Correction

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The authors note that on page 3597, right column, the third equation (for soft threshold nonlinearity) appeared incorrectly. The corrected equation appears below:

\[ \Gamma[x] = x + \alpha \exp \left( -\frac{x}{\alpha} \right) \]
Dissociable prior influences of signal probability and relevance on visual contrast sensitivity

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According to signal detection theoretical analyses, visual signals occurring at a cued location are detected more accurately, whereas frequently occurring ones are reported more often but are not better distinguished from noise. However, conventional analyses that estimate sensitivity and bias by comparing true- and false-positive rates offer limited insights into the mechanisms responsible for these effects. Here, we re assessed the prior influences of signal probability and relevance on visual contrast detection using a reverse-correlation technique that quantifies how signal-like fluctuations in noise predict trial-to-trial variability in choice discarded by conventional analyses. This approach allowed us to estimate separately the sensitivity of true and false positives to parametric changes in signal energy. We found that signal probability and relevance both increased energy sensitivity, but in dissociable ways. Cues predicting the relevant location increased primarily the sensitivity of true positives by suppressing internal noise during signal processing, whereas cues predicting greater signal probability increased both the frequency and the sensitivity of false positives by biasing the baseline activity of signal-selective units. We interpret these findings in light of “predictive-coding” models of perception, which propose separable top-down influences of expectation (probability driven) and attention (relevance driven) on bottom-up sensory processing.

decision making | psychophysics | visual perception

Signal detection theory (SDT) proposes that sensitivity can be calculated by comparing true- and false-positive rates (1, 2). In a typical detection task, subjects are asked to judge whether a noisy stimulus does or does not contain a low-energy signal, allowing researchers to classify stimuli judged as containing the signal into true and false positives (“hits” and “false alarms,” respectively), and stimuli judged as not containing the signal into true and false negatives (“correct rejections” and “misses”). SDT posits that performance can be summarized by two statistics: d’, indexing sensitivity to signal occurrence in signal-to-noise units, and c, reflecting a bias to report signal occurrence (modeled as a decision criterion). Using this approach, it is now well established that cues that predict the location of a behaviorally relevant signal increase sensitivity (3–6) by improving the precision of visual processing (7–10). By contrast, cues that predict a greater probability of signal occurrence alone are believed to have no influence on sensitivity (11, 12) but instead bias observers to report signal occurrence by adopting a more liberal decision criterion.

Over the past 50 years, SDT has provided a versatile description of decision processes, both in laboratory experiments and in real-world situations such as medical diagnostics, by dissociating between an observer’s sensitivity and bias, two quantities that had traditionally been difficult to tease apart (13). However, SDT has remained largely silent about the computational mechanisms by which sensitivity and bias are influenced by contextual information such as the prior probability and relevance of the signal. Indeed, changes in signal-to-noise sensitivity can occur either by amplifying the responses of signal-selective units (14) or by suppressing performance-limiting noise without amplifying the signal per se (15). Similarly, changes in bias can arise either by increasing the baseline activity of signal-selective units or by shifting the observer’s decision criterion toward one of the two responses. However, the binary classification of stimuli as signal-present (S+) and signal-absent (S−) used by conventional SDT analyses makes it difficult to arbitrate between these different possibilities, for a number of reasons. First, the conventional approach does not distinguish between the two successive sources of performance-limiting noise in the decision process: external noise (physical noise in the stimulus itself) and internal noise (physiological noise during stimulus processing). This conflation makes it hard to pinpoint the locus of contextual influences on signal detection (e.g., whether effects occur upstream or downstream from internal noise) (16). Second, the binary classification of stimuli does not allow to measure sensitivity separately in the S+ and S− categories. This is important, because different mechanisms make distinct predictions as to whether their effects on sensitivity should grow or shrink with signal strength (17).

Reverse-correlation analyses offer a powerful complement to conventional analyses, by permitting the measurement of observer sensitivity to small, noise-driven changes in image statistics (18, 19). Here we adopted a reverse-correlation approach to identify the mechanisms by which signal probability and relevance influence signal detection. To do so, we quantified the amount of signal energy present in each noisy stimulus by convolution with a pool of visual filters that approximate the receptive fields of orientation-selective neurons in early visual cortex (20, 21). This parametric characterization of external noise allowed us to estimate the sensitivity of human observers to signal-like fluctuations separately in S+ and S− stimuli. In conjunction with a signal detection task in which two types of cues provided mutually independent information about probability and relevance, this approach allowed us to dissociate and arbitrate between their candidate mechanisms.

Results

Probability × Relevance Cueing Procedure. While fixating centrally, subjects viewed two simultaneously presented stimuli in colored placeholders located in their left and right visual fields (Fig. L4). Their task was to report whether a signal was present (S+) or absent (S−) in one of the two placeholders, indicated by a color-matched probe presented after stimulus offset. The target signal was a vertical Gabor pattern of two cycles per degree of visual angle, presented at a fixed contrast titrated for each subject before the experiment. All stimuli were embedded in visual noise whose frequency characteristics closely matched those of the signal (Methods). We manipulated signal probability at the block level, using a 2 × 2 within-subjects design, with block probability and relevance as factors. The former permitted us to dissociate the influences on sensitivity of signal probability from those of signal relevance, whereas the latter enabled us to distinguish between their candidate mechanisms.

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level using a cue indicating the prior probability of signal occurrence in each of the two colored placeholders (0.67/0.33, 0.50/0.50, or 0.33/0.67), and signal relevance at the trial level using a prestimulus cue indicating the most likely color of the poststimulus probe (0.67/0.33, 0.50/0.50, or 0.33/0.67). Signal occurrence in the probed placeholder was made independent from the other placeholder (i.e., signals could occur in both, one, or neither of the placeholders). This feature ensured that the relevance of the signal (i.e., the fact that its correct detection would yield a positive reward) did not depend on its presence in any of the two placeholders but on its presence in the placeholder that was probed afterward. Consequently, the relevance cue did not provide any prior information about whether or where a signal was likely to occur. So unlike typical cueing studies based on the Posner paradigm (22), the two types of cues provided mutually independent information about signal probability and relevance.

**Conventional Signal Detection Analyses.** When we estimated sensitivity $d'$ and bias $c$ using conventional methods (1, 2), we replicated previous studies in that signal relevance increased sensitivity $d'$ (repeated-measures ANOVA, $F_{2,18} = 23.4$, $P < 0.001$), whereas signal probability lowered bias $c$ ($F_{2,18} = 10.2$, $P = 0.001$) but did not increase $d'$ ($F_{2,18} < 1$, $P > 0.5$) (Fig. 1B and C and Fig. S1). Sensitivity $d'$ increased for stimuli cued as relevant ($F_{1,9} = 19.8$, $P = 0.001$) and decreased for stimuli cued as irrelevant ($F_{1,9} = 15.5$, $P < 0.005$) relative to neutral ones, thereby matching known effects of spatial attention on visual contrast sensitivity (4). By contrast, stimuli cued as likely to contain the signal were associated with an increased false-alarm rate ($F_{1,9} = 10.0$, $P = 0.01$) (i.e., a more liberal decision criterion according to signal detection theory) (11).

**Reverse-Correlation Analyses.** Rather than classifying stimuli in a binary fashion as signal-present (S+) or signal-absent (S-), we then assessed whether trial-to-trial fluctuations in external noise could further account for variability in signal detection. To do so, we first processed each stimulus through a pool of Gabor energy filters of varying preferred orientations and spatial frequencies (Methods). The energy response of each filter corresponds to the contrast of the stimulus with respect to its preferred orientation and spatial frequency. We then estimated the sensitivity of detection judgments to trial-to-trial fluctuations in stimulus energy within S+ and S- stimulus categories using binomial parametric regression (Methods). The regressed energy sensitivity provides an estimate of the strength of the relationship between the amount of signal-like energy present in each stimulus and the internal response upon which detection judgments are made. In contrast to $d'$, this measure of sensitivity capitalizes exclusively on the influence of within-category fluctuations in signal energy on choice (i.e., precisely the trial-to-trial variability being discarded by conventional analyses).

Before assessing the influences of signal probability and relevance on energy sensitivity, we first verified that parametric fluctuations in stimulus energy within each stimulus category (S+ or S-) predicted trial-to-trial variability in signal detection, over and above between-category differences in signal strength (Fig. 2). We first plotted energy sensitivity across varying orientations and spatial frequencies centered around the attributes of the target signal (Fig. 2B) and found that detection judgments were maximally sensitive to signal-like fluctuations in stimulus energy in the probed stimulus ($t$ test against zero, $t_9 = 12.3$, $P < 0.001$). Importantly, this was not the case for the other, unprobed stimulus ($t_9 = -0.7$, $P > 0.5$). When considering S+ and S- stimulus categories independently, we found that both hits and false alarms were sensitive to fluctuations in signal energy binned into quartiles (Fig. 2B and Fig. S2). Indeed, hits increased by 27.9% $\pm$ 2.2% ($F_{1,9} = 167.2$, $P < 0.001$) and false alarms by 10.0% $\pm$ 2.4% ($F_{1,9} = 17.3$, $P < 0.005$) between the first and fourth energy quartiles. In other words, both hit and false-alarm rates increased parametrically with signal energy, a finding predicted by signal detection theory but unaccounted for when using conventional analyses.

This regression-based approach can also be used to recover conventional estimates of sensitivity $d'$ and bias $c$, by simply substituting the within-category fluctuations in signal energy with ones and zeros for S+ and S- stimuli, respectively. This allowed us to compare the conventional (binary) and reverse-correlation (parametric) approaches head-to-head and ask which could account better for trial-to-trial variability in choice (SI Methods). We found that the reverse-correlation approach was a better predictor of choice, as measured by the area under the receiver operating characteristic curve (conventional: 0.684 $\pm$ 0.012; reverse-correlation: 0.721 $\pm$ 0.013; paired $t$ test, $t_9 = 9.8$, $P < 0.001$).
Although both hits and false alarms were sensitive to signal energy, we also found that false alarms were significantly less sensitive than hits to signal-like fluctuations in stimulus energy (paired t test, \( t_9 = 4.2, P < 0.005 \)). This finding implies that the internal response upon which detection judgments are made does not grow linearly with signal energy but rather indicates the presence of a soft-threshold nonlinearity at low signal strength, in accordance with previous psychophysical observations (21) (Methods).

**Probability x Relevance Effects on Energy Sensitivity.** Turning to our main analyses of interest, we went on to assess the influences of signal probability and relevance on energy sensitivity (Fig. 3 and Fig. S3). These analyses were performed using trial-to-trial fluctuations in signal energy in the probed stimulus only. In contrast to conventional analyses, we found that both types of cues increased energy sensitivity, but that they did so in a dissociable fashion. Energy sensitivity was significantly increased at the target orientation for the stimulus cued as signal-present relative to the stimulus cued as signal-absent (\( F_{1,9} = 10.5, P = 0.01 \)) (Fig. 3A).

Furthermore, the separate analyses of signal-present and signal-absent stimuli revealed that probability increased the energy sensitivity of false alarms (interaction: \( F_{1,9} = 5.2, P < 0.05 \)); cued as signal-present: \( F_{1,9} = 16.4, P < 0.005 \); cued as signal-absent: \( F_{1,9} = 1.4, P > 0.2 \) but not of hits (interaction: \( F_{1,9} < 1, P > 0.5 \) ) (Fig. 3B). In other words, a greater probability of signal occurrence increased not only the global frequency of false positives but also their sensitivity to signal-like fluctuations in stimulus energy.

To ensure that this effect of probability cues was not due to a spurious interaction with relevance cues, we ran a control task on another group of subjects for which we manipulated exclusively signal probability, in the same fashion as in the main task, and obtained the same pattern of results (Fig. S4 and SI Results).

As expected from the effect of signal relevance on \( d' \), the peak of the energy sensitivity profile at the vertical orientation was also significantly higher for the stimulus cued as relevant (\( F_{1,9} = 18.6, P = 0.001 \)) (Fig. 3C). However, unlike probability, relevance increased the energy sensitivity of hits (interaction: \( F_{1,9} = 16.5, P < 0.005 \); cued as relevant: \( F_{1,9} = 180.7, P < 0.001 \); cued as irrelevant: \( F_{1,9} = 6.5, P < 0.05 \) ) but not of false alarms (interaction: \( F_{1,9} = 1.7, P > 0.2 \) ) (Fig. 3D). Therefore, although the global frequency of hits did not differ between cued and uncued stimuli (\( F_{1,9} < 1, P > 0.5 \)), their sensitivity to signal-like fluctuations in stimulus energy was significantly increased for the stimulus cued as relevant. These dissociable effects of probability and relevance cues on energy sensitivity can be summarized by the interaction between four factors—cue type, cue content, stimulus category, and signal energy—on detection rate (\( F_{1,9} = 5.3, P < 0.05 \).

**Computational Modeling of Probability x Relevance Effects.** To account for these findings, we described the effects of signal probability and relevance on signal detection using a computational model of visual contrast processing (Fig. S5). Importantly, the model relies on the same basic assumptions as signal detection theory, namely, that detection judgments are based on the level of a continuous internal response R corrupted by additive Gaussian noise, \( \sigma \) (1, 2):

\[
R = \Gamma [E(S[T]) + \delta] + N(0, \sigma),
\]

where \( E(S[T]) \) corresponds to the energy of the noisy stimulus \( S \) conditional to a target signal \( T \), \( \delta \) to an additive bias to signal-selective units, \( \Gamma [\ . \ . \ . ] \) to a soft-threshold nonlinearity capturing the contrast-response function of visual neurons, and \( \sigma \) to the SD of the performance-limiting internal noise (Methods). Consistent with signal detection theory, each decision made by the model is based on the comparison between the level of the internal response \( R \) and an adjustable decision criterion \( \theta \) (yes if \( R > \theta \), no otherwise).

Importantly, although changes in \( \delta \) and \( \theta \) both influence bias \( c \) in conventional terms, a change in \( \delta \) corresponds to an early shift of
the contrast-response function of signal-selective units, upstream from internal noise, whereas a change in $\theta$ corresponds to a phase shift in response criterion, downstream from internal noise.

We used maximum-likelihood estimation to fit the hit and false-alarm rates predicted by each model at the first and fourth energy quartiles for stimuli cued as signal-present vs. signal-absent, and for stimuli cued as relevant vs. irrelevant (Methods). We compared the quality of the best fits for three competing models with respect to a fourth control model: (i) a model in which $\delta$ was allowed to vary between cueing conditions but all other parameters were fixed ("input bias" model), (ii) a model in which only $\theta$ could vary ("response bias" model), (iii) a model in which only $\sigma$ was free ("response gain" model), and (iv) a control model in which all parameters were fixed between cueing conditions ("null" model).

We began by testing the ability of each model to capture the changes in hit and false-alarm rates between stimuli cued as signal-present vs. signal-absent. The effects of signal probability were best accounted for by the input bias model, that is, by increasing the additive bias $\delta$ for the stimulus cued as signal-present and decreasing it for the stimulus cued as signal-absent (cued as signal-present: +3.6%; cued as signal-absent: −1.6%; likelihood-ratio test against null model, $\chi^2 = 20.5, df = 1, P < 0.001$) (Fig. 4A). Importantly, the input bias model captured the observed effects of signal probability both on bias $c$ ($F$ test between data and input bias model, $F_{1,9} < 1, P > 0.5$) and on energy sensitivity ($F_{1,9} < 1, P > 0.5$). Although the response bias model also vastly outperformed the null model ($\chi^2 = 19.0, df = 1, P < 0.001$), it could not capture the effect of signal probability on energy sensitivity, indicating that the response bias model can be formally rejected ($F$ test between data and response bias model, $F_{1,9} = 12.5, P < 0.01$) (Fig. 4B). The response gain model did not perform better than the null model ($\chi^2 = 0.2, df = 1, P > 0.5$). No combination of the three models outperformed the winning input bias model (SI Methods).

By contrast, the model that best captured the changes in hit and false-alarm rates between stimuli cued as relevant vs. irrelevant was the response gain model (likelihood-ratio test against null model, $\chi^2 = 14.7, df = 1, P < 0.001$) (Fig. 4C). The amount $\sigma$ of internal noise estimated by the model was suppressed by more than half between the cued stimulus and the uncued one (cued as relevant: 8.6%; cued as irrelevant: 13.3%). This response gain model captured the observed effects of signal relevance on sensitivity $d'$ ($F$ test between data and response gain model, $F_{1,9} < 1, P > 0.5$) and on energy sensitivity ($F_{1,9} < 1, P > 0.5$). Unsurprisingly, neither the input bias model nor the response bias model outperformed the null model (both $P > 0.5$). As for signal probability, no combination of the three models outperformed the winning response gain model (SI Methods).

Discussion

We designed a signal detection task that allowed us to dissociate the prior influences of signal probability and relevance on visual contrast sensitivity. Using a reverse-correlation approach that quantifies how noise-driven fluctuations in signal energy predict the trial-to-trial variability in choice unexplained by conventional SDT analyses, we reveal that signal probability and relevance both influence energy sensitivity, albeit in a dissociable fashion: relevance increases energy sensitivity primarily for signal-present stimuli, whereas probability increases energy sensitivity only for signal-absent stimuli. These separable effects can be accounted for using a computational model in which (i) relevance increases the signal-to-noise precision of signal processing by suppressing internal noise, and (ii) probability biases signal detection by increasing the baseline activity of signal-selective units.

The computational dissociation between these two types of prior information maps broadly onto the theoretical difference between “expecting” a particular signal to occur because of the statistical regularities of the environment, and “attending to” that signal on the basis of its behavioral significance (23). In everyday life, these two functions can, and often are, deployed in an orthogonal fashion. For example, some events may be motivationally highly salient (e.g., cues that are associated with impending rewards, or punishments, and demand attention to be deployed to them). However, events also differ with regard to their probability of occurrence, independent of whether they are relevant to the current task set.

The reverse-correlation technique used here constitutes a refinement of conventional SDT analysis with no alteration to its basic assumptions: both approaches assume that detection judgments are based on the comparison between a continuous internal response and an adjustable decision criterion (1, 2). In fact, our regression-based approach allows to verify empirically one of the main predictions of SDT: that hit and false-alarm rates both increase parametrically with signal energy. In this respect, the finding that false alarms are not pure strategic guesses constitutes in itself a validation of SDT and allows the ruling out of other, finite-state models of detection, such as the high-threshold model (24).

Characterizing the mechanisms by which attention enhances sensory processing at the behavioral and neuronal levels is a key goal of the neurosciences, and a large body of literature has used signal detection theory to measure increases in contrast sensitivity when a relevant stimulus is presented at an expected location.
relative to an unexpected one (3–10). Most, if not all, of these studies have manipulated top-down attention using spatial cues that predict the occurrence of a target stimulus at a particular location (22). However, such cues provide mixed information about the forthcoming stimulus. First, relative to uninformative cues, these predictive cues reduce uncertainty about where the target stimulus is likely to appear. Whether their facilitatory effects on detection sensitivity can be attributed to uncertainty reduction alone is still a matter of debate (25–27) [i.e., by weighting differently the sensory evidence available at cued and uncued locations in the decision process (28, 29)]. Here we used a poststimulus probe specifically to suppress uncertainty about which stimulus was relevant before each choice. Second, most previous studies have used a single cue to concurrently (i) indicate an increase in the conditional probability that a signal would occur at the cued location, and (ii) mark the cued location as potentially relevant for subsequent behavior (30). By contrast, we manipulated these two types of prior information orthogonally using two cues and showed that they produce dissociable effects on visual contrast processing.

Our study is not the first to investigate the mechanisms of visual attention using computational modeling (5, 6, 28, 29). Here, our reverse-correlation analysis indicates that the facilitatory influence of signal relevance on sensitivity grows with signal strength: it is weak for signal-absent stimuli and stronger for signal-present stimuli. Our model demonstrates that this pattern of results can be best accounted for as a suppression of internal noise during signal processing, without any change in the mean activity of signal-selective units. This multiplicative mechanism is highly consistent with recent results from electrophysiological recordings in monkey visual cortex (9, 10), which have revealed that most of the facilitatory effects of spatial attention on visual processing can be explained by a suppression in pair-wise neuronal correlations rather than by an increase in firing rates.

Signal probability has been much less studied in the absence of spatial uncertainty (25–27) but has classically been thought to increase hit and false-alarm rates to a similar extent. This finding has been interpreted as an idiosyncratic bias occurring at late response stages, unrelated to visual signal processing per se (11, 12). In contrast to this view, we show that probability increases energy sensitivity and that its influence shrinks with signal strength (i.e., stronger for signal-absent stimuli). By comparing two models in which probability facilitates signal detection either at the input stage or at the response stage (31, 32), we confirm that only an early influence on signal processing can account for its observed effects. This distinction is not possible using conventional analyses that can only assess the frequency of false alarms, not their sensitivity to signal-like fluctuations in noise.

At the computational level, the finding that prior probability can bias the baseline activity of signal-selective units during early visual processing is in agreement with “predictive-coding” models of perception (33–35). This theory of brain function argues that probabilistic expectations about future sensory events flow backward from higher associative regions to supplement or “complete” bottom-up sensory signals. This top-down mechanism allows for optimal perceptual inference by minimizing the amount of surprise (or prediction error) left to be encoded by bottom-up signals (36) and is mathematically equivalent to computational descriptions of how attention biases visual processing (37–39). The early influence of signal probability is also supported by functional imaging studies showing increases in blood oxygen level-dependent (BOLD) signals for expected stimuli in ventral visual cortex (40, 41) and stronger BOLD responses to false alarms relative to misses or correct rejections in primary visual cortex (42).

To conclude, we demonstrated that the prior probability and relevance of a visual signal can modulate visual contrast processing in a dissociable manner. Visual signals cued as relevant are processed with an increased signal-to-noise precision by suppressing internal noise, whereas signals cued as probable are biased positively by increasing the baseline activity of signal-selective units. While offering psychophysical evidence for separable top-down influences of expectation and attention on bottom-up sensory processing, these findings also call into question an assumption that has endured for more than 50 years, namely, that prior probability biases signal detection only at late response stages.

Methods

Subjects. Ten human subjects aged 19–28 y (six female) participated in the study after giving informed written consent. All had normal or corrected-to-normal vision, and all were naive to the purpose of the experiment. Subjects were paid £45 for their participation.

Psychophysical Procedures. Each of the stimuli consisted of a Gabor pattern (the target signal) that could be added to a Gaussian noise patch. The diameter of the stimulus was 4° of visual angle, and their center was positioned at 4° of visual angle to the left and right of fixation. The orientation of the Gabor patterns was always vertical, their spatial frequency was fixed at two cycles per degree of visual angle (cpd), and their phase was sampled from a uniform random distribution. The noise patch was created by smoothing pixel-by-pixel Gaussian noise through a 2D Gaussian smoothing filter. The dimension of the smoothing filter was chosen to maximize the trial-to-trial variability of the convolution between the smoothed noise and the target signal (i.e., to maximize the influence of the noise on the detectability of the signal). Both this smoothing dimension (0.083° of visual angle) and the contrast of the noise (50% of 10%) were fixed across subjects and stimuli. Further information about the psychophysical procedures is presented in SI Methods.

Reverse-Correlation Procedures. Each stimulus was processed through a pool of Gabor energy filters with varying preferred orientations and spatial frequencies using the following equation:

$$E(S|T) = \sqrt{(S \cdot \cos(T))^2 + (S \cdot \sin(T))^2}$$

where E(S|T) corresponds to the energy of the stimulus S conditional to the preferred signal T (uniquely defined by its orientation and its spatial frequency), and < > corresponds to the cross-correlation operator. Intuitively, the response of each energy filter corresponds to the effective contrast of the stimulus with respect to its preferred signal.

We submitted these single-trial energy filter responses and the corresponding detection judgments to binomial regression to estimate energy sensitivity—the strength of the relationship between within-category fluctuations in signal-like energy and the internal response upon which detection judgments are made. Mathematically, the generalized linear model used for the regression is:

$$P(\text{yes}) = \Phi(\beta_0 + \beta_1 \cdot E(S|T))$$

where P(\text{yes}) corresponds to the energy of the stimulus S with respect to the template signal T, \(\Phi(\cdot)\) to the normal deviate function (mean of the stimulus category of S, SD of the signal-absent energy distribution), and \(\beta_0, \beta_1\) to the cumulative normal function. As for conventional signal detection theory (1,2), two parameters are fitted simultaneously: (i) \(\beta_0\) is independent from the stimulus S and corresponds to the normal deviate of the overall detection rate (e.g., the false-alarm rate for signal-absent stimuli), and (ii) \(\beta_1\) indexes the strength of the parametric relationship between E(S|T) and the internal response upon which detection judgments are made (i.e., their energy sensitivity). Further information about the reverse-correlation procedures is presented in SI Methods.

Modeling Procedures. The equation for the soft-threshold nonlinearity is:

$$\Gamma(x) = x + \exp\left(-\frac{x}{\alpha}\right)$$

where x corresponds to the input contrast/energy level, and \(\alpha\) corresponds to the soft threshold, expressed in contrast units. The soft-threshold nonlinearity becomes linear at high contrast levels (>\(\alpha\)) and saturates at low contrast levels (<\(\alpha\)). We fitted \(\alpha\) to match the within-subject difference in energy sensitivity between hits and false alarms using maximum-likelihood estimation. The best-fitting \(\alpha\) estimate (11.2%) was fixed across conditions for all computational simulations reported in the manuscript. This static nonlinearity, commonly used in computational studies of visual contrast processing.
processing (5, 6), captures the contrast-response function of noisy population responses at low contrast levels. Further information about the modeling procedures is presented in SI Methods.

Statistical Procedures. All analyses were performed at the single-subject level (see Fig. S6 and Fig. S7 for a representative subject) and followed by standard parametric tests at the group level (e.g., paired t tests, repeated-measures ANOVAs) to assess reliable within-subject differences between cueing conditions (signal-present vs. signal-absent, relevant vs. irrelevant).


This scheme ensures that between-subject variability in overall detection performance is appropriately controlled for and cannot account for significant group-level effects. Further information about the statistical procedures is presented in SI Methods.

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Supporting Information

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SI Results

Control Task. To ensure that the effect of signal probability on energy sensitivity was not due to a spurious interaction with signal relevance, we ran a control task on another group of subjects for which we manipulated exclusively signal probability, in the same fashion as in the main task, and obtained the same pattern of results (Fig. S4).

Conventional analyses confirmed that signal probability lowered bias $c$ ($F_{1,9} = 52.9, P < 0.001$) but did not increase $d'$ ($F_{1,9} < 1, P > 0.2$). Nevertheless, energy sensitivity was again found to increase at the target orientation for the stimulus cued as signal-present ($F_{1,9} = 27.7, P < 0.001$) (Fig. S4B). In addition, as observed in the main task, probability increased the energy sensitivity of false alarms (interaction: $F_{1,9} = 5.3, P < 0.05$; cued as signal-present: $F_{1,9} = 4.8, P = 0.05$; cued as signal-absent: $F_{1,9} < 1, P > 0.5$) but not of hits (interaction: $F_{1,9} < 1, P > 0.5$) (Fig. S4C). Together, these findings replicate the effects of signal probability observed in the main task.

SI Methods

Psychophysical Procedures. Stimuli were presented on a γ-corrected cathode ray tube screen using a resolution of 1024 × 768 pixels at a refresh rate of 60 Hz. Stimulus design and presentation were programmed and controlled using the Psychtoolbox-3 package (1, 2) and custom functions for MATLAB (MathWorks). Subjects responded via key presses using their left hand (index finger: no; middle finger: yes) when probed about the left stimulus, and their right hand (using the same response mapping) when probed about the right stimulus.

The experiment consisted of two sessions, taking place on different days. The first session was a training session, during which subjects were progressively trained on the different aspects of the task. The data analyzed here were recorded during the second session, corresponding to 725 ± 20 trials per subject (mean ± SEM). Each session started with an adaptive titration procedure to determine the contrast of the Gabor pattern for which detection accuracy was 69% (i.e., $d' ≈ 1$ for an unbiased observer). This titration procedure converged toward a mean threshold contrast of 14.9% ± 1.3%. The main task was divided into blocks of 92 trials. Each trial started with the appearance of pink and blue placeholders to the left and right of a fixation point. After a variable delay of 1000–1500 ms, the fixation point flashed for 50 ms in pink, blue, or gray to indicate to subjects which stimulus was likely to be probed (gray: 0.50/0.50; pink: 0.67/0.33 in favor of the pink placeholder; blue: 0.67/0.33 in favor of the blue placeholder). One thousand milliseconds after this relevance cue, two noisy stimuli were briefly presented in the pink and blue placeholders for 50 ms. Subjects were asked to monitor the presence of the target signal in each of the stimuli and were also explicitly told that the presence of the signal in one of the two stimuli provided strictly no information about the presence of a signal in the other stimulus. Five hundred milliseconds after the onset of the stimuli, the fixation point turned pink or blue to probe for signal presence in one of the two stimuli. The trial timed out after 3 s without response.

The probability contingencies were fixed within blocks: in some blocks, the pink placeholder was 0.67 likely to contain a signal, whereas the blue placeholder was 0.33 likely to contain the signal, as indicated by an instruction cue at the beginning of the block. In other blocks, these probability contingencies were reversed (0.67 for the blue placeholder, 0.33 for the pink placeholder). Finally, in one third of the blocks, both pink and blue placeholders were equally likely (both $P = 0.50$) to contain the signal. The locations of the pink and blue placeholders varied randomly between left and right locations across trials, so that the left and right locations had the same overall frequency of signal occurrence within each block. Participants received an auditory feedback tone 250 ms after each response (correct: 880 Hz; error: 440 Hz).

Importantly, this paradigm allowed us to dissociate the influence of signal probability from that of response probability (i.e., the prior probability that either response is correct) until the onset of the poststimulus probe. This feature prevented subjects from preparing a response on the basis of the probability cue alone.

Reverse-Correlation Procedures. Because signal energy corresponds to the theoretical amount of signal information present in each stimulus, we could quantify the sensitivity $d^*$ of the ideal observer by computing the normalized distance (in $d'$ units) between the distributions of signal energy in the $S^+$ and $S^-$ stimulus categories using the following equation:

$$d^* = \left[ \frac{\mu[E(S/T, S^+)] - \mu[E(S/T, S^-)]}{\sqrt{\sigma^2[E(S/T, S^+)]^2 + \sigma^2[E(S/T, S^-)]^2}} \right] / 2,$$

where $E(S/T, S^+)$ and $E(S/T, S^-)$ correspond to the distributions of signal energy for the two categories, $\mu[ . ]$ corresponds to the average operator, and $\sigma[ . ]$ corresponds to the SD operator. We found that this ideal signal-to-external-noise sensitivity $d^*$ of 4.93 ± 0.41 was much higher than participants’ sensitivity $d'$ of 0.96 ± 0.07, corresponding to a detection efficiency $\eta^*$—the squared ratio between each subject’s sensitivity and ideal sensitivity—of 0.041 ± 0.004.

Importantly, the main difference between conventional signal detection theory (SDT) analyses and our reverse-correlation approach comes from the use of a parametric estimate of the amount of signal information available in each stimulus rather than a binary flag corresponding to its category (signal-present or signal-absent). This allowed us to compare directly the conventional (i.e., binary) and reverse-correlation (i.e., parametric) approaches, by asking which could account better for trial-to-trial variability in choice using receiver operating characteristic (ROC) analysis (3, 4). Conventional SDT analyses allow the expression of sensitivity $d'$ as the area under a predicted ROC curve (often coined as “choice probability”) using the following equation:

$$A_{ROC} = \Phi\left[ d' / 2 \right],$$

where $\Phi[ . ]$ corresponds to the normal cumulative function.

By contrast, single-trial estimates of signal energy afford the estimation of $A_{ROC}$ in a nonparametric fashion. We traced the empirical ROC curve by varying continuously a threshold on signal energy, from high to low, and computing for each threshold level (i) the proportion of “yes” responses for which signal energy exceeds that threshold, and (ii) the proportion of “no” responses for which signal energy exceeds that threshold. The area under the empirical ROC curve $A_{ROC}$ corresponds to the trapezoidal integral of these two monotonically increasing values, ranging from 0 to 1. This formulation of $A_{ROC}$ indexes the ability to predict choice from single-trial signal energy.

Interestingly, it can be shown that this trapezoidal estimate of $A_{ROC}$ is mathematically equivalent to the Mann-Whitney $U$ statistic, that is, the nonparametric degree of separability between two continuous distributions, in this case, between the distributions of signal energy observed for “yes” and “no” responses (5).
Modeling Procedures. As described in Results, our model relies on the same basic assumptions as signal detection theory, namely, that binary detection judgments are based on the level of a continuous internal response \( R \) corrupted by additive Gaussian noise:

\[
R = \Gamma \left[ E(S|T) + \delta \right] + \mathcal{N}(0, \sigma),
\]

where \( E(S|T) \) corresponds to the energy of the noisy stimulus \( S \) conditional to a target signal \( T \), \( \delta \) to an additive bias to signal-selective units, \( \Gamma \) to a soft-threshold nonlinearity capturing the contrast-response function of visual neurons, and \( \sigma \) to the SD of the performance-limiting internal noise. Consistent with signal detection theory, each decision made by the model is based on the comparison between the level of the internal response \( R \) and an adjustable decision criterion \( \theta \) (yes if \( R > \theta \), no otherwise).

The critical difference between the conventional SDT model and our model is its ability to distinguish between two types of biasing mechanisms: a response bias that influences choice via a late shift in decision criterion \( \theta \) without altering signal processing, and an input bias that influences choice via a leftward shift of the contrast-response function \( \Gamma \) of signal-selective units. Consequently, a change in response bias does not influence energy sensitivity [i.e., the relationship between \( E(S|T) \) and the strength of the internal response \( R \) upon which detection judgments are made]. By contrast, a change in input bias is mathematically equivalent to a left- or rightward shift of the soft threshold \( \alpha \), hence modifying energy sensitivity mostly for weak signal contrasts (much smaller than \( \alpha \)), not for signal contrasts above \( \alpha \), where \( \Gamma \) becomes approximately linear.

We verified empirically the single-sidedness of the soft-threshold nonlinearity \( \Gamma \) that we have used in our computational simulations, by assessing whether energy sensitivity differed between low- and high-energy \( S^+ \) stimuli (binned using a median split). When entering the energy sensitivity for \( S^- \) stimuli, low-energy \( S^+ \) stimuli and high-energy \( S^+ \) stimuli, we found that energy sensitivity differed significantly along this dimension indexing signal strength (repeated-measures ANOVA, \( F_{2,14} = 8.8, P < 0.01 \)). Precisely, energy sensitivity for \( S^- \) stimuli was lower than energy sensitivity both for low- and high-energy \( S^+ \) stimuli (low: \( F_{1,9} = 5.9, P < 0.05 \); high: \( F_{1,9} = 40.8, P < 0.001 \)); and importantly, energy sensitivity did not differ between low- and high-energy \( S^+ \) stimuli (\( F_{1,9} = 1.3, P > 0.2 \)). This pattern of energy sensitivity across signal strength confirms the shape of soft-threshold nonlinearity \( \Gamma \).

Model fitting was performed in the following way. Model predictions regarding hit and false-alarm rates for the first and fourth signal energy quartiles were computed across a large set of model parameters (\( \delta, \sigma \) and \( \theta \)), using \( 10^6 \) trials per simulation. We performed constrained maximum-likelihood estimation to recover the best-fitting parameter changes for explaining the observed effects of signal probability (cued as signal-present vs. signal-absent) and relevance (cued as relevant vs. irrelevant). We used group-level means and SEM to estimate log-likelihood sums for different sets of parameters, and likelihood-ratio tests to compare between nested models with different number of free parameters. Finally, we computed the model predictions for the effects of signal probability and relevance on sensitivity \( d' \), bias \( c \), and energy sensitivity and verified using standard \( F \) tests that the observed effects did not differ significantly from model-predicted effects.

Statistical Procedures. As described in Methods, energy sensitivity estimates were regressed across trials at the single-subject level. Importantly, they were found to be significantly positive at the target orientation for each of the ten subjects (all \( P < 0.01 \)).

On the basis of the observation that human subjects were more sensitive to signal-like fluctuations in signal-present (\( S^+ \)) stimuli than in signal-absent (\( S^- \)) stimuli, we assessed whether the difference in energy sensitivity between high- and low-probability cueing conditions could have been due to the different proportions of \( S^+ \) stimuli in the two conditions. To do so, we applied a bootstrap subsampling procedure at the single-subject level to compute energy sensitivity estimates with matched proportions of \( S^+ \) and \( S^- \) stimuli in high- and low-probability cueing conditions. We repeated this subsampling procedure \( 10^3 \) times and averaged the matched energy sensitivity estimates separately for the high- and low-probability cueing conditions. These subsampled energy sensitivity estimates still differed significantly between high- and low-probability cueing conditions (bootstrap \( P = 0.01 \)), indicating that the difference in energy sensitivity observed between probability cueing conditions could not have been due to the higher proportion of \( S^+ \) stimuli in the high-probability condition.

We applied nonparametric cluster-level statistics on energy sensitivity maps and profiles to extract clusters of energy sensitivity significantly different from zero (6). We used the sum of single-point statistics within a given cluster exceeding an uncorrected threshold (\( P < 0.05 \)) as the cluster-level statistic. The null distribution for this cluster-level statistic was estimated by randomly permuting data across conditions at the single-subject level and extracting the maximum cluster-level statistic for the difference between shuffled conditions (\( 10^3 \) permutations). We highlight significant clusters for which the cluster-level \( P \) value was smaller than 0.01. This cluster-level statistic provides an appropriate control for the type-I error rate and takes advantage of the spread of the differences between conditions to increase statistical sensitivity for large clusters (at the expense of small clusters).

Control Task Procedures. The control task used exactly the same psychophysical procedures as the main task, except that the signal relevance factor was eliminated: on each trial, both placeholders had a 0.50/0.50 probability of being probed at the end of the trial. As in the main task, the probability contingencies were fixed within blocks: in half the blocks, the pink placeholder was 0.67 likely to contain a signal, whereas the blue placeholder was 0.33 likely to contain the signal, as indicated by an instruction cue at the beginning of the block. In the other blocks, these probability contingencies were reversed (0.67 for the blue placeholder, 0.33 for the pink placeholder). As before, the locations of the pink and blue placeholders varied randomly between left and right locations across trials, so that the left and right locations had the same overall frequency of signal occurrence within each block.

Fig. S1. Conventional signal detection analyses. (A) Signal probability lowers bias c but does not increase sensitivity $d'$, suggesting a more liberal criterion at the high-probability location according to conventional SDT. (B) By contrast, signal relevance increases sensitivity $d'$ but does not change bias c, indicating a higher signal-to-noise precision at the location cued as relevant. **$P < 0.01$; ***$P < 0.001$; ns, nonsignificant. Error bars indicate SEM.

Fig. S2. Sensitivity of hits and false alarms to parametric fluctuations in stimulus energy. (A) Hit rate change maps corresponding to the increase in hit rate between the first and fourth energy quartiles for varying preferred orientations and spatial frequencies in the probed stimulus (Left) and in the unprobed/other stimulus (Right). (B) False-alarm rate change maps corresponding to the increase in false-alarm rate between the first and fourth energy quartiles in the probed stimulus (Left) and in the unprobed/other stimulus (Right). Highlighted clusters indicate significant energy sensitivity at $P < 0.01$ corrected for multiple comparisons.
Fig. S3. Signal selectivity of the effects of signal probability and relevance on energy sensitivity. (A) Energy sensitivity maps for the high- (Left) and the low-probability (Right) stimuli. The increase in energy sensitivity for the high-probability stimulus is only found around signal attributes (dashed lines). (B) Energy sensitivity maps for the cued (Left) and uncued (Right) stimuli. The increase in energy sensitivity for the stimulus cued as likely to be relevant is also selective to signal attributes (dashed lines). Highlighted clusters indicate significant energy sensitivity at $P < 0.01$ corrected for multiple comparisons.

Fig. S4. Control task results. (A) Task structure. While fixating centrally, subjects viewed two simultaneously presented stimuli in colored placeholders located in their left and right visual fields. As in the main task, their task was to report whether a signal was present or absent in one of the two placeholders, indicated by a color-matched probe presented after stimulus offset. We manipulated exclusively signal probability using a block-level cue indicating the prior probability of signal occurrence in each of the two colored placeholders. (B) Signal probability increases the energy sensitivity profile at the target orientation. (C) Signal probability increases the sensitivity of false alarms, not hits, to parametric changes in signal energy. Black lines indicate significant effects at $P < 0.05$. *$P < 0.05$; **$P < 0.01$. Shaded areas and error bars indicate SEM.
Computational model of visual contrast processing and decision making. Binary detection judgments are based on the level of a continuous internal response corrupted by additive Gaussian noise. First, each noisy stimulus $S$ is convolved with the target signal $T$ to calculate the amount of signal energy $E(S|T)$ available in $S$ (template matching stage), mimicking orientation processing in signal-selective visual neurons. Signal energy is biased by an additive input $\delta$, corresponding to the baseline activity of signal-selective units. Then, signal energy passes through a soft-threshold nonlinearity mimicking the contrast-response function of visual neurons (nonlinearity stage). Finally, the output internal response is corrupted with additive Gaussian noise of spread $\sigma$ and compared with a decision criterion $\theta$, following signal detection theory (statistical decision stage). The input bias model corresponds to a change in the additive input bias $\delta$. The response gain model corresponds to a change in the spread $\sigma$ of the performance-limiting internal noise. The response bias model corresponds to a change in the decision criterion $\theta$.

Reverse-correlation analyses for a representative subject. (A) Left: Energy sensitivity maps for probed (Left) and unprobed (Right) stimuli. The highlighted cluster is significant at $P < 0.01$ corrected for multiple comparisons. Right: Energy sensitivity profile for the probed stimulus. The black line indicates significance at $P < 0.05$. (B) Hit rate (Left) and false-alarm rate (Right) both increase parametrically with signal energy in the probed stimulus.
Fig. S7. Dissociable effects of signal probability and relevance on energy sensitivity for the same representative subject. (A) Signal probability increases the sensitivity of false alarms, not hits, to parametric changes in signal energy. (B) Signal relevance increases primarily the sensitivity of hits to parametric changes in signal energy.