



Dissociable prior influences of signal probability and relevance on visual contrast sensitivity

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Edited by Ranulfo Romo, Universidad Nacional Autonoma de Mexico, Mexico City, DF, Mexico, and approved January 18, 2012 (received for review December 7, 2011)

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 reassessed 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 $\times$ Relevance Cueing Procedure. While fixating centrally, subjects viewed two simultaneously presented stimuli in colored placeholders located in their left and right visual fields (Fig. 1A). 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

Author contributions: V.W., A.C.N., and C.S. designed research; V.W. performed research; V.W. contributed new reagents/analytic tools; V.W. and C.S. analyzed data; and V.W., A.C.N., and C.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1120118109/-DCSupplemental.

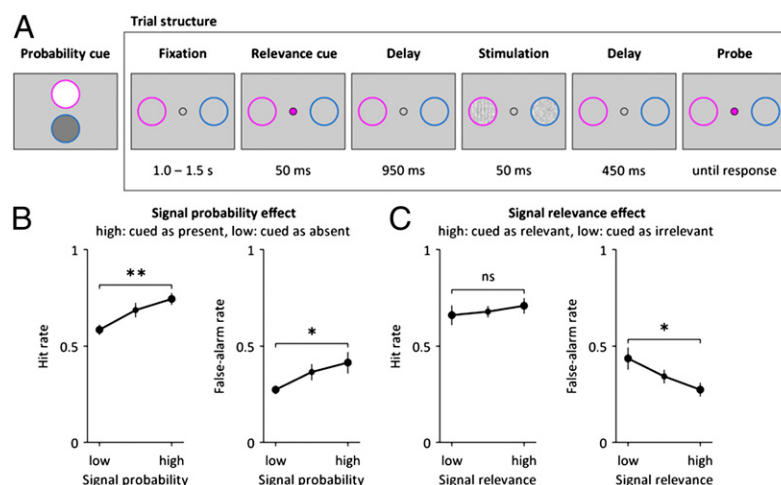


Fig. 1. Task structure and conventional signal detection analyses. (A) Task structure. Subjects viewed two simultaneously presented stimuli in colored placeholders located in their left and right visual fields. Their task was to report whether a signal was present or absent in one of the two placeholders, indicated by a color-matched probe. We manipulated signal probability at the block level using a cue indicating the prior probability of signal occurrence in each of the two colored placeholders, and signal relevance at the trial level using a prestimulus cue indicating the most likely color of the poststimulus probe. (B) Signal probability biases detection judgments by increasing hit and false-alarm rates to a similar extent. (C) Signal relevance improves the precision of signal processing by selectively decreasing the false-alarm rate for cued stimuli. * $P < 0.05$; ** $P < 0.01$; ns, nonsignificant effect. Error bars indicate SEM.

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. 2A) 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 ± 0.012 ; reverse-correlation: 0.721 ± 0.013 ; paired t test, $t_9 = 9.8$, $P < 0.001$).

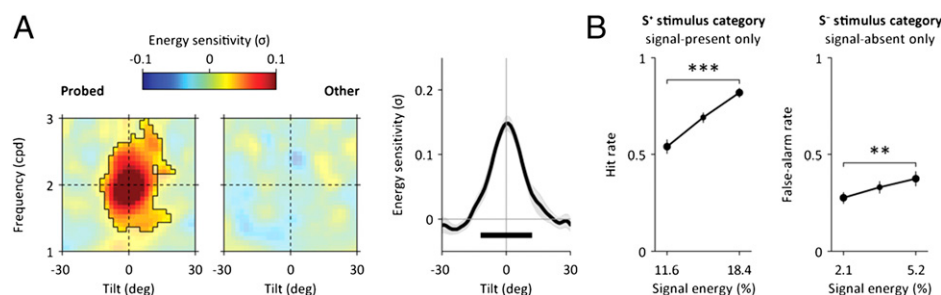


Fig. 2. Reverse-correlation analyses. (A) *Left*: Energy sensitivity maps for probed and unprobed stimuli. Subjects' choices are sensitive to signal-like fluctuations in stimulus energy in the probed stimulus (*Left*), not in the other stimulus (*Right*). The highlighted cluster is significant at $P < 0.01$ corrected for multiple comparisons. *Right*: Energy sensitivity profile for the probed stimulus. The black line indicates significance at $P < 0.05$. The shaded area indicates SEM. (B) Hit rate (*Left*) and false-alarm rate (*Right*) both increase parametrically with signal energy in the probed stimulus. $**P < 0.01$; $***P < 0.001$. Error bars indicate SEM.

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 $\times$ 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 $\times$ 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 (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 , δ to an additive bias to signal-selective units, $\Gamma[\cdot]$ to a soft-threshold nonlinearity capturing the contrast-response function of visual neurons, and σ 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 θ (yes if $R > \theta$, no otherwise). Importantly, although changes in δ and θ both influence bias c in conventional terms, a change in δ corresponds to an early shift of

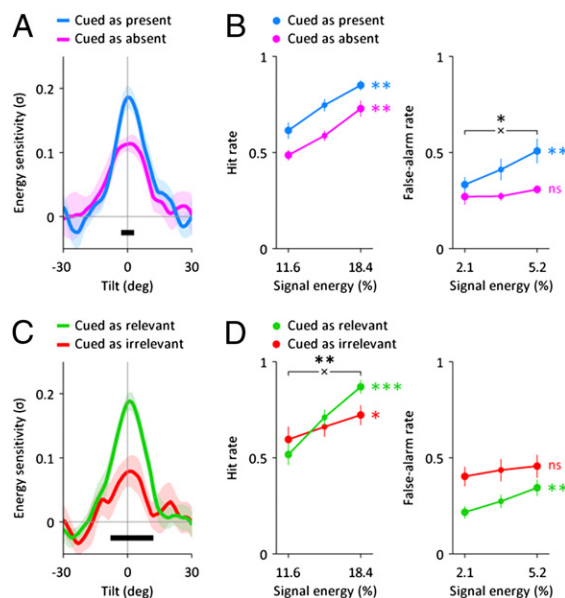


Fig. 3. Dissociable effects of signal probability and relevance on energy sensitivity. (A) Signal probability increases the energy sensitivity profile at the target orientation. (B) Signal probability increases the sensitivity of false alarms, not hits, to parametric changes in signal energy. (C) Like probability, signal relevance increases the energy sensitivity profile at the target orientation. (D) Unlike probability, signal relevance increases primarily the sensitivity of hits to parametric changes in signal energy. Black lines indicate significant effects at $P < 0.05$. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. Shaded areas and error bars indicate SEM.

the contrast-response function of signal-selective units, upstream from internal noise, whereas a change in θ corresponds to a late 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 δ was allowed to vary between cueing conditions but all other parameters were fixed ("input bias" model), (ii) a model in which only θ could vary ("response bias" model), (iii) a model in which only σ 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 δ 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 σ 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: 18.3%). 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

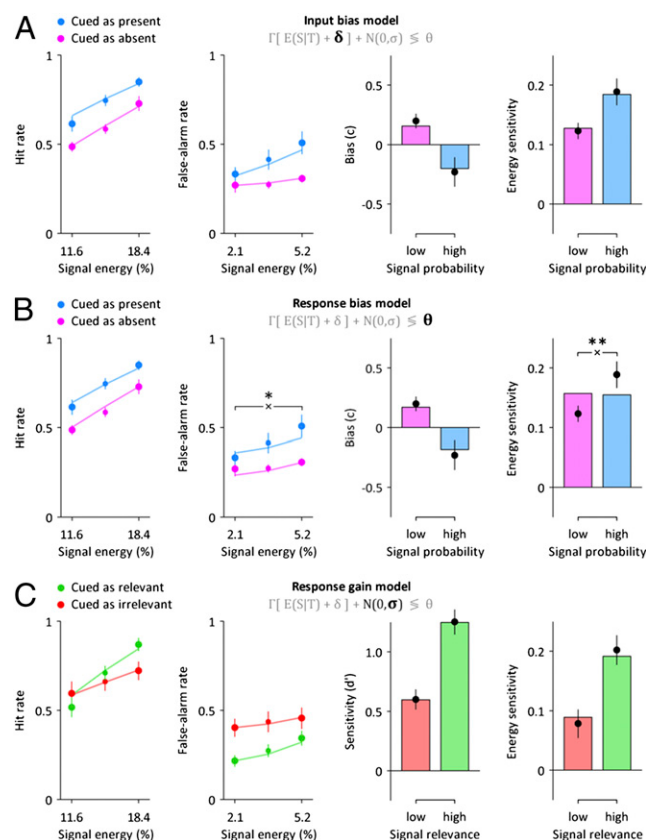


Fig. 4. Computational modeling of the effects of signal probability and relevance. (A) Input bias model. The input bias model predicts successfully the effects of signal probability on bias c and on energy sensitivity. (B) Response bias model. The response bias model does not predict the effect of signal probability on energy sensitivity. (C) Response gain model. The response gain model predicts quantitatively the effects of signal relevance on sensitivity d' and on energy sensitivity. Points correspond to observations, lines to best-fitting models (Left), and bars to model predictions (Right). Model predictions vs. observed effects: * $P < 0.05$; ** $P < 0.01$. Error bars indicate SEM.

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., strongest 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 naïve 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 stimuli 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 (SD 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:

$$E(S|T) = \sqrt{\langle S * \cos(T) \rangle^2 + \langle S * \sin(T) \rangle^2},$$

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 $\langle * \rangle$ 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:

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

where $E(S|T)$ corresponds to the energy of the stimulus S with respect to the template signal T , $Z[\cdot]$ to the normal deviate function (mean of the stimulus category of S , SD of the signal-absent energy distribution), and $\Phi[\cdot]$ to the cumulative normal function. As for conventional signal detection theory (1, 2), two parameters are fitted simultaneously: (*i*) β_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*) β_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 α 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 α to match the within-subject difference in energy sensitivity between hits and false alarms using maximum-likelihood estimation. The best-fitting α 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 (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*.

ACKNOWLEDGMENTS. We thank Vincent de Gardelle, Gustavo Rohenkohl, Mark Stokes, and two anonymous reviewers for useful suggestions and comments. This work is supported by a postdoctoral research grant from the Fyssen Foundation (to V.W.).

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