection Theory to such an experiment. We shall then carry out the limited model in detail. We follow this calculation with a description of the psychophysical experiment and its results, and compare these results, and those of related published works, with the predictions of the model. Finally, in order to strengthen our claim to robustness of the model, we apply it to responses of a monkey cortical cell. We find that the resulting curves correspond quite well to the human psychometric functions. This correspondence may also be taken to indicate that the human psychophysical decisions are based on the responses of no more than a few cells, but the differences in conditions preclude firmer conclusions at this point.

2 Signal Detection and the Parallel Search Task

In a typical "pop out" task, a field of bars may be briefly presented and the observer required to detect the presence or absence of a horizontal target bar among vertical distractors (Julesz 1981; Treisman and Gelade 1980; Sagi and Julesz 1985; Treisman 1985). The target appears in half the presentations, randomly chosen, and its position is varied randomly from trial to trial. In order to succeed in such a behavioral task the subject must of course make use of visual mechanisms which can discriminate between the presentation of a horizontal and a vertical bar of light.

We shall consider a neuron whose response firing rate is orientation-selective. This tuning is statistical, however, since there is a considerable variance in the response firing rate of the cell to a given stimulus. Thus, we shall need to define probability distributions for the firing rates in response to presentation in the cell's receptive field of a bar of the preferred orientation (target or stimulus 1) and a bar of the orthogonal orientation (distractor or stimulus 2). We shall begin by assuming both these distributions to be Gaussian and to have the same standard deviation (Green and Swets 1974). We later drop these constraints by dealing with real neuron data.

We shall show that as more processing time is available the variance in the mean firing rates decreases so that if correct identification is limited by this variance, this reliability improves with time. That is, there is an increase in the discriminability between the target (horizontal bar) and the distractor (vertical bar) elements, as the degree of overlap between the two distributions decreases. We shall use the formalism of Signal Detection Theory to show that, for the present simplified case, the probability of correct element identification by this neuron is a monotonically increasing, saturating, function of the processing time.

In principle, the available processing time can be limited by the integration time of the system or by the duration of the signal (the response of the system to a stimulus presentation). This duration in turn may be limited by the duration of the stimulus, or of the response if it is intrinsically transient, or by the imposition of a masking stimulus which erases the response. Use of such a masking stimulus makes possible a mapping of the time course of discrimination reliability as a function of the time between stimulus onset and masking onset (Stimulus Onset Asynchrony or SOA). The present model assumes both an integration time and a response duration long compared with the SOA.

In order to derive a psychometric function we shall assume that each neuron (processor) is an independent channel analyzing the element in its receptive field. We shall use a multiple noisy channel approach to tackle the problem of combining these signals (Shannon and Weaver 1949). We calculate the expected rates of Hits, Misses, Correct Rejections, and False Alarms as functions of time.

In Sects. 4 and 5 we present data of our own experiments and those previously published by others for parallel processing tasks and compare the results to the model's predictions. In the Postscript (Sect. 7) we present electrophysiological data from cortical neurons and use the model to predict neuron "psychometric functions" from these data.

3 Model

Consider a visual neuron whose response orientation tuning is such that the cell is better driven by a horizontal bar than a vertical bar. We start by assuming for computational convenience that the neuron's reaction to the presentation of a stimulus is a step increase in firing rate degraded by noise lasting until the mask is presented. We call the mean firing rate of the cell for a horizontal "target" stimulus X_T. However, due to the stochastic nature of the cell's response to such a stimulus a normal probability distribution of mean firing rates is expected around the mean X_T with a standard deviation, σ. The same holds for a less effective stimulus such as a vertical bar, the "distractor" stimulus, for which the mean firing rate is X_D. We assume that the standard deviation is the same for these two distributions. These probability distributions, with arbitrary equal widths, are plotted in Fig. 1A. For this case, the mean firing rates are located at the peaks of the distributions for horizontal and vertical bar stimuli, respectively, and they constitute two points on the orientation tuning curve of this hypothetical neuron.

The critical point is that the longer the stimulus is available for processing, the more action potentials there are, and the more reliable is the average firing rate. Thus, for a square wave response, the variance σ^2 of both distributions is inversely proportional to the available processing time of the stimulus. This is illustrated by the two narrower distributions around the same means displayed in Fig. 1B, which is for a processing period that is four times longer than in Fig. 1A. As a result of the decrease in σ the detectability of the target element increases with time. The same point can be seen in the comparison of the inset panels of Fig. 1, which display the action potential *count*, that is, the rate integrated over 50 ms (upper inset panel) and 200 ms (lower inset panel). The smaller degree of overlap between the two distributions in the lower inset panel compared with the upper inset panel reflects higher discriminability.

We may now compute the percent of correct detections based on the responses of our detector neuron, as a function of the time the stimulus image is available for analysis before the mask "erases" the image (the SOA). Let $p_1(t)$ be the probability that a cell "recognizes" correctly a target (horizontal bar) when presented to it (by firing at a rate over some fixed criterion k). This probability of a Hit is equal to the area under the Gaussian distribution between k and infinity:

$$p_1(t)=\frac{1}{\sqrt{2\pi}\sigma(t)}\int_{k}^{\infty} e^{-[X-X_T]^2/2\sigma(t)^2}\mathrm{d}X\,. \qquad (1)$$

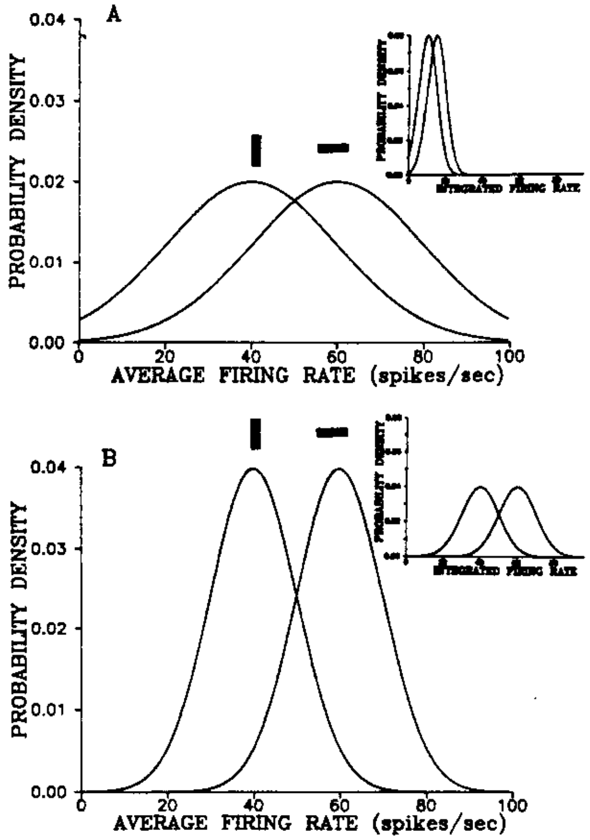

Fig. 1A and B. A model of a visual neuron's responses based on Signal Detection Theory. Gaussian probability distributions of response of a hypothetical visual neuron to the presentation of a horizontal light bar (target – right curves) or a vertical light bar (distractor – left curves). For purposes of the model we have assumed the standard deviations of the two distributions to be equal. Although the cell's preferred stimulus is a horizontal bar, variability in the mean response rates reduces the neuron's ability to convey reliable information about the orientation of the stimulus. However, the variance in the mean firing rate decreases with the available processing time due to a larger sample size. This is shown in the narrower probability distributions of the lower panel (B) compared to the upper panel (A). Equivalently, this is seen in the smaller area of overlap between the distributions of the integrated firing rate as shown in the insets. Processing times for the lower panels were four times those of the upper panels. Thus, the reliability of the processor's "decision" about the stimulus orientation is a monotonically increasing function of the processing time

Similarly, the probability of a Correct Rejection of a stimulus not containing the target is:

$$p_0(t)=\frac{1}{\sqrt{2\pi}\sigma(t)}\int_{-\infty}^{k} e^{-[X-X_D]^2/2\sigma(t)^2}\mathrm{d}X\,, \qquad (2)$$

where the negative firing rates implied by the $-\infty$ limit correspond to inhibition of ongoing activity. Note that in (1) and (2) we have expressly indicated the dependence of σ on processing time.

The reliability index of a neuron, that is, the probability of correct responses is then the mean of $p_1(t)$ and $p_0(t)$. This index, however, is dependent on the choice of criterion (Green and Swets 1974). An alternative criterion-independent parameter is the detectability

$$d'(t)=\frac{X_T-X_D}{\sigma(t)}, \tag{3}$$

where $\sigma(t)$ is the standard deviation of the probability distributions of the response to the target (T) and nontarget (D) stimuli, for a stimulus of duration t.

As discussed above, $\sigma(t)$ narrows as the square root of time. Then,

$$\sigma(t)=\frac{\sigma(\tau)}{\sqrt{(t/\tau)}}, \tag{4}$$

where $\sigma(\tau)$ is defined as the difference between the mean responses to the target and the distractor, $\sigma(\tau) \equiv X_T-X_D$, and τ is therefore the time when the detectability, $d'(\tau)$, is unity. Then

$$d'(t)=\sqrt{(t/\tau)}\,. \tag{5}$$

Thus an improvement in the reliability of the neuron's "decision" is expected with time.

If one chooses a criterion one can calculate the probability of correct responses from either of the above approaches. In our model case of two equal Gaussians, the optimal criterion is the crossover point between the two curves. The resulting prediction of the model is shown in Fig. 2, where we plot the percent of correct responses (Hits plus Correct Rejections as a percent of trials) expected at the single neuron level (the reliability index) as a function of processing time.

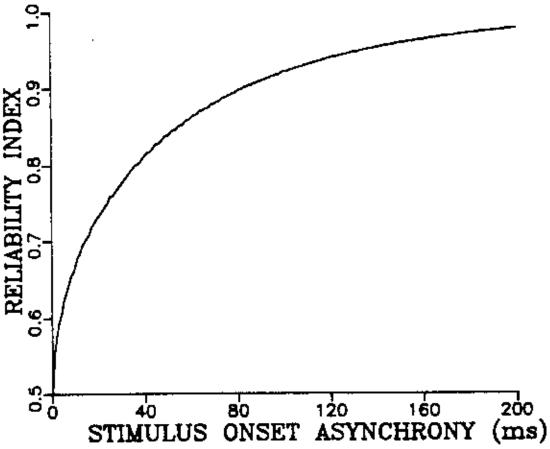

Fig. 2. Reliability index (RI), the fraction of correct identifications, [Hits + Correct Rejections]/2, of the stimuli presented to our model neuron is plotted as a function of processing time. Hits and Correct Rejections were calculated by integrating the area under the appropriate Gaussian distribution between some fixed criterion k and $\pm\infty$, respectively [see Eqs. (1) and (2) of the text]. k was assumed to be optimal, that is, 50 spikes/s in Fig. 1; in this case Hits and Correct Rejections are equal and the curve is then also valid for either separately. RI begins at the chance rate of 0.5 since the two stimuli are presented with equal probability

In order to analyze the observer's performance for a multi-element display we must now combine information from the different processors (Shannon and Weaver 1949). Consider a noisy binary channel with two possible inputs $\{0,1\}$ and outputs $\{0,1\}$. Let a vertical bar be equivalent to 0 and a horizontal bar equivalent to 1. Such a channel is drawn in Fig. 3. The transition probability matrix:

$$\begin{bmatrix} p_0 & q_0 \\ q_1 & p_1 \end{bmatrix}$$

will be calculated according to (1) and (2) with the appropriate integral limits. Notice that the channel's reliability improves with time according to (4).

It is assumed that in a parallel search situation all processors are activated simultaneously. Furthermore, if N elements are present they are all scanned with the same degree of reliability depending on the SOA. In the special case where the type and density of distractor elements projected on the screen is kept constant, to eliminate variability in the effects of lateral inhibition (Sagi and Julesz 1986; see Discussion), we may assume independence between channels and use a multiplicative model to compute the observer's expected response. The observer's response is then "yes" (a target was present in the stimulus) if at least one of the processors signals so and "no" otherwise. Since the processors' answers are assumed to be independent there can be occasions of false detections of more than one target and in all such circumstances we expect the observer to respond "yes" rather than "no". Thus, the probability that the subject will correctly report that

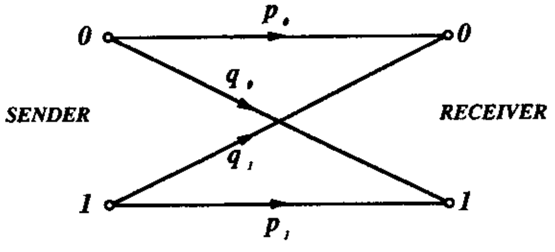

Fig. 3. A noisy binary channel analogy. Each orientation processor can be seen as a binary channel with two possible inputs (0 = vertical bar, 1 = horizontal bar) and outputs. The dependence of the transition probability matrix on time can be directly calculated by using the Signal Detection Theory model (see Fig. 2 for the special case of optimal criterion). Assuming that the channels are independent of one another, one can predict the observer's overall performance as a function of the processing time

there was no target present in the display (Correct Rejection) is the product of the probabilities of N processors correctly signalling that there is no target:

$$P(CR)=[f_0(t)]^N, \tag{6}$$

where f_0 is the probability of a Correct Rejection by a particular neuron in whose receptive field there is a distractor element.

The likelihood that any detector neuron will encounter a target is $1/2N$ since there are N stimulus elements and a target is present in half the trials. Accordingly, neurons must be strongly biased against False Alarms. In the symmetrical model we develop, for optimal performance the bias must ensure that the number of False Alarms equals the number of Misses. The a priori probability for Correct Rejection by a neuron is thus increased from 0.5 to $(2N-1)/2N$, and this probability increases with processing time by a degree proportional to p_0 from (2). The probability of a Correct Rejection by a neuron in whose receptive field a distractor element is displayed therefore becomes

$$f_0(t)=\frac{2N-1}{2N}+\frac{1}{2N}p_0(t). \tag{7}$$

The probability of a subject incorrectly reporting the presence of a target (False Alarm) is the complement of the probability for a Correct Rejection,

$$P(FA)=1-P(CR). \tag{8}$$

The probability of failing to report the presence of a target (Miss) is the product of $(N-1)$ processors correctly signalling that there is no target in their receptive fields and a single processor failing to report the presence of a target in its field:

$$P(M)=[f_0(t)]^{(N-1)}*[1-f_1(t)], \tag{9}$$

where the probability, $f_1(t)$, of a Hit by the neuron in whose receptive field there is the target element is the a priori probability of the element being the target, $1/2N$, increased towards 1 by a degree proportional to $p_1(t)$ from (1), that is,

$$f_1(t)=\frac{1}{2N}+\frac{2N-1}{2N}p_1(t). \tag{10}$$

The probability of correctly reporting the presence of a target (Hit) is the complement of the probability of a Miss,

$$P(H)=1-P(M). \tag{11}$$

The probability of correct responses for the array of neurons then becomes

$$\%\ \text{correct}=\frac{P(H)+P(CR)}{2}, \tag{12}$$

where these variables can be obtained from the cell firing rates and variances by using (6)–(11) and (1) and (2). The corresponding curve looks quantitatively like that of Fig. 2, departing from the origin with a monotonically declining positive slope. In the following sections we present data from psychophysical experiments and compare their results with the predictions of this model, using (6)–(11) to modify Fig. 2.

4 Comparison with Psychophysics

4.1 Experimental Design

The experiments conducted to test this model were a typical pop-out search task. Briefly flashed stimuli were followed by a mask after a variable time interval (SOA), and the mean percent of correct answers for the various SOAs (the psychometric function) was measured. This method (Bergen and Julesz 1983b) has an advantage over previously used reaction time techniques for understanding early vision, because the brief stimulus presentations ensure that no eye movements are involved. Observers had to report the presence or absence of an odd-man-out. This was a red horizontal element that in some experiments was embedded in an array of green horizontal distractor elements, so that a color judgment had to be performed, and in other experiments was embedded in an array of red vertical distractor elements, so that correct target identification was based on orientation differences.

4.2 Methods

4.2.1 Visual Stimulus. The stimuli were displayed on the face of a Barco CD-233 short-persistence color monitor. The display was controlled by a PDP 11/23 computer via a Peritek VCG-Q color graphics video interface. Data collection and analysis were carried out on the same computer. Figure 4 illustrates the temporal and spatial pattern of the stimuli used. The number of elements was 64 (8 × 8), and the entire stimulus grid covered 10 × 8 cm. The target never appeared as one of the outer shell elements. This ensured that the target always had distractor element neighbors on all sides. A jitter of 20% of the inter-element distance was introduced into the location of elements to prevent detection based on luminance differences or on a departure from overall symmetry. A fixation point of size 2 × 2 min of arc was present throughout the experiment at the center of the stimulus. The stimulus was viewed from a distance of 170 cm. Distractor elements were either red vertical or green horizontal bars. Bar length and width were 14 and 3.5 min of arc, respectively. The target was a red

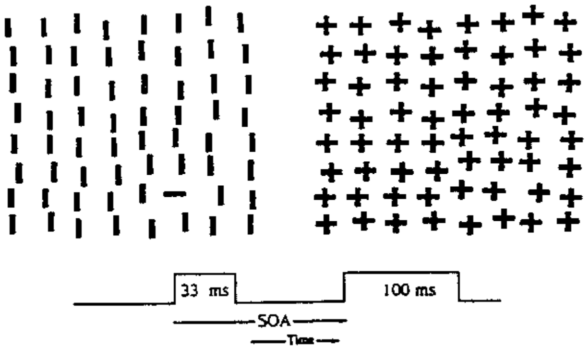

Fig. 4. Spatiotemporal properties of the stimulus. The stimulus was presented for 33 ms and was followed by a mask after a variable delay (stimulus onset asynchrony or SOA; range 50–200 ms). The target was present in half the trials and was randomly positioned anywhere except in the outer shell of elements. The case shown is for 64 elements with the target being a horizontal bar and the distractors vertical bars. Other experiments were done with target and distractors differing in color rather than orientation. Jitter was introduced into the exact location of the elements to prevent detection based on luminance differences or symmetry breaking

horizontal bar of the same size. The colors were nearly isoluminant using the flicker criterion so that distractor differences in the color dimension were mainly the result of chrominance rather than luminance differences. The arrangement of the distractors and the position of the target were randomized between trials. The SOA was randomized between trials (range 50–200 ms in steps of 16.6 ms) and the stimulus presentation time was 33.3 ms to prevent a second fixation. Mask duration was 100 ms.

4.2.2 Task Procedure. Subjects were asked to report the presence or absence of the target by pressing the appropriate key on the computer keyboard. The target was present in half of the trials and an auditory feedback tone was given following every error made by the subjects. The rate of correct responses was calculated as the sum of the Hits and Correct Rejections divided by the total number of stimulus presentations. In this way effects on the psychometric function of subjective differences in the decision criterion were reduced. Performance was measured as the mean correct response rate at various SOAs, and described by a psychometric function for each subject. Each data point in these psychometric functions is the average of 50 repetitions.

4.2.3 Subjects. Five subjects participated in the pop-out experiments. All were naive to the purpose of the experiment and had normal or corrected-to-normal vision. All subjects were given 100 practice trials before data collection was begun.

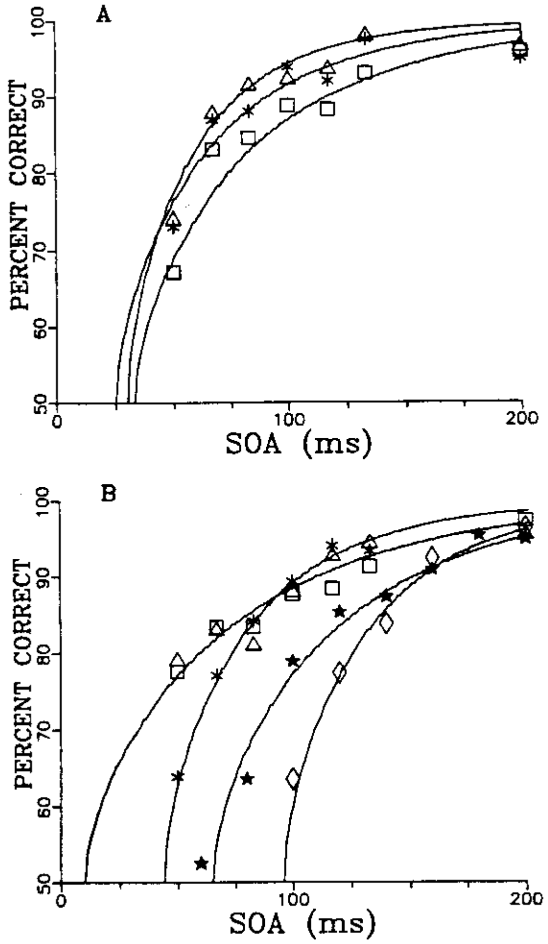

Fig. 5A and B. Percent of correct identifications of a target element in the presence of background elements (100 × Hits plus Correct Rejections divided by the total number of trials). **A** Data and psychometric functions for three subjects using horizontal colored bars. A red target replaced in half the trails one of the central 36 green distractors in a field of 64 elements. **B** Data and psychometric functions from three subjects for detection of a horizontal target which replaced in half the trials one of the central 36 vertical bars in a field of 64 bars. In addition, the stars and diamonds represent data from two subjects of Bergen and Julesz (1983b) for an "*L*" target in a field of 35 "+" distractors. The same function fits all the data well; the different values of parameters in our data and those of Bergen and Julesz may be due to different stimulation conditions. In all cases the curves show the best fit to the data of the prediction of the model described in the text

4.3 Results

The percent of correct responses as a function of SOA was measured for both the color and the orientation pop-out tasks. Figure 5A and B shows examples of the psychometric data obtained for a stimulus containing 64 elements in which the target was present as one of the inner 36 elements in half of the trials. The data confirm earlier results (Bergen and Julesz 1983b) that both color and orientation may serve as textons for rapid and effortless detection of an odd man out.

The data of Fig. 5 exhibit a sigmoidal or threshold form which differs from the curve predicted from (12) which looks like that of Fig. 2. However, a single reasonable addition leads to a good fit: The assumption that there is a threshold time, t_0, which is a minimum processing time, or equivalently that there is a minimum number of neuron action potentials below which no information gain is achieved. The resulting psychometric functions are shown in Fig. 5 by the continuous lines. There are now two free parameters, t_0, the threshold time, and τ, the time for which the standard deviation of the Gaussian distributions of the firing rates equals the difference between the means of the firing rates for vertical and horizontal bar stimuli, that is when $d' = 1$. The best-fit psychometric curves are shown in Fig. 5. The fit is quite good in all cases. τ was in the range 25–96 ms for different observers; and t_0 was in the range 10–96 ms. These curves were constructed using (12) of Sect. 3, where $N = 36$ elements.

5 Comparison of the Model with Other Psychometric Data

We have also checked our model's performance with data from experiments done by Bergen and Julesz (1983a). The main purpose of their experiments was to show that performance decreases as texton gradients become smaller. They reduced the gradients by changing the orientation differences between the background elements (distractors) and the target from 90 deg down to 10 deg. This is equivalent to bringing the two Gaussian distributions of Fig. 1 closer together, as the two mean firing rates are in most cases closer when the orientation differences between the two stimuli are smaller. Thus, we expect discriminability to deteriorate as texton gradients decrease in our model as well. This does not mean that we rule out effects due to lateral inhibition (Sagi and Julesz 1986) which may also contribute to the deteriorating performance, but discrimination performance deteriorates also in the case of absolute judgement of the orientation of a single element in consequence of reductions in the difference between the two orientations from which the stimulus is chosen (Dick and Hochstein 1988). Thus, lateral inhibition does not seem to be the sole factor underlying this phenomenon (see Discussion).

Figure 6 shows the data from Bergen and Julesz (1983a), for 6 different background orientations (90, 75, 60, 45, 30, and 20 deg) while the target was always vertical (0 deg). Data for SOAs longer than 200 ms have been omitted. The continuous lines represent the model's best fit to the data. The model parameter whose value should be varied as a function of the distractor element orientation is the mean firing rate of the response to the non-target stimulus X_D. This could affect the values of both t_0 and τ. The values chosen for best fit to the data (Fig. 6, inset) suggest that there is in both cases a monotonic dependence on the orientation angle difference between the two stimuli.

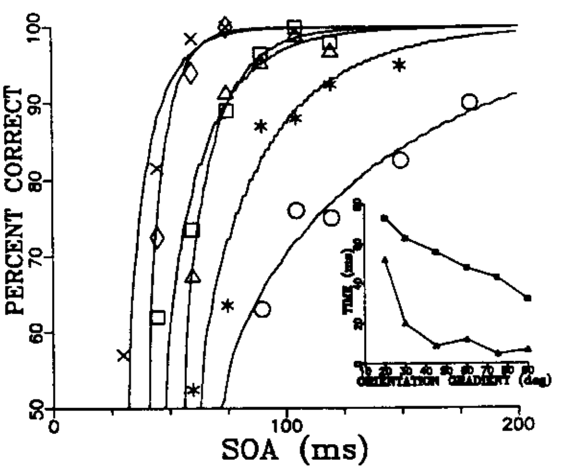

Fig. 6. Data (from Bergen and Julesz 1983a) and psychometric functions (from our model) obtained for five different texton gradients. The target stimulus was always a vertical bar while the distractors differed from the target by 90° (X's), 75° (diamonds), 60° (squares), 45° (triangles), 30° (asterisks), and 20° (circles). As the orientation gradient becomes smaller target detection becomes harder and slower (greater τ and t_0), as seen in the inset (τ: triangles; t_0: squares)

6 Discussion

Our main goal in this paper is to suggest a plausible model at the level of the single cortical neuron that may account for the improved performance with SOA that has been shown for a number of simple detection tasks (such as orientation and color discrimination). We have proposed that the discrimination is limited by the signal-to-noise ratios of the firing rates of single cells, integrated over the available processing time (SOA). Neurons capable of carrying out these tasks – that is, having limited tuning curves – are common in visual cortex. Given these tuning curves and the variability of each point on them we were able, using Signal Detection Theory, to calculate the percent correct responses an ideal decision maker would achieve. This variability decreases and therefore the percent correct response increases with increasing available processing time (SOA).

The available processing time is the integration time of the decision process, or the duration of the useful signal, whichever is shorter. This duration is longer than that of the stimulus by 100–200 ms (e.g.

Spitzer et al. 1988, Fig. 1) so the integration time optimally should be at least this number.

The signal-to-noise ratio or detectability depends not only on the signal and noise variability, which corresponds to the widths of the Gaussians of Fig. 1A, but also on the widths of the tuning curves which corresponds to the separation of the Gaussians. These widths can be affected by task difficulty (contrast: Barlow et al. 1987; stimulus separation along the relevant dimension: Spitzer et al. 1988) and by attentional shifts (Hochstein and Maunsell 1985), as well as other factors such as brightness, color, and size.

An independent factor which may also affect the tuning curves and therefore the detectability and which we have not included in our model is element density. Sagi and Julesz (1986) have shown the effect of element density on the detection of feature differences and claim that "preattentive processing is limited to short range interactions that operate only at a high density of elements. ... The operation of the preattentive system can then be accounted for by a simple system of feature detectors with local connections of inhibitory or excitatory type between similar detectors." There have been several reports of inhibitory surround effects outside the classic receptive field (Allman et al. 1985). Furthermore, cells which are sensitive to orientation gradients or color gradients were found in extrastriate areas $V2$ and $V4$, respectively (De-Yoe et al. 1986; Desimone et al. 1985). This effect, like the temporal integration effect we propose, is passive in nature (i.e. there is no need for active attention to turn it on).

A point of view similar to the one presented here was taken by Tolhurst et al. (1983) and Skottun et al. (1987). Tolhurst et al. (1983) argued that "the variability of the discharge of visual cortical cells in cats and macaque monkeys limits the reliability with which such neurons can relay signals about weak stimuli. ... The probability that a neuron will fire a criterion number of impulses in a stimulus trial grows monotonically with the contrast of a sinusoidal grating stimulus." Bradley et al. (1987) have followed this line of thought in trying to estimate the minimal difference in orientation or spatial frequency that could produce reliable changes in the response characteristics of individual neurons in the cat visual cortex. They compared these values with orientation and spatial frequency thresholds determined behaviorally. Their results point to a correspondence between the behavioral thresholds and those estimated from the most selective single cortical cells in the cat. Furthermore, the existence of a true threshold in the contrast discrimination ability of cortical neurons, which is comparable with the psychophysical threshold (Barlow et al. 1987), corresponds to our finding that there is a true temporal threshold (t_0) in ability to discriminate orientations in brief presentations, both at the perceptual and the neuronal levels.

We conclude that the improvement with available processing time of psychophysical performance tasks may consistently be modelled as arising from decision making at the level of the single cortical neuron. In order to show that the model we have developed is robust against changes in its specific assumptions and that the psychophysical performance predicted from the responses of real neurons is in the right range, we now carry out our model for a monkey $V1$ cell.

7 Post-Script: Comparison with Physiological Data

Real neurons violate at least two of the model assumptions: That the response rate has a square-wave form and that the target and distractor rate distributions are Gaussian and of equal width. We shall now demonstrate that the qualitative correspondence between the model predictions and the psychophysical observations is unaffected by this violation. Furthermore, it is more plausible that neurons compute by a counting process (integrated response over some period) than by directly averaging firing rates and we refine the model accordingly.

Our present data were collected from monkey $V1$ neurons while the monkey was performing an orientation discrimination task. However, we do not have monkey psychophysical data and use human data for comparison. Furthermore, we did not use masking stimuli in these experiments and simulate the SOA paradigm by integrating data over various response periods. Accordingly, we claim only to demonstrate the reasonableness of the model.

It has been reported that the variance of cortical cell responses is roughly proportional to the magnitude of the response itself (Dean 1981; Tolhurst et al. 1983), rather than constant for all responses, as assumed in our model. The standard deviation of the response is then proportional to the square root of the integrated response. Thus, the basic notion of improvement of identification with increased available processing time is expected to remain firm when using neuron action potential data. In fact, we did find that for our $V1$ data, as well, this relationship holds. This finding is most easily related to the psychometric function if we remember that the detectability of the signal is a function of the distance between the mean integrated responses to the signal and distractor, divided by the square root of the sum of the squares of the standard deviations of the two responses.

We check these ideas by considering the variability of the response of single units in the primary visual cortex ($V1$) in the awake, behaving monkey.

7.1 Single Neuron Electrophysiology

7.1.1 Methods. Recordings were made from 17 *V*1 neurons in a female rhesus monkey (*Macacca mulatta*) trained to move between its cage and a primate chair. A head bolt, scleral search coil, and recording chamber were implanted under aseptic conditions using barbiturate anesthesia. Transdural recordings were made from striate cortex with glass-coated Pt/Ir electrodes. The electrode signal was amplified and filtered, and monitored on an oscilloscope and audio-monitor. Single units were identified on the basis of waveform, and their impulses were digitized using a window discriminator.

Sinusoidal gratings of 4 different orientations (0–135° in steps of 45°) were projected sequentially in quasi-random order on an oscilloscope screen for 500 ms. Contrast was 36–57%; mean luminance 3 cd/m^2. The monkey had to identify the stimulus that was identical to a cue stimulus, which was always the first stimulus presented, by releasing a lever. He was rewarded for a correct response with a drop of fruit juice. After training, the monkey's mean reaction time was 330 ms at a success rate of 85%.

7.1.2 Results. Figure 7 shows a typical cell's tuning curve for the different orientations. The inset peristimulus time histograms (PSTHs) show the cell's mean response firing rate as a function of time for each of the four stimuli over 150 trials on average.

It is evident from the PSTHs that the cell is selective for orientation. However, it is not clear how well it can discriminate between two differently oriented gratings since the PSTH conveys no information about the variance about the mean response. We plot in Fig. 8 the distributions of the integrated responses of the cell for the four fixed orientations as a function of the width of the window of integration, starting from stimulus presentation. As this window is increased the integrated response (the number of action potentials occurring inside the window) increases and so does the variance of the integrated response.

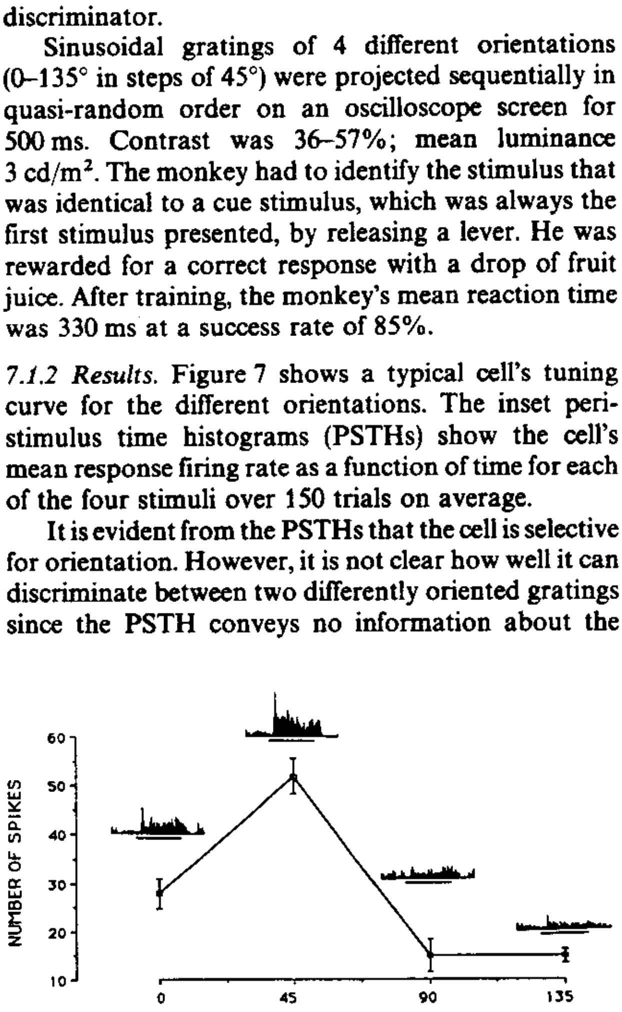

Fig. 7. Orientation tuning curve of a cortical cell in *V*1 of an alert monkey. The figure shows the dependence of the integrated responses on orientation. The integration was started 50 ms after stimulus presentation and lasted 200 ms. Error bars are the standard errors of the mean ($N \simeq 150$). The insets show the PST histograms for the four different stimuli. (Stimulus duration was 500 ms.) The reliability with which the cell can differentiate between two different orientations depends both on the separation of the values of the integrated responses and on their variability

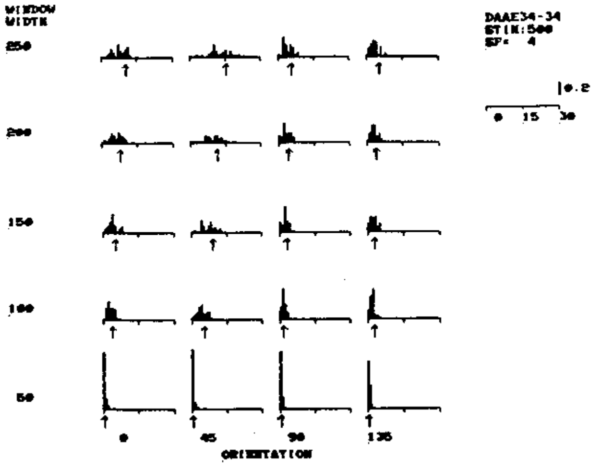

Fig. 8. Histograms of integrated responses of the visual neuron whose tuning curve and PSTH are shown in Fig. 7. These histograms are plotted for each of four different orientations (columns) and give different integration times (50–250 ms) beginning at stimulus onset. Notice that both the mean response (denoted by an arrow) and the variance increase as the integration time is increased. Calibrations are shown at the top right. *X* axis: Integrated firing rate. *Y* axis: Relative Frequency

The variance, however, is roughly proportional to the integrated firing rate. Thus, the degree of overlap between the two response distributions (for instance, to 45° and 135° gratings) decreases, making it easier to discriminate between the two stimuli. This is demonstrated in Fig. 9 which compares the results of integration over 60 and 100 ms. Note the qualitative resemblance of the distributions in Fig. 9 to the theoretical distributions in the insets of Fig. 1.

If we assume the decision-maker's criterion to be at the point of intersection of the two response distributions to target and distractor elements, respectively (arrows in Fig. 9) we can calculate the rates of Hits, Misses, False Alarms, and Correct Rejections and we can reconstruct the dependence of the percent of correct "identifications" of a stimulus on the action potential integration time by this unit. This is shown in Fig. 10 (triangles). This psychometric function at the single neuron level will be called the neurometric function. We measured the neurometric functions for 11 neurons in primate *V*1 as in Fig. 10. The neurometric functions passed 75% reliability in 5 of these cells. In these five, the integration time required to

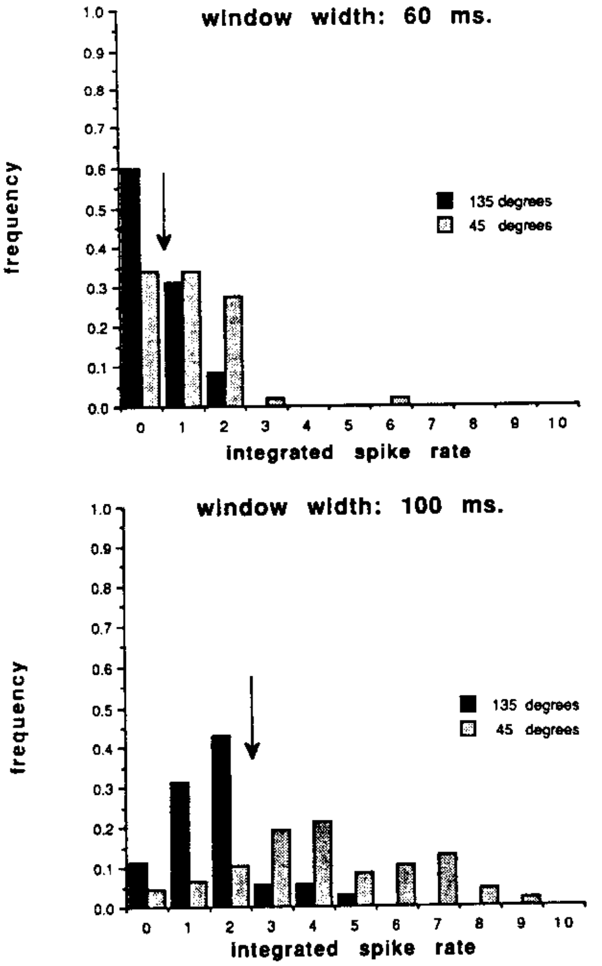

Fig. 9. Integrated response distributions for 45° (cross hatched) and 135° (black) stimuli for two different integration periods. The window of integration was 60 ms and 100 ms in the upper and lower panel, respectively. In both panels the point of intersection between the response distributions to the target and the distractors is indicated by an arrow. The degree of overlap between the two distributions is reduced as the available processing time is increased. Thus discriminability increases with increasing integration time at the single detector level

reach a criterion of 75% correct discriminations between a target of the neuron's preferred orientation and a distractor of the orthogonal orientation was 140 ± 37 ms and the average maximal reliability was 85 ± 5%.

There are two problems with the above approach, however. There is a need to determine a criterion in order to decide whether a particular response indicates a vertical or a horizontal stimulus and in order to set this criterion optimally, the response distributions must be known. Furthermore, this criterion is time dependent: Note the different positions of the arrows in Fig. 9. It is not clear how this criterion could be determined physiologically.

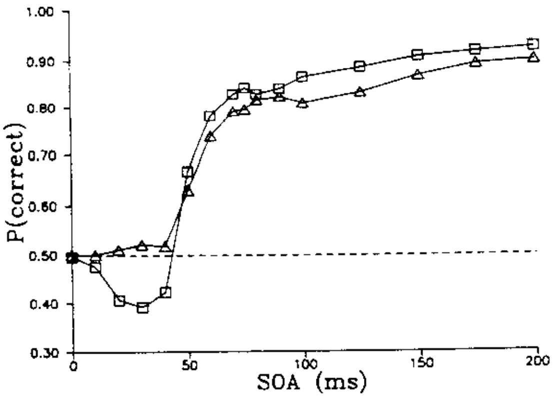

Fig. 10. The percent of correct discriminations between two stimuli (45° and 135°) as a function of the integration time at the level of the single unit (triangles). This neurometric function was calculated by applying Signal Detection Theory to the results of Fig. 9 with the cell criteria set at the points of intersection of the two distributions (arrows in Fig. 9). Alternatively, the neurometric function of the decision cell in the next layer (see Fig. 11) is plotted by calculating the area under the ROC for each integration time (see text for details). These curves may be compared with the psychometric data and model of Figs. 5 and 6

However, improved performance and criterion independence may be obtained by the use of a simple network of the sort described in Fig. 11a (see also Newsome et al. 1989). The cells of the first layer are similar to the *V*1 neurons from which we recorded (e.g. Fig. 7) which display orientation preference, for example for horizontal (*h*) or vertical (*v*) stimuli, respectively. The next layer's cells (the decision neurons – e.g. the *H* neuron) are excited by one preference neuron (e.g. *h*) and inhibited by the other (e.g. *v*). This computed difference in the response of the preference neurons, at any time, is a measure of the degree to which the criterion has been surpassed, and of the reliability with which the orientation of the stimulus has been detected. There is no criterion dependence on time. For example, the horizontal decision neuron (*H*) would respond if the horizontal preference neuron (*h*) gave a stronger response than the vertical one (*v*), irrespective of the integration period or the absolute strength of the responses.

This case is similar to the results of a 2AFC procedure in psychophysics with the response of the vertical preference neuron corresponding to the observer's internal representation of the first stimulus, and the response of the horizontal preference neuron corresponding to the representation of the second stimulus. It may thus be shown that the percentage of correct responses of a decision neuron is simply the area under the receiver operating characteristic (ROC), assuming the noise of the two preference neurons is uncorrelated (see Green and Swets 1974).

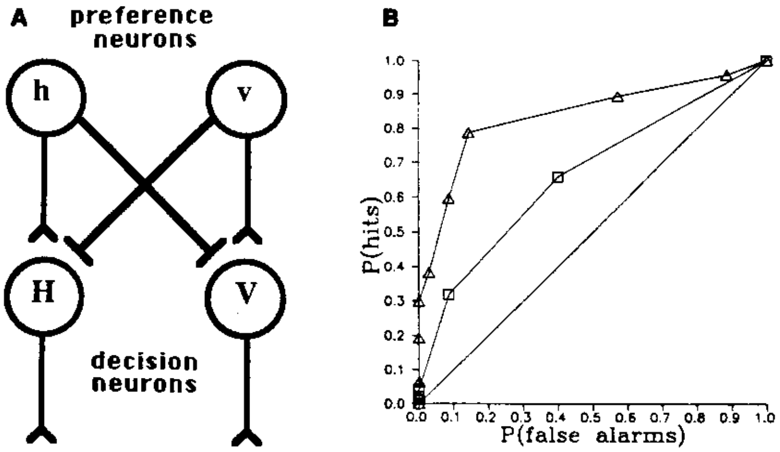

Fig. 11. **A** A simple two layered network to compute orientations effectively. The first layer of preference neurons have response distributions similar to the ones described in Fig. 1. The *h* and *v* stand for horizontal and vertical preference neurons, respectively. Thus the *v* neuron has interchanged response distributions to horizontal and vertical stimuli with respect to the *h* neuron. The next layer cells (decision neurons *H*, *V*) summate the responses of the preference cells with opposite signs. Their output reflects the reliability of the detection of horizontal or vertical stimuli, respectively, for any time and is criterion independent (see text). **B** ROC curves computed from the response distributions displayed in Fig. 9 by varying the criterion for two different integration periods: 60 ms (squares), 100 ms (triangles). The diagonal line is the ROC for zero integration time where the response distributions for the two stimuli are the same. The area under the ROC corresponds to the percent of correct responses made by the decision neuron (see text) and its dependence on integration time is plotted in Fig. 10 (squares)

We plot two ROC curves in Fig. 11b, by varying the criterion in Fig. 9 for each of the two different integration times: 60 ms (squares) and 100 ms (triangles). The performance of a decision neuron for a particular integration time may be calculated as the area under the appropriate ROC. The integration time dependence of this performance measure is displayed in Fig. 10 (squares).

In theory, if the inputs from the *h* and *v* preference neurons were uncorrelated and the response distributions were Gaussian, with mean responses to a horizontal stimulus, X_h and X_v, respectively, and with the same standard deviation σ, one would expect the detectability of the *H* decision neuron to improve by a factor of the square root of *N*, where *N* is the number of preference neurons [with *N*/2 vertical (*v*) and *N*/2 horizontal (*h*) neurons]:

$$d' = \sqrt{N} * \frac{X_h - X_v}{\sigma}.$$

Note that the neurometric function based on the ROC (Fig. 10 squares) is above that based on an "optimal" criterion (Fig. 10 triangles). That some points on this curve are somewhat below the 50% level may be due to noise at times shorter than the cell's response latency and before the neuron's response threshold is reached. This noise would decrease in the same way with $\sqrt{N}$.

The correspondence between the psychometric function (Figs. 5 and 6) and the neurometric function (Fig. 10) supports the hypothesis that binary decisions regarding simple features such as bar orientation can be based on the activity of single units in the primary visual cortex. Improved neuron performance with increased processing time may be a basis for a better target discrimination during simple search tasks.

We conclude that the results of the model analyzed in the body of this report do not derive from the assumptions made there regarding neuron response time course or their Gaussian distributions of equal width. Rather the results are robust and valid as well for real neuron firing rate data in the behaving, unanesthetized animal.

More quantitative conclusions require a study in which both physiology and psychophysics are carried out on the same animal. For instance, if the rise time of identification success is faster behaviorally than it is for a single neuron, it may be assumed within the model that more than one unit participates in the computation of a stimulus orientation.

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