Disentangling signal from noise in visual contrast discrimination

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Human ability to detect stimulus changes (ΔC) decreases with increasing reference level (C). Because detection performance reflects the signal-to-noise ratio within the relevant sensory brain module, this behavior can be accounted for in two extreme ways: first, the internal response change ΔR evoked by a constant ΔC decreases with C (that is, the transducer $R = f(C)$ displays a compressive nonlinearity), whereas the internal noise is independent of R; second, ΔR is constant with C but the noise level increases with R. A newly discovered constraint on human decision-making helps solve this century-old problem: in a detection task where multiple changes occur with equal probabilities, observers use a unique response criterion to decide whether a change has occurred. For contrast discrimination, our results supported the first account above: human performance was limited by the contrast transducer nonlinearity and an almost constant noise.

Human performance in detecting a stimulus change, the discrimination threshold, is assumed to reflect the sensitivity of the corresponding sensory module in the brain and is used to infer the response characteristics of that specific module. Because this sensitivity measure reflects the signal-to-noise ratio at the processing stage where decisions are made[1], changes in sensitivity may reflect changes in either signal or noise. Psychophysical methods available so far are unable to distinguish between these two alternatives. Figure 1a demonstrates the problem using standard signal detection theory (SDT)[1]. As a result of the stochastic nature of neuronal responses, any two (just discriminable) stimulus values, call them C and $C + \Delta C$, generate two distributions of internal response values (the pairs of dashed and solid Gaussian functions), with sensitivity (d') computed as the difference between the means divided by the (equal) standard deviation of the two distributions. In practice, d' is estimated from the observer's frequency of correct responses on the two types of available stimuli (C and $C + \Delta C$; see below). For a constant stimulus increment (or decrement; ΔC), d' typically decreases with the increasing base value, C (or 'pedestal'), a behavior known to hold for all sensory dimensions. This behavior (coined Weber's law when $\Delta C_\theta/C$ is constant[2–4], with ΔC_θ being the discrimination threshold) is believed to reflect a basic limitation on sensory processing[2,5–12]. Given the ambiguity in interpreting psychophysical sensitivity changes, this limitation may result from an increasing noise, from a reduced response gain as the internal activity level increases, or both.

Here we present a psychophysical method to discriminate between these two possibilities. The method was applied to contrast discrimination but it can be generalized to any other dimension. The key feature of this method is that it permits the gauging of the noise factor across the sensory (that is, internal response) continuum. This gauging was achieved by using a newly discovered constraint on human decision-making[13] (A. Gorea and D. Sagi, *Invest. Opthalmol. Vis. Sci.* Suppl. 40, S796, 1999): in a multiple detection task during which multiple signals are presented with equal probabilities, observers use a unique decision criterion (see below).

In an increment detection task (Fig. 1a and b), repetitive presentations of a stimulus produce a variable internal response, generating an internal response distribution, here assumed to be Gaussian. Figure 1a presents, on an 'absolute' internal response continuum, the internal response distributions generated by two different strength contrasts (or pedestals; dashed curves) and by two equally discriminable contrast increments (or signals; solid curves) added to each pedestal. Stronger stimuli are assumed to generate a larger variability of the internal response. To the extent that observers' discrimination judgments in each of the two conditions are always referenced to the corresponding pedestal, the internal responses generated by each of these two baseline contrasts can be mapped on a decision space such that their means are aligned at the zero point of a 'relative' internal response continuum (Fig. 1b).

To discriminate between two stimulus values, observers must use a decision criterion on the decision axis in reference to which the current internal response, if stronger, is attributed to an actual stimulus increment (that is, to a signal, a 'yes' response), or, otherwise, to the comparison baseline (the noise, a 'no' response). Observers are free to select any internal response value as the decision criterion but are constrained so that they use only one such value for the two baseline conditions when they are mixed within the same experimental block[13]. This unique criterion, c_U (heavy vertical line with an arrow in Fig. 1b), is somewhere in between the values (c_1 and c_2) used by observers when each stimulus pair is tested in isolation[13].

In SDT, the value of the decision criterion, c (relative to the mean of the noise distribution generated in this particular case by

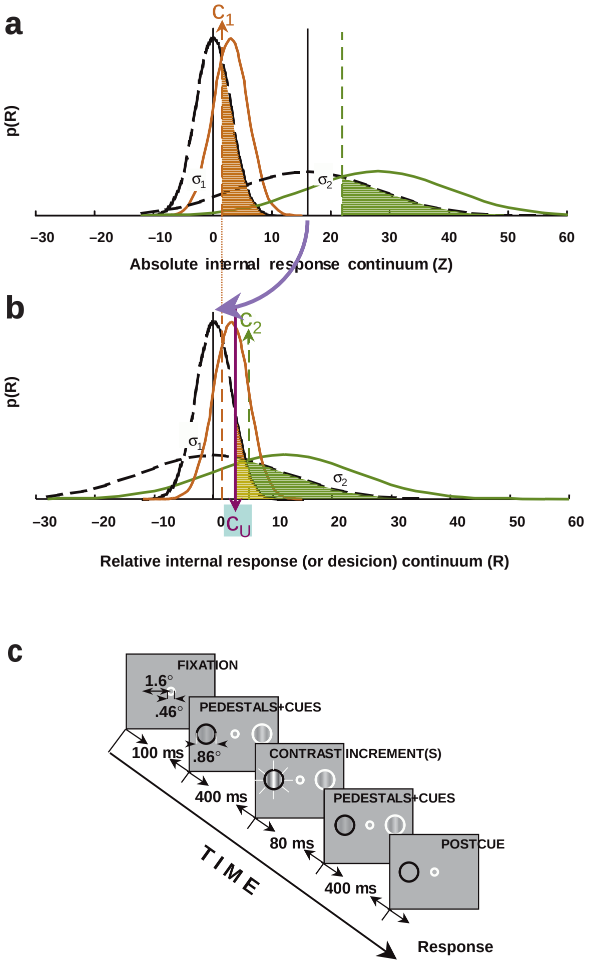

Fig. 1. Signal detection theory[1] framework and the trial sequence. (**a**, **b**) Gaussian functions describe the probability density, *p*(*R*), of the internal response distributions (in arbitrary units; abscissa) for two equally visible contrast increments (signal, S; solid curves) added to two different strengths baselines (noise, N; dashed curves). The illustration assumes that the standard deviation, σ, of the S and N distributions increases with the strength of the latter ($\sigma_2 > \sigma_1$) and that, close to threshold, the σ associated with N and S are practically identical ($\sigma_N = \sigma_S$). When S and N have equal occurrence probabilities, an optimal observer should place his absolute response (seen/not seen) criterion, *c*, at the crossing point of each of the two S–N distribution pairs (vertical dotted lines). The location of *c* on the internal response continuum relative to the mean of N (solid vertical lines) is derived from the negative *Z*-score of the 'false alarms' (shaded areas) recorded for each pedestal. In (**a**), the two internal response distributions pairs are displayed on an 'absolute' internal response continuum axis. However, observers' discrimination judgments for each of the two baseline conditions are referenced to that baseline so that the internal responses generated by each of them is mapped in (**b**) on a 'relative' decision continuum where their means are aligned at the zero point. Under this representation as well, the optimal observer should use distinct response criteria, c_1 and c_2; the unique criterion constrain requires that he use a unique *c*, c_U, located somewhere in between c_1 and c_2 (solid vertical line with an arrow). Because equal decision performances involve equal internal response differences, Δ*R*, and because the latter are equal to *c* when measured in the appropriate σ-units, it is true that $c_1 = c_2 = c_U$. (**c**) One trial sequence (see text).

the baseline contrast), is given in units of the standard deviation of the noise (σ). This criterion is estimated from the measured error rate for 'yes' responses, that is, when observers report a signal in its absence (false alarms, FA; shaded areas in Fig. 1); it is the negative *Z* score of the probability density function of such responses, –ZFA. The unique criterion constraint requires that, when measured in internal response units, any two criteria c_1, c_2 assessed for two jointly presented baselines (C_1 and C_2) be equal: $c_1 = c_2 = c_U$, with $c_1 = \mathrm{ZFA}_1 \cdot \sigma_1$ and $c_2 = \mathrm{ZFA}_2 \cdot \sigma_2$; thus, the following is true.

$$\frac{\sigma_1}{\sigma_2} = \frac{\mathrm{ZFA}_2}{\mathrm{ZFA}_1} \tag{1}$$

Because ZFA_i is experimentally measurable, the noise ratio σ_1/σ_2 can also be estimated as a function of the reference contrast ratio C_1/C_2. For equally likely signals, models assuming constant noise at the decision stage predict $\mathrm{ZFA}_2/\mathrm{ZFA}_1 = 1$. The present results supported this view: for contrasts up to 60% (about 12 times the detection threshold), discrimination was essentially limited by a close-to-constant internal noise (at the decision level) and it decreased with baseline contrast mostly because of a gain reduction (compressive nonlinearity) in the transducer.

RESULTS

For suprathreshold baselines (*C*), the threshold-versus-contrast (TvC) functions obtained in the two-alternative forced choice (2AFC) experiments (four observers) exhibited a typical power low behavior[7,14,15], $\Delta C_\theta \propto C^{\omega}$, with an average $\omega_{2AFC} = 0.57 \pm 0.02$ (mean and standard error across observers; Fig. 2). Thus, contrast discrimination deviated significantly from Weber's law ($\omega = 1$). On the condition that *d*′ is linear with Δ*C* and has a zero intercept[1,9,16,17] (also see Methods), the discrimination threshold, $\Delta C_\theta = \Delta C/d'$ could also be derived from the main yes/no experiment. When fit to this set of data, the TvC function yielded $\omega_{y/n} = 0.59 \pm 0.03$; ω_{2AFC} and $\omega_{y/n}$ were practically identical. The exponent ω may result from the nonlinearity of the transducer, that is, of the relationship between the internal response *R* (at the decision stage) and *C*: $R \propto C^{\gamma}$ (Steven's law[11]); from an equivalent dependency of the noise, σ, on *R*: $\sigma \propto R^{\beta}$ (refs. 8, 9); or from both. On the latter assumption and given that at the discrimination threshold, $\Delta R_\theta = \sigma$ (ref. 1), one may derive the discrimination threshold ΔC_θ by taking the derivative of *R* with respect to *C*:

$$\Delta C_\theta \propto C^{\,\omega = 1 - \gamma + \gamma\beta} \tag{2}$$

To proceed along the logic presented in the Introduction, we needed to establish, on the one hand, that at equal sensitivities, observers used the same criteria (ZFA values) whatever the 'same'-baseline contrasts, and that these criteria were sensitivity-dependent. On the other hand, we needed to confirm that observers adopted a unique criterion when the different sensitivity increments (ΔC) applied to equal baseline stimuli, were mixed together. In Fig. 3a, *d*′ and ZFA values (averaged over the four observers) are shown for stimulus pairs of identical baselines and increments (same-*d*′) at the four baseline contrasts used in the main experiment (different symbols). The main observation was that both *d*′ and ZFA values lied within very narrow ranges (respectively, 1.45–1.90 and 0.94–1.17) indicating, on the one hand, that the ΔC values were appropriately chosen and, on the other hand, the absence of a criterion drift due to the contrasts of the paired baselines. When tested at two different ΔC

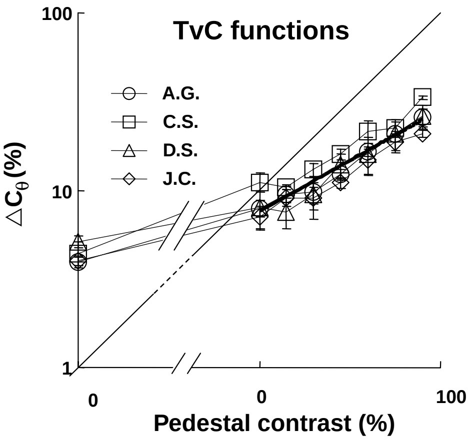

Fig. 2. Threshold increments versus contrast functions for four observers (different symbols). Within the 10–60% contrast range, the data are well fit by a power function with an exponent ω = 0.57 (thick black line). This is substantially different from a power function with an exponent of one as required by the Weber's law (thin black line).

values, each paired with itself (Fig. 3b; open symbols), the criteria closely followed the expected ZFA = $d'/2$ relationship (dotted line). A different behavior is observed for different-d' conditions where the paired ΔC values were chosen to yield rather large d' differences. This condition yielded about identical ZFA values despite the fact that the d' values remained practically unchanged (with respect to the same-d' condition): this demonstrates the unique criterion constraint previously revealed in absolute detection experiments[13]. Note that it was realized by means of a rather large upward drift and of a smaller downward drift of the originally low and high ZFA values, respectively.

The substantiation of the unique criterion constraint with suprathreshold stimuli validated Eq. 1 and allowed the derivation of the noise ratio, $\sigma_R = \sigma_i/\sigma_j$ from the criterion ratio ZFA_j/ZFA_i for all baseline contrast ratios $C_R = C_j/C_i$ (with $j > i$). Referring back to the form of the transducer ($R \propto C^\gamma$) and to the relationship between noise and the internal response ($\sigma \propto R^\beta$) and using Eq. 1 yields the following.

$$\sigma_R = \frac{ZFA_2}{ZFA_1} = \left(\frac{C_2}{C_1}\right)^{-\gamma\beta} \qquad (3)$$

The estimated σ_R was almost independent of C_R for each observer (different symbols in Fig. 4a); it yielded a log–log slope $-\gamma\beta = -0.1 \pm 0.08$. Indeed, the best power fit for three of the four observers yielded a $\gamma\beta$ exponent of zero.

Next we determined γ, the exponent of the transducer $R = f(C) \propto C^\gamma$. For small C increments (or decrements), $\Delta R = f'(C)\Delta C$ with $f'(C) = \alpha = \gamma C^{\gamma-1}$, the slope of the transducer at C (see inset in Fig. 4b). It follows that the α_2/α_1 ratio for a given baseline pair C_2, C_1 is given by $(C_2/C_1)^{\gamma-1}$. On the other hand, by SDT, $d' = \alpha\Delta C/\sigma$. Thus, the following equation applies.

$$\frac{\alpha_2}{\alpha_1} = \frac{d'_2 \cdot \Delta C_1 \cdot \sigma_2}{d'_1 \cdot \Delta C_2 \cdot \sigma_1} = \left(\frac{C_2}{C_1}\right)^{\varphi = \gamma - 1} \qquad (4)$$

From the unique criterion constraint (Eq. 1), the following is true.

$$\frac{\alpha_2}{\alpha_1} = \frac{d'_2 \cdot \Delta C_1 \cdot ZFA_1}{d'_1 \cdot \Delta C_2 \cdot ZFA_2} = \left(\frac{C_2}{C_1}\right)^{\varphi = \gamma - 1} \qquad (5)$$

The α-ratio was measurable, as the mid-term of Eq. 5 could be estimated from the data. If the transducer were linear, α_R should have equaled unity for any baseline contrast ratio $C_R = C_2/C_1$. The linear regression line (on log–log coordinates), $\alpha_2/\alpha_1 \propto (C_2/C_1)^\varphi$, fit to the data of all observers, yielded a log–log slope $\varphi = -0.42 \pm 0.07$ with $\gamma = \varphi + 1 = 0.58$ (Fig. 4b). Thus, the transducer displayed a strong compressive nonlinearity. The noise dependency on R could then be computed from $\gamma\beta = 0.1$ and $\gamma = 0.58$, to yield an exponent $\beta = 0.17$. Because $\omega = 1 - \gamma + \gamma\beta$ (Eq. 2), our analysis predicted $\omega = 0.52$, very close to the observed value (0.57).

DISCUSSION

The present work offers psychophysical means of directly and unambiguously separating the contribution of noise and signal to the human decision process. For sensory discriminations, it

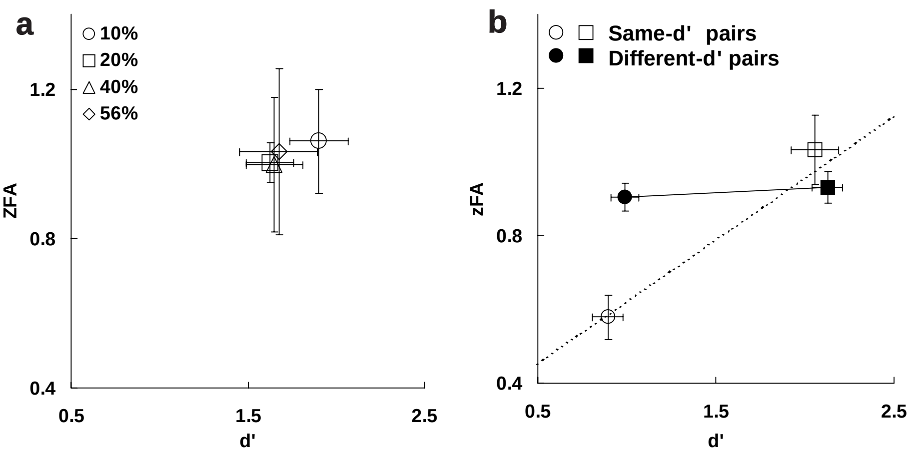

Fig. 3. Response criteria expressed in *Z*-scores of false alarms (ZFA) as a function of the sensitivity index, d'. ZFA values are averaged over the four observers. In (**a**), the data are for all baselines paired with themselves with contrast increments (ΔC) chosen so as to yield close to identical d' values. Different symbols are for the different baselines. In (**b**), the data are for ΔC values chosen so as to yield d' values close to 1 and 2 when applied to baseline contrasts of either 10 or 40%. Open and solid symbols are for same-d' and different-d' conditions, respectively. The former involved the pairing of identical stimuli (baselines and increments); the latter refer to ΔC pairs yielding different d' values also applied to identical baselines. For both conditions, datum points are averages computed over stimuli yielding low (circles) and high (squares) d' values. The same-d' data lie close to the SDT prediction (the dotted line with a slope of 0.5). The different-d' data (connected by the solid line) lie close to the horizontal demonstrating that under such conditions observers use a unique response criterion (ZFA).

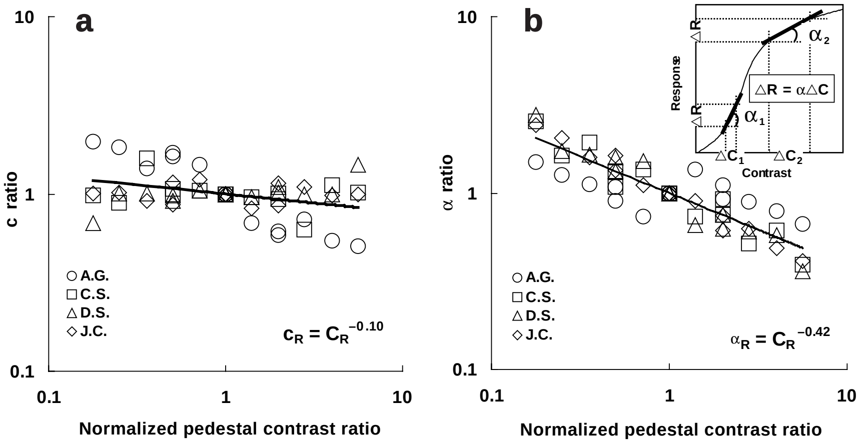

Fig. 4. Criterion (ZFA) ratio and α-ratio as a function of the normalized pedestal-contrast ratio for all possible pairwise combinations of the four baseline contrasts used in the main experiment. Different symbols are for different observers. The power functions fit to all the data yield an exponent of –0.1 and –0.42 for the criterion ratio (**a**) and the α-ratio (**b**). The inset in (**b**) shows an arbitrary transducer characterized by its local slope, α. The standard assumption that any liminar contrast increment (or decrement), ΔC, yields a constant internal response increment (or decrement), ΔR, entails $\Delta R = \alpha\Delta C$.

enabled the identification of the transducing process at the level of the relevant neural module and of its associated noise at the decision stage. Applied to contrast discrimination, our analysis revealed a strongly compressive nonlinearity (in the form of a power function with an exponent $\gamma = 0.58$) and an internal noise only moderately dependent on contrast (described by a power function with an exponent $\gamma\beta \approx 0.1$). When combined, the two components accounted well for the measured TvC behavior. The small and non-significant discrepancy between the predicted ($1 - \gamma + \beta\gamma = 0.52 \pm 0.11$) and the actually estimated ω-exponent (of the TvC function; $\omega_{2AFC} = 0.57 \pm 0.02$; $\omega_{Y/N} = 0.59 \pm 0.03$) may be due to various inaccuracies, including that of the linearity assumption between d' and ΔC (refs. 9, 18, 19) (that is, $\Delta C/d' = \Delta C_\theta$) and of the representation of the transducer (and therefore of the TvC behavior) as a straightforward power function ($R \propto C^\gamma$, Stevens law[11]; within the presently tested contrast range, this approximation accounted for about 90% of the variance in the fit of the measured TvC functions).

Our paradigm is meant to assess the overall noise at the decision stage, that is, after the last transduction stage. As such, it encompasses a whole sequence of transduction steps and noise sources that may well be contrast-independent (additive) and/or contrast-dependent (multiplicative). Others have examined the noise level at earlier stages of visual processing. Using the fine details of the psychometric function (d' versus ΔC), the noise added to the output of the first nonlinear transduction stage was estimated to be a power function of the corresponding internal response with an exponent of 0.8 (ref. 9). However, their method is not sensitive to nonlinearities following the processing stage where the limiting noise is added as these nonlinearities preserve the signal-to-noise ratio (and thus the d') estimated by these experiments. Similar conclusions were reached by using external noise to estimate the critical internal noise[19,20]. Because the external noise passes through the same transduction nonlinearities as the signal, it can serve only as a relative estimator of the system variability (measured in, for example, contrast units), thus leaving its internal equivalent unknown[21]. Whatever the specific dependency of the internal noise on contrast at intermediate processing levels, the combination of these noise sources yielded an overall noise that was practically contrast-independent. It follows that the standard increase in the contrast discrimination threshold with the base contrast (Fig. 2) is due to the reduced response gain of the overall transducer.

A number of direct, neurophysiological observations support the notion of an activity-dependent noise process[8,22–24]. The difficulty with bridging this neurophysiological evidence and the psychophysically assessed sensory process rests in the uncertainty about how local neural processes average up to yield a measured sensation. The response to contrast of visual neurons in the lateral geniculate nucleus and/or in the striate visual areas displays a large variability across neurons both in its range and in its saturation index[23,25–27]. This variability is substantially larger than the response variability of each neuron with contrast. To the extent that the detection/discrimination performance reflects some sort of optimal pooling over a large neural population[23], the noise resulting from this averaging will partly override the response-dependent noise of each neuron (in the same way that a relatively high external noise controls the sensitivity of a system to the exclusion of its own internal noise[20,21,28–31]). Thus, the global (psychophysical) processes would be essentially limited by a (practically) constant, averaging-related noise.

The presently used (unique criterion constraint) method may (and should) reveal very different transducers and noise contributions to discrimination tasks along other dimensions and modalities. A case in point is the detection or discrimination of luminance increments. Tasks of this sort frequently yield TvC functions with an exponent $\omega \approx 0.5$ (the de Vries–Rose range[32–34]) suggesting, on the assumption of a linear transducer, that they are exclusively limited by photon noise in the eye[5,6,28]. Larger ω exponents (sometimes close to Weber's regime[35]) require, in addition to photon noise, a compressive nonlinearity of the (luminance) transducer. Photon noise cannot be such a limiting factor for contrast detection/discrimination as it involves a comparison between two stimuli of the same average light intensity (and thus number of photons). Under such conditions, photon noise limitations are expected to be minor. Thus, the presently identified noise limiting contrast discrimination must be neural noise[30,31].

METHODS

Observers had to report the presence of a short (80 ms) contrast increment (ΔC) presented on either one of two suprathreshold, 3 cycles-per-degree vertical Gabor patches (baselines or pedestals). The pedestals appeared 400 ms before the putative increment and lasted 400 ms after. They were displayed on a 29 cd/m^2 gray background 1.6° to the left and to the right of a white fixation circle (0.5° in diameter) within two cue circles (see below) 0.9° in diameter.

A first set of experiments assessed the TvC function by means of a 2AFC staircase. The two baseline Gabors were of equal contrasts (C; 1 of 8 values ranging from 0 to 80%) and ΔC was randomly applied to one of them in only one of the two temporal intervals. Observers had to specify this interval. Three correct responses in a row entailed a 2-dB decrement and one wrong response entailed a 2-dB ΔC increment (yielding an average of 80% correct responses). One session consisted of two interleaved staircases (for the left and right locations) with C fixed. The cue-circles were both white or both black with the color randomized across sessions. A session was ended after at least 16 reversals (in each staircase) and the threshold was taken as the average of the last 8. Final thresholds were based on at least two repetitions per C yielding at least four threshold values (two per side). Final thresholds were the average of these values.

The main experiment used the SDT 'yes/no' format. On each trial (Fig. 1c), observers were presented with, in sequence, a fixation white circle present during the whole trial, the two baseline Gabors displayed within two precue circles, the contrast increment(s) occurring with a probability of 0.5 independently for each Gabor, and the ΔC value offset(s) followed 400 ms later by the offset of the Gabors and of one of the two precues. Observers had to report whether or not a target was presented within the persistent (postcue) circle only. Incorrect responses were signaled by a short tone. This experimental format required that observers monitored both locations until the 'appearance' of the postcue (for more details, see ref. 13). The two baseline Gabors had equal ('same' condition) or different ('different' condition) C values. There were four baseline contrasts (ranging from 10% to 56%) yielding four pairs in the 'same' condition and six in the 'different' condition. Within one experimental block (characterized by 200 trials of a given baseline pair), the colors (white and black) of the cue circles were consistently matched with each baseline Gabor in a pair and their locations were randomized across trials (this pairing was meaningless in the 'same' conditions). The use of fixed spatial phase, high-contrast baselines and constant increments together with their systematic association with the colored precues insured that observers had full knowledge of the signal characteristics, a factor that minimizes variance differences between noise and signal plus noise distributions[1,18].

One d' and one ZFA value were estimated from 100 trials for each baseline in a pair. Final d' and ZFA values were estimated from up to 600 (and not less than 300) trials (that is, 3–6 repeats). Based on the 2AFC incremental thresholds and on preliminary experiments, ΔC values were chosen so as to yield d' values close to 1.5 (that is, 1.5× the traditional threshold) for all C values. In an additional experiment meant to demonstrate the unique criterion constraint, ΔC values were chosen to yield d' values close to 1 and 2 for pedestal C values of 10% and 40%. It is of interest to point out that within the tested range and for each observer d' was a quasi-linear function of ΔC with a slope decreasing with the pedestal contrast. Four observers (including the first author) participated in all experimental conditions.

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