Integration, segregation, and binocular combination

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The human visual system can accurately judge the mean of a distribution of different orientation samples. We ask whether the site of this integration is before or after the sites of binocular combination and disparity processing. Furthermore, we are interested in whether the efficiency with which local orientation information is integrated depends on the eye of origin. Our results suggest that orientation integration occurs after binocular integration but before disparity coding. We show that the effectiveness of added orientation noise is not only less than expected on signal or noise grounds but also that it depends on the dominance of the eye to which it is presented, suggesting an interocular opponent interaction in which the dominant eye input has higher gain.

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1. INTRODUCTION

Early visual processing consists of a patchwise local decomposition of the retinal image into its spatial, orientational, contrast, motion, and chromatic components.[1] These local operations are represented in the firing patterns of individual cells in V1 of the cortex.[2] Subsequent nonlinear operations reveal and consolidate global patterns of activation that allow the extraction of ecologically relevant global image features. We know more about the initial quasi-linear local processing than we do about the later nonlinear global processes of integration and segregation.

In terms of orientation processing there have been a number of psychophysical studies that bear on these later global operations, particularly with reference to shape discrimination.[3–7] A simpler form of integration is one in which subjects are asked to report on the mean value (e.g., orientation) of a group of local, randomly positioned spatial samples in which global shape is irrelevant. Such a task involves integration in its purest form. Using such an integration task, Dakin[8] has shown that normal observers can integrate local orientation information efficiently over a large range of stimulus size, numerosity, and density. His results were well described by the equivalent noise model used to estimate the visual system's internal noise and sampling efficiency. He showed that such integration is robust to changes in stimulus size, element numerosity, and density. More recently it was shown that a similar type of integration occurred for second-order stimuli (i.e., in which orientation is defined by a contrast variation), thereby extending its generality, although the underlying mechanisms may be different.[9]

It is of interest to know where in the visual processing hierarchy such a basic type of integration takes place. For example, is it before or after binocular combination? If it is after binocular combination, is it before or after the site of disparity processing? The site of visual integration of local orientation is of interest for a number of reasons. First, being one of the simplest forms of integration, it may occur early in the pathway. Second, a comparable integration for motion direction is thought to occur in extrastriate area MT,[10–12] and it would be of interest to know if there is also an extrastriate locus for orientation information. Third, by introducing a noise distribution into this integration task, one might be able to assess whether the processes of integration and segregation occur at the same site or at different sites along the pathway.

At present, there have been no studies on the site of this specific form of orientation integration involving estimation of the mean. However, some research has been done on the site of other types of global orientation processing relevant to shape processing. For example, the integration of orientation information for the extraction of global contours[13] is thought to involve disparity-tuned (i.e., V2) as well as binocular (i.e., superficial layers of V1) mechanisms because not only can dichoptic versions of the stimulus be detected[14] but also contours that oscillate between different depth planes can be easily detected.[15] The integration of local orientation information to define

object shape and, in particular, circularity has been shown to involve area V4 of the ventral pathway.[15,16] On the other hand, texture boundaries based on local orientation can be discriminated only at a monocular site (e.g., layer 4B of V1) in the pathway.[17]

To determine the site of this form of orientation integration (i.e., involving mean estimation), we measured the ability of normal subjects to estimate the mean orientation of an array of oriented Gabor patches. The orientations of the Gabors were sampled from a signal population, which had different variances under monocular, dichoptic, and stereoscopic viewing conditions. In some conditions, these signal stimuli were accompanied by a set of randomly oriented Gabors (our noise stimuli). If the visual system averages over all the available stimuli, then introducing this orientation noise will enormously disrupt the visual system's performance. However, if the visual system applies extra mechanisms, such as segregation, it might be, to some extent, robust to the effect of the added randomly oriented noise Gabors.

We used an equivalent noise model to derive the best-fitting estimates of internal noise and number of samples from the threshold data. Our results suggest that the site of orientation integration is after the site of binocular integration but before the site of disparity encoding. In a separate manipulation we introduce noise (i.e., samples unrelated to the orientation distribution whose mean is to be estimated) to our stimulus to assess the role of segregation under our stimulus conditions. We find that the effectiveness of noise depends on the eye to which it is presented, suggesting that the eye of origin influences interocular segregation processes.

2. METHODS

Observers. Three observers who were naïve to the purposes of the experiments and the first author were tested. All observers wore their usual optical correction.

Eye dominance. Eye dominance was assessed for each subject with a sighting test.[18] Three subjects were right-eye dominant, and one was left-eye dominant.

Apparatus. A Power Macintosh 6600/800 computer was used to generate and display the stimuli. Stimulus presentation was controlled by the Matlab environment (MathWorks Ltd) and Psychophysics Toolbox.[19] In the main experiment all stimuli were displayed on a 20-in. (1 in. = 2.54 cm) NANAO FlexScan 6600 monitor; however, we used a 20-in. Sony Trinitron GDM-F520 monitor for the disparity and control experiments. Both monitors were calibrated and linearized by use of a Graseby S370 photometer and the Video Toolbox[20] package. Pseudo-12-bit contrast accuracy was achieved with a video attenuator,[21] which combined the red-blue-green outputs of the graphic card (ATI Rage 128) into the green gun. Both monitors had refresh rates of 75 Hz. The mean luminance of the screens was 28 cd/m^2. The resolution was 1152 × 870 pixels for both. One pixel on the screen was 0.32 mm, which was 2.12-arc min of the observers' visual angle from the viewing distance of 52 cm.

Stimuli. Separate stimuli were presented to the left and right eyes, by use of a mirror stereoscope. Each eye viewed an independent image. These images were 6° × 6° wide and arranged on the screen centrally and adjacent to each other. The left- and right-eye images were fused into one cyclopean image by the observer.

Stimuli were arrays of Gabor micropatterns presented on a 30° (height) × 38° (width) (from the observer's distance) mean luminance background. The envelope of each Gabor had a standard deviation of 0.4 deg of visual angle. The spatial frequency of sinusoidal modulation within the Gabors was 0.52 cycles per degree (cpd). Typically, eight Gabors were presented to each eye. These were positioned randomly within a circular area inside the box outline, centered on the center of the box. When the patches overlapped (as could occasionally occur), their gray levels were added; if this led to brightness levels outside the possible luminance range, they were clipped appropriately at the maximum or minimum contrast values.

The orientation of each Gabor was controlled by its parent distribution. Two types of parent distribution were used, producing two Gabor populations: noise and signal. The orientation of each Gabor micropattern in the signal population was selected from a Gaussian distribution with a mean equal to the orientation cue (i.e., 90° ± the cue generated by adaptive probit estimation, an adaptive method of constant stimuli[22]) and a variable bandwidth. The distribution's standard deviation, σ_{ext}, was varied from 0° (all elements aligned) to 28° (high orientation variability). The orientations of Gabors in the noise population were selected from a Gaussian distribution with a standard deviation of 90°. We used the same method to generate the parent distribution of the noise Gabors as we used to generate the parent distribution of the signal array. This meant that the noise population distributions had a randomly selected (on each trial) mean orientation; however, given the breadth of the distribution, this was not discernible. Note also that, since orientation is a circular variable (i.e., any orientation beyond 180° or below 0° is equivalent to its fellow in the 0° to 180° range), our noise populations were equivalent to uniform distributions between 0 and 180 deg. Different combinations of signal and noise were tested. Depending on which condition was tested, each eye's image could contain a signal population, a noise population, both, or just a fixation point. A stereoscope was used to show the left image to the left eye and the right image to the right eye [see Figs. 1(A) and 1(B)]. To prevent any bias, the observers were not informed which population (e.g., signal or noise) was being presented at any time, and, if different Gabor populations were presented to different eyes, the process was randomized within a run so that observers were unaware of which stimulus was presented to which eye. Observers did not receive feedback.

Six combinations of signal and noise were tested (see Fig. 1). In the first five conditions (A)–(E) the signal population, the noise population, and the fixation point were presented in the same disparity plane.

(A) Signal population presented to the dominant eye, and the fixation point presented to the nondominant eye and vice versa.

(B) Signal populations presented simultaneously to the dominant and nondominant eyes.

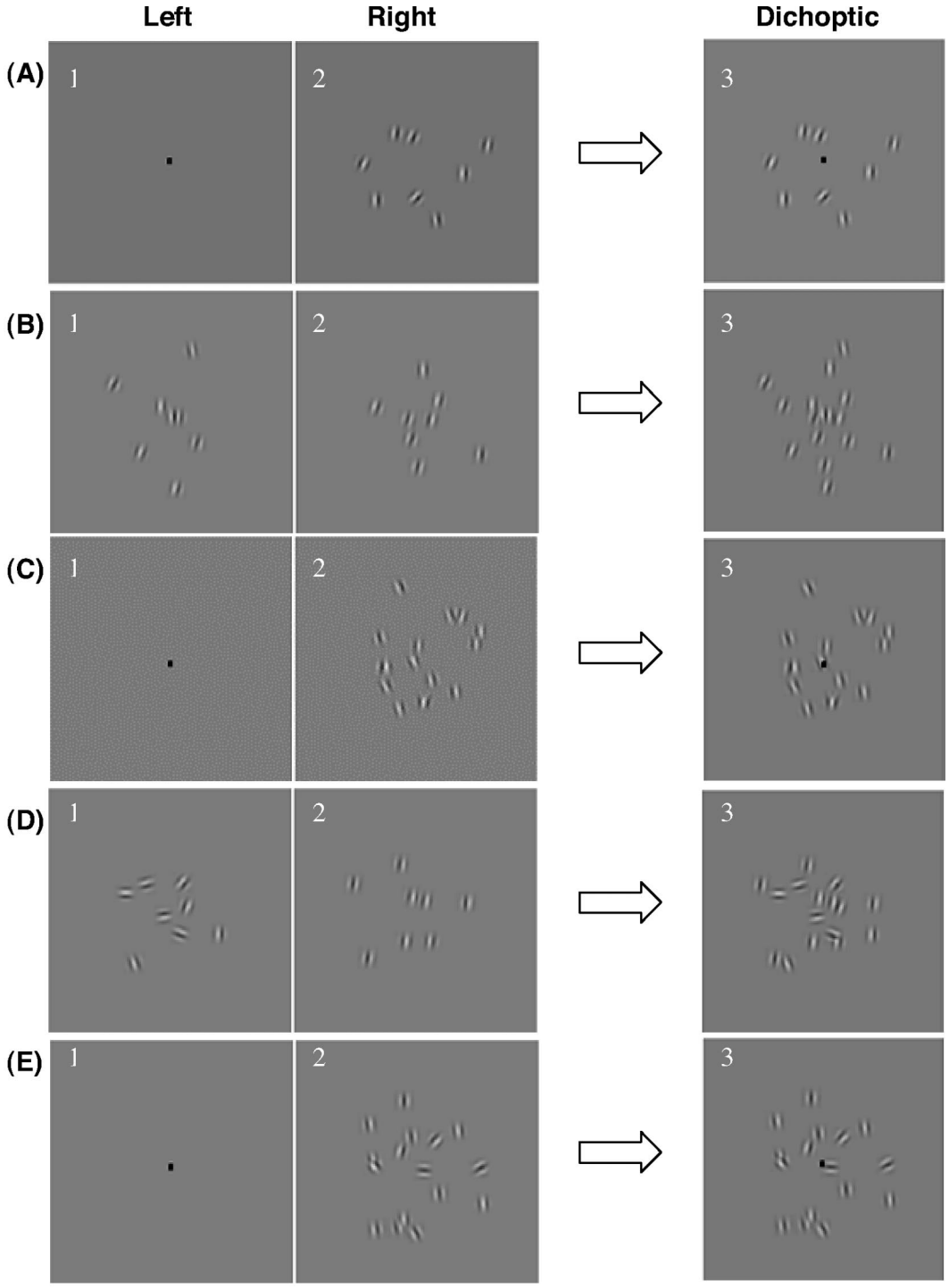

Fig. 1. Two adjacent boxes (1, 2), each holding either stimuli or a fixation point, were located at the center of the screen. Looking through a stereoscope, observers could see one box (3), which contained a fused image. However, the left eye could see only the left box, and the right eye could see the right box. The stimuli could be the signal or noise or both (see Section 2). (A) Eight signal Gabors are presented to one eye, and the fixation point is presented to the other eye. (B) Eight signal Gabors are presented to each eye. (C) Sixteen signal Gabors are presented to one eye, and the fixation point is presented to the other eye. (D) Eight signal Gabors are presented to one eye, and eight noise Gabors are presented to the other eye. (E) Eight signal Gabors and eight noise Gabors are presented to one eye, and one fixation point is presented to the other eye.

(C) Sixteen signal Gabors (two times the typical eight Gabors) presented to the dominant eye, and the fixation point presented to the nondominant eye and vice versa.

(D) Signal population presented to the dominant eye, and the noise population presented to the nondominant eye and vice versa.

(E) Signal and noise populations presented to the dominant eye, and the fixation point presented to the nondominant eye and vice versa.

In a separate condition, (F), signal and noise populations were presented in different disparity planes.

When the signal Gabors are presented to the dominant eye and nondominant eye, they are called StoD and StoND, respectively.

As stated above, typically, the signal and noise populations each comprised eight Gabors. In a later control experiment, one observer (SS) was tested with populations comprising two and 32 Gabors, in all first five conditions (A)–(E).

3. PROCEDURE

A single-temporal-interval two-alternative forced-choice paradigm was used. The observers' task was to judge whether the mean orientation of the array of Gabors was rotated clockwise or counterclockwise (tilted to right or left of vertical) (see Fig. 1). The stimulus presentation time was 500 ms in the main experiment. In a later control experiment this was reduced to 100 ms. On each trial, observers indicated their decision with a button press. The mean orientation of the signal population was controlled by adaptive probit estimation, an adaptive method of constant stimuli[22] that sampled a range of orientations around vertical.

Given that thresholds are estimates of response variance, the nonideal behavior of observers with noiseless stimuli can be expressed as an additive internal noise. The level of internal noise is measured by increasing the amount of external noise in the stimulus and determining the point at which observers' performance begins to deteriorate. If the task requires integration, then observers' robustness to increasing amounts of external noise will depend decreasingly on internal noise and increasingly on how many samples are averaged. Thus the form of the equivalent noise model is

$$\sigma_{\mathrm{obs}}^2 = (\sigma_{\mathrm{int}}^2 + \sigma_{\mathrm{ext}}^2)/n, \tag{1}$$

where σ_{obs} is the observed threshold, σ_{ext} is the external noise, σ_{int} is the estimated equivalent intrinsic or internal noise, and n is the estimated number of samples that is employed. In terms of the orientation-discrimination task, σ_{obs} corresponds to the threshold for orientation discrimination, σ_{ext} to the standard deviation of the distribution from which the samples are derived, and σ_{int} to the noise associated with the measurement of each orientation sample and their combination; n corresponds to the estimated number of orientation samples being combined by the visual system. It is important to note that this is an equivalent noise model and that the model supplies equivalent estimated parameters. This is especially important in the later section in which oriented noise populations (randomly oriented Gabors) are combined with signal Gabor populations. In this case, since the model has no *a priori* knowledge of what is signal and what is noise, the equivalent noise estimate increases and the equivalent sampling rate declines.

Orientation-discrimination thresholds were derived from between 192 and 340 presentations for each of a number of standard deviations of the parent distribution, i.e., external noise (ten levels, typically between 0° and 28°). The orientation threshold for each level of variance of the parent distribution was estimated as the slope of the best-fitting cumulative Gaussian function with a maximum-likelihood procedure in which the threshold was equal to 82% correct.[23] One thousand bootstrap replications of the fitted function were carried out and used to generate 95% confidence intervals (CIs) for the threshold estimates.[24] The orientation-discrimination thresholds at each level of external noise were fitted by the equivalent noise model (see above) to derive the measures of internal noise and number of samples. The model fit was also replicated 1000 times, and this distribution of parameters was used to generate 95% CIs for the model parameter estimated. These CIs were used to compare the interocular differences in each individual observer.

To analyze the model parameters, we performed a two-way mixed analysis of variance with two correlated variables (within subjects). The first variable was the eye with two levels: dominant and nondominant. The second variable is the condition, which had five levels [see Figs. 1(A)–1(E)]. If there were significantly different levels in one variable, we continued the analysis with a pairwise Tukey's *post hoc* test. However, if the interactions of the variables were significant, we applied a simple effect test before the *post hoc* test. The q values were calculated with the *post hoc* Tukey's test. Since we had two correlated variables, we adjusted the degrees of freedom of the error terms. We tested each model parameter (i.e., internal noise and number of samples) separately.

4. RESULTS

Orientation-discrimination thresholds are shown in Fig. 2. In each figure the threshold orientation offset is plotted against the standard deviation of the population from which the local orientation samples were derived. The solid and dotted curves are the fits of the model from which the parameters of internal noise (σ_{int}) and number of samples (n) are derived (insets in figures). The internal noise parameter is determined by the asymptotic thresholds at low variances, whereas the sampling rate determines how rapidly thresholds rise with increasing variance. Results for four subjects' dominant (dotted curve) and nondominant eyes (solid curve) are shown for the stimulus conditions (A)–(E) previously outlined in Fig. 1.

Parameters from the fitted equivalent noise model are summarized in Fig. 3.

Figure 3(A) shows the internal noise parameter for each condition, averaged over the observers. We compared conditions when the signal was presented to the dominant eye (StoD, open bars) with the case when the signal was presented to the nondominant eye (StoND, filled black bars). Depending on the condition (for the key to column titles, see Fig. 1), noise Gabors might have accompanied the signal Gabors. In terms of the internal noise, the interaction of the two variables was significant [$F(4, 12) = 14.55, p = 0.0001$]. Therefore the following analyses have been extracted from simple effect and *post hoc* tests.

1. Comparing StoD [compare open bars in Fig. 3(A)] across all observers, there is no statistically significant difference between these five conditions [A(StoD)–E(StoD)] [$F(4, 20) = 2.17, p > 0.05$]. However, the re-

sults from individual subjects showed a trend of increasing internal noise when noise Gabors were added to the signal. The fact that dichoptically (to nondominant eye) and monocularly presented noise Gabors have the same effect on performance as signal Gabors presented to the dominant eye [compare D(StoD) and E(StoD)] suggests that signal and noise are linearly combined in the dominant eyes' visual stream when they are presented dichoptically.

2. When the signal is presented to the nondominant eye (StoND) and the noise is presented to the dominant eye [condition D(StoND)] or nondominant eye [condition

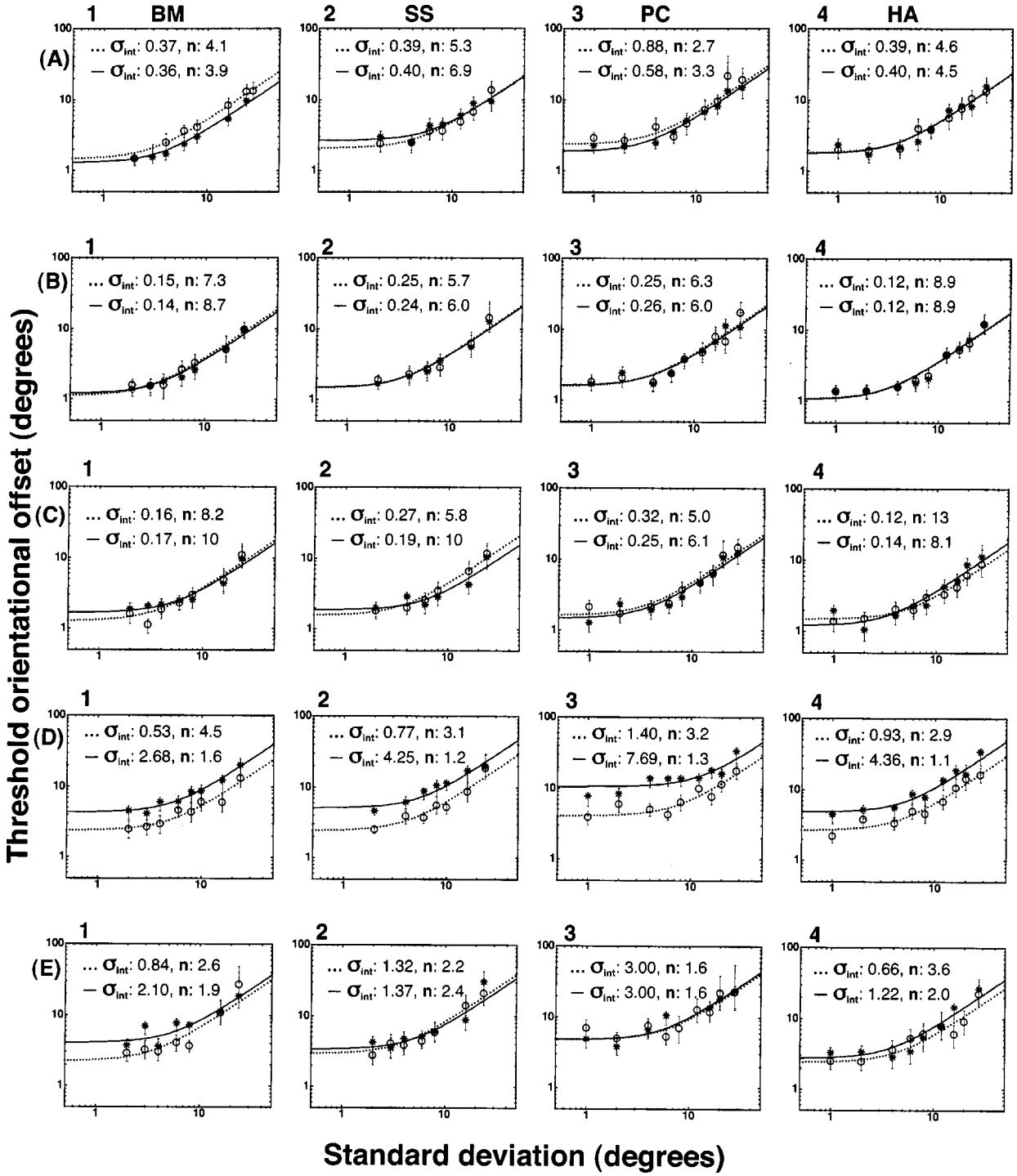

Fig. 2. Data from observers (BM, SS, PC, and HA) are presented in four columns (1, 2, 3, and 4), respectively. Five conditions (A), (B), (C), (D), and (E) are tested as described in Section 2. The orientation threshold offset is plotted for each standard deviation of the signal population (external noise). Circles represent the data from presenting the signal to the dominant eye (StoD), and the stars show the data from presenting the signal to the nondominant eye (StoND). In condition B, both eyes are presented with the signal (StoB). The best fits for StoD and StoND data are shown, respectively, as dotted and solid curves. The parameters of internal noise (σ_{int}) and number of samples (n) from the fitting model (see Section 2) are shown for each observer and for each condition (StoD and StoND). Error bars represent 95% CIs.

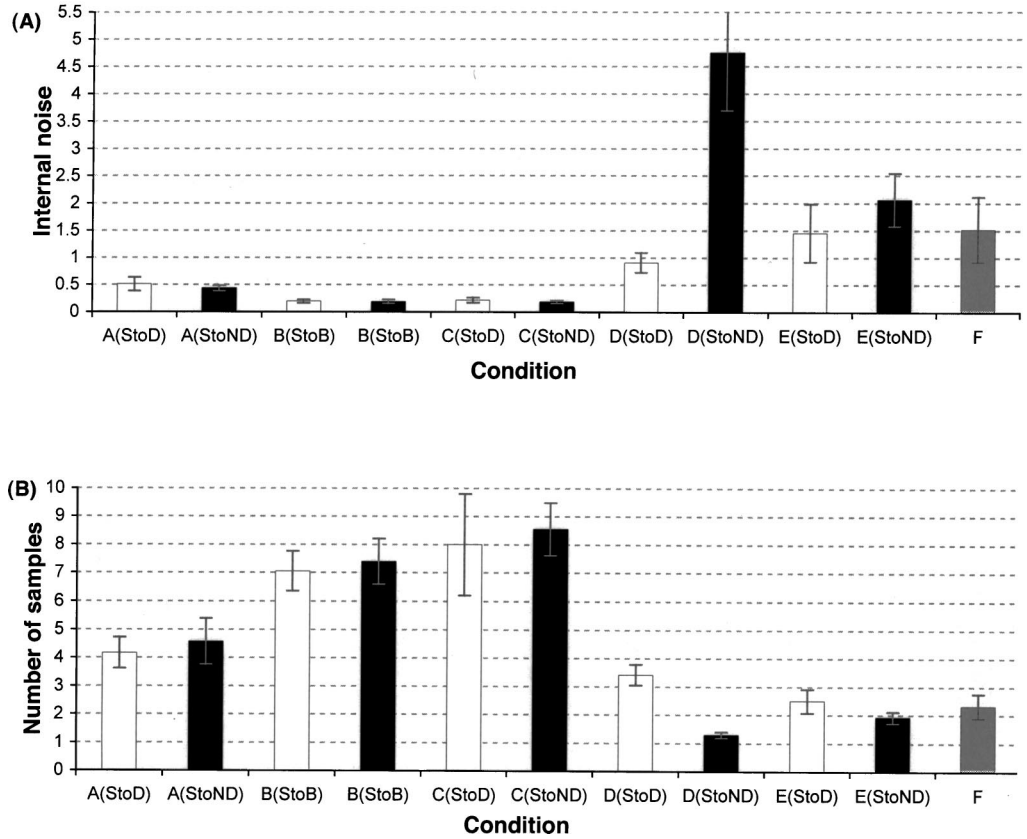

Fig. 3. (A) Internal noise and (B) number of sample parameters are shown from the different conditions (see Section 2). Open and black bars represent StoD and StoND, respectively. In condition B, both eyes are presented with the signal (StoB). Gray bars (F) represent the condition in which the signal and noise are presented in different disparity planes. Error bars represent ±0.5 standard deviations.

E(StoND)] [compare black bars in Fig. 3(A)], internal noise is significantly higher than when only the signal is presented to the nondominant eye either monocularly or binocularly [conditions A(StoND), B(StoB), and C(StoND)] [$q(5, 19.49) = 9.2$ (in average), $p < 0.01$]. These differences were more prominent when the noise Gabors were dichoptically presented to the dominant eye [D(StoND)] [$q(5, 19.49) = 12.6$ (on average), $p < 0.01$], which were also significantly higher than the internal noise in noise to the nondominant eye [E(StoND)] condition [$q(5, 19.49) = 7.82, p < 0.01$].

3. When we compare dominant eyes with nondominant eyes [compare open and black bars of Fig. 3(A)], internal noise is significantly different only in condition D, where signal Gabors were presented to the dominant eye and randomly oriented noise Gabors were presented to the other eye. The internal noise in StoND [D(StoND)] is significantly higher [$F(1, 13.67)$, $p < 0.0001$] than the internal noise in condition D(StoD).

In Fig. 3(B), the differences in condition variable were significant [$F(4, 12) = 25.09, p < 0.0001$] when we tested the number of sample parameters. Figure 3(B) summarizes the number of sample parameters for each condition, averaged over all observers. The number of samples is significantly higher when signal populations are presented to both eyes (condition B), rather than to just one eye (condition A) [$q(5, 12) = 5.09, p < 0.05$], suggesting an improvement with binocular viewing. The number of samples is significantly greater when a population of twice the size is presented monocularly (condition C) than when the regular-sized population is presented to the dominant eye (condition A) [$q(5, 12) = 6.98, p < 0.05$]. When the signal population is evenly distributed between the two eyes in binocular viewing, however, the number of samples is equal to the case in which a signal population of twice the size is presented to just one eye (compare conditions B with C) [$q(5, 12) = 1.9, p > 0.05$]. This suggests binocular linear combination. Adding a noise population decreases the estimates from sampling efficiency of both eyes. Conditions D and E have a lower number of sample estimates than any of the conditions without noise Gabors (conditions A, B, and C) [$q(5, 12) = 7.87, p < 0.01$]. However, this decrease did not reflect a decrease in the visual system's sampling efficiency because the randomly oriented noise Gabors, which the visual system integrates, are not useful in estimating the mean and must automatically be registered as lower estimates of the number of samples by the model.

In a separate experiment we tested whether noise presented in a different disparity plane was effective in raising the internal noise and lowering the number of samples as illustrated above for stimuli in the same depth plane. Two disparity planes were used: One was in the fixation plane and contained the eight signal elements, and the other was at a crossed disparity of 33.92 arc min and contained eight noise elements. Observers were not

aware of which population (e.g., signal or noise) was presented to which plane. The results are shown in Fig. 4, and the parameter summaries are given in Fig. 3(A) condition F for internal noise and Fig. 3(B) condition F for the number of samples. The internal noise and the number of samples found when noise is added in a different depth plane in condition F(StoND) are more similar to those found when the noise is added in the same plane as the signal (conditions D and E) than they are when there is no noise (condition A). This suggests that noise presented in a different depth plane is equivalent to noise presented in the same depth plane.

In the main experiment when signal or noise elements were presented to separate eyes, we did not prevent the few cases in which left- and right-eye elements overlapped. Consequently, we wondered whether rivalry could have played a part in our initial finding that noise presented to the dominant eye is more effective. Since rivalry takes some time to build up and can be disrupted by brief presentations,[25] we undertook a control experiment in which the stimulus was presented for 100 ms rather than the 500 ms that we had used previously. These results are shown in Fig. 5 for the dichoptic condition when the signal is presented to one eye and the noise to the other [as in Fig. 1(D)]. Circles are for StoD (and noise to the nondominant eye), and stars are for StoND (and noise to the dominant eye). There are a significant increase in internal noise (the CI is 95%, $p < 0.05$) and a significant decrease in the number of samples (the CI is 95%, $p < 0.05$) when noise is presented to the dominant eye and the signal to the nondominant eye compared with the other way round. This confirms that the asymmetry observed in our main experiment is also present when the exposure duration is shortened to 100 ms, making it unlikely that binocular rivalry played a major role.

Finally, we show in Fig. 6 the results for one subject (SS) for populations of Gabors ranging from 2 to 32 elements, displayed in the same manner as that already described for Fig. 2.

Model parameters (internal noise and number of samples) derived from the continuous (solid and dotted) curve fits to these data are summarized in Fig. 7 in a manner comparable with that already described for Fig. 3. The results show that our conclusions derived from a

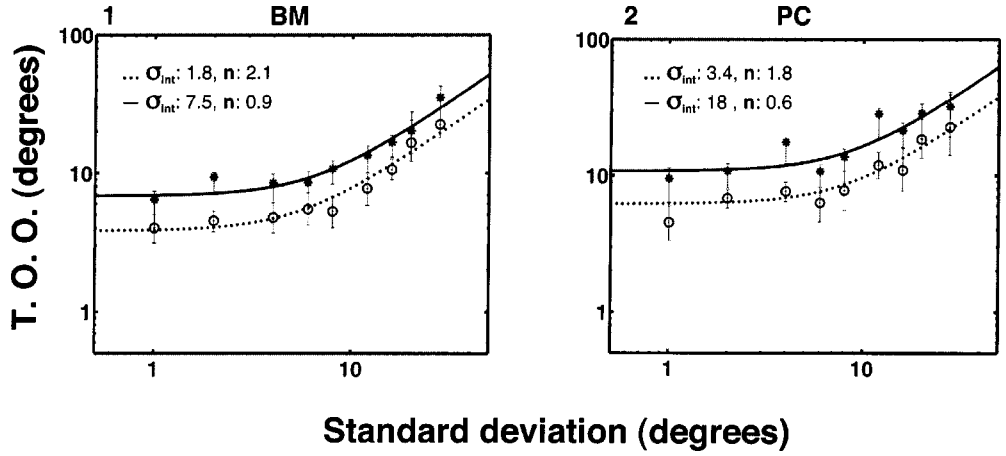

Fig. 4. Orientation-discrimination thresholds and the parameters from the equivalent noise model are presented for conditions F(StoD) and F(StoND). The disparities are 33.92 arc min and zero. The orientation-discrimination thresholds, internal noise, and number of samples in condition F(StoD) are not significantly different (the CI is 95%, $p > 0.05$) from those of the control condition F(StoND). Error bars represent 95% CIs. T.O.O., threshold orientation offset.

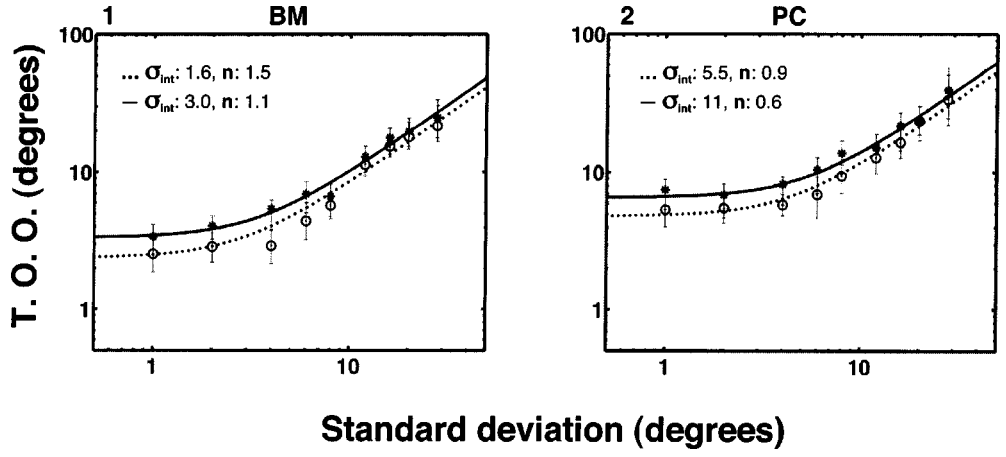

Fig. 5. Data from a control experiment that reduced presentation duration for conditions D(StoD) and D(StoND). Presentation time was 100 ms for two observers. The differences in thresholds, internal noise, and number of samples are significant (the CI is 95%, $p < 0.05$). Error bars represent 95% CIs. T.O.O., threshold orientation offset.

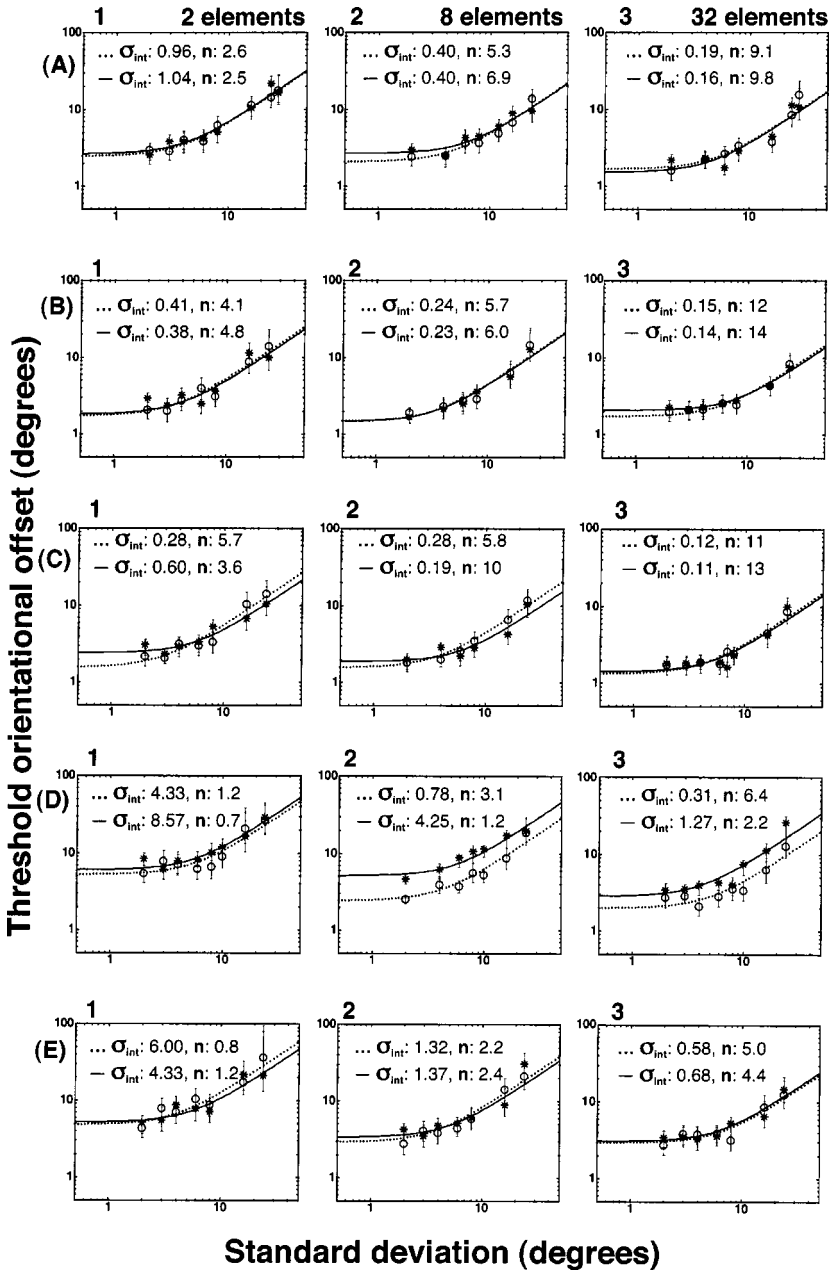

Fig. 6. Beside the eight Gabors in the main experiment, two numbers of Gabors (2, 32) were tested with one observer (SS). Five conditions are presented in the same configuration as used in Fig. 1. Internal noise is generally decreased and the number of samples is increased when the number of Gabors is increased. The significant differences in condition D is replicated within the cases of 2 and 32 Gabors. Error bars represent 95% CIs.

population of eight Gabors (Figs. 2 and 3) can be generalized to populations from 4 to 32 elements. In particular, signal summation is comparable within eyes [A(StoD) and A(StoND)] and between eyes [B(StoB) and B(StoB)], even in the presence of added noise [E(StoD) and E(StoND)]. However, noise to the dominant eye D(StoD) is statistically more effective in raising the internal noise and lowering the number of samples than noise to the nondominant eye [D(StoND)].

5. DISCUSSION

We have used a task that involves the integration of local orientation information and that is processed in an efficient and preattentive fashion by the visual system.[8] What appears to limit performance on this task is more the informational capacity of the stimulus rather than the visual processing *per se*.[8] By varying the standard deviation of a Gaussian distribution from which the samples are drawn, one can quantify integrative performance in terms of a two-parameter model (equivalent noise model) in which the parameters are internal noise and number of samples.

A. Integration Site

Our first issue concerned the site of this integration relative to binocular and disparity processing. Since we find that our two model parameters (internal noise and num-

ber of samples) are similar under monocular [Fig. 2(C)] and dichoptic [Fig. 2(B)] conditions, we conclude that this form of orientation integration is likely to occur after binocular combination. This is strengthened by the findings that dichoptically presented noise [Fig. 2(D)] can be, in some situations, more detrimental than the same noise presented monocularly [Fig. 2(E)] and that the addition of signal or noise dichoptically and monocularly is equivalent. Furthermore, we found that the effects of such noise cannot be reduced when it is presented in a different depth plane [Fig. 2(F)]. This suggests that the site of this form of integration is prior to the site of disparity processing. This indicates that the integration of arrays of Gabors occurs after the processing of simple texture boundaries[17] but at a stage similar to contour integration.[14,15] Since the earliest site of binocular combination is in layer 4 of V1[26] and the earliest site where relative disparities are processed is V2,[27] it would seem that this form of orientation integration occurs somewhere between the input cells in layer 4C of V1 and the input layer 4 in V2.[28] The finding that orientational opponency is present in V1[29] is suggestive that the site of integration may be in the more superficial layers of V1.

B. Segregation

With the addition of randomly oriented Gabor patches, our noise never reduced performance as much as would have been predicted if the visual system was blindly sampling from the orientation elements and integrating these samples. We devised an ideal observer model that blindly integrated signal and noise Gabors. We used the model to estimate the internal noise that would arise if observers took the observed number of samples but blindly selected either signal or noise. For example, when signal and noise Gabors were presented to one eye, the mean estimate of number of samples was 2.21, and the average estimated internal noise was 2.82. Blindly integrating signal and noise elements by an ideal observer model predicts an internal noise estimate of approximately 19.49. If the model takes the samples from a more restrictive range of orientations around the mean, instead of averaging every element, the ideal observer is more robust to the effect of added noise. Our simulations show that internal noise comparable with that found experimentally is found when our ideal observer model takes the samples over a range of 50 deg (mean ±25 deg). However, this assumes that the more restrictive region

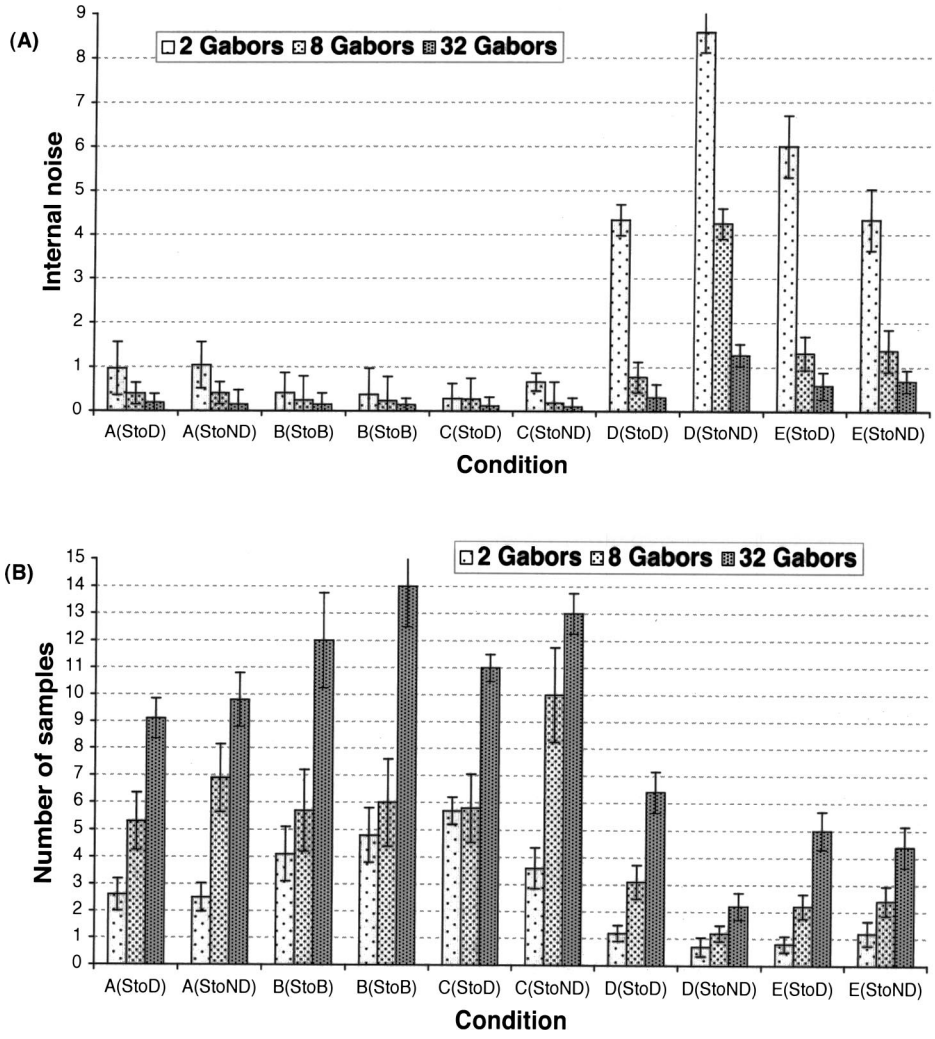

Fig. 7. Internal noise and number of sample parameters are shown for three numbers of Gabors (2, 8, and 32) and all conditions displayed in Fig. 6 (see Section 2). Dotted and solid curves represent StoD and StoND, respectively. In condition B, both eyes are presented with the signal (StoB). Error bars represent 95% CIs.

over which signal and noise integration takes place is fixed, an assumption that has, as yet, no experimental support. It should be stressed that the signal and noise Gabor populations were identical in every way except orientation distribution. Some segregation of signal and noise elements must have taken place. This suggests that there are monocularly based segregation processes at work to reduce the effectiveness of the noise and, by analogy to luminance adaptation in the retina, this may involve an opponent interaction. An opponent mechanism that estimated the magnitude of orientation noise presented by, for example, the response of a population of nonoriented neurons could regulate sensitivity.

C. Eye Dominance

We also investigated the effect of noise on signal integration. We show that the two key model parameters for signal integration are statistically identical between dominant and nondominant eyes of our observers. This is also the case when a population of noise elements is introduced. When this population of noise elements is introduced through one eye and the signal through the other eye, the effectiveness of that noise depends on the eye of origin. At the binocular site where we suggest integration takes place, segregation (i.e., involving signal and noise), but not integration (involving just signal), is less effective when the noise comes from the dominant eye rather than vice versa. This segregation can take place only after binocular combination for these dichoptic stimuli. These results suggest that the monocular input weights at the site of binocular combination are different for integration compared with segregation.

Of particular interest is the finding that the effect of the so-called dominant eye, defined by sighting tests,[18] is shown to be selective for segregation. We found no eye-based differences for pure signal integration under either monocular [Figs. 2(A) and 2(C)] or dichoptic [Fig. 2(B)] conditions. When the task had a segregation component, there was a clear eye-based difference only in the dichoptic condition [Fig. 2(D)], not in the monocular condition [Fig. 2(E)]. It is unlikely that this can be explained by other than low-level processes, since the eye through which the noise entered was randomly interleaved across trials. It is not that the monocular performance of one eye is superior to that of the other [Fig. 2(E)] but rather that, under dichoptic conditions, noise through one eye can be better segregated from a signal through the other eye when that noise comes from the nondominant eye. A mechanism similar to that proposed above for monocular segregation, but having interocular inputs, may also underlie the benefit of nondominant eye noise on the integration of dominant eye signal, if one assumes that the input gain varies between eyes.

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