Feature expectation heightens visual sensitivity during fine orientation discrimination

Sam Cheadle Department of Experimental Psychology, University of Oxford, Oxford, UK

Tobias Egner Center for Cognitive Neuroscience, Duke University, Durham, NC, USA

Valentin Wyart Laboratoire de Neurosciences Cognitives, Inserm U960, Département d'Etudes Cognitives, Ecole Normale Supérieure, Paris, France

Claire Wu Department of Experimental Psychology, University of Oxford, Oxford, UK

Christopher Summerfield Department of Experimental Psychology, University of Oxford, Oxford, UK

Attending to a stimulus enhances the sensitivity of perceptual decisions. However, it remains unclear how perceptual sensitivity varies according to whether a feature is expected or unexpected. Here, observers made fine discrimination judgments about the orientation of visual gratings embedded in low spatial-frequency noise, and psychophysical reverse correlation was used to estimate decision 'kernels' that revealed how visual features influenced choices. Orthogonal cues alerted subjects to which of two spatial locations was likely to be probed (spatial attention cue) and which of two oriented gratings was likely to occur (feature expectation cue). When an expected (relative to unexpected) feature occurred, decision kernels shifted away from the category boundary, allowing observers to capitalize on more informative, "off-channel" stimulus features. By contrast, the spatial attention cue had a multiplicative influence on decision kernels, consistent with an increase in response gain. Feature expectation thus heightens sensitivity to the most informative visual features, independent of selective attention.

Introduction

Spatial attention increases the sensitivity of visual detection and discrimination judgments. Consider a task where participants are asked to discriminate whether a noisy grating was tilted clockwise (CW), or counterclockwise (CCW) of vertical. The grating can occur at one of two locations, and the participant is provided with a prestimulus cue that indicates the location at which the grating is likely to be shown. When the stimulus occurs at a spatial location that is validly cued, discrimination performance improves, as measured by d', a statistic that indexes an observer's ability to distinguish one category from another (Bashinski & Bacharach, 1980; Carrasco, 2011; Posner, Snyder, & Davidson, 1980). This effect is predicted by an ideal observer model, in which more weight is given to noisy inputs arriving at the validly cued location, where information is more likely to be relevant for the decision (Eckstein, Peterson, Pham, & Droll, 2009).

By contrast, in the discrimination task described above, consider the influence of a probabilistic cue that indicates whether the grating is more likely to be tilted CW than CCW, but provides no information about its likely location (to avoid confusion, in what follows we refer to this as the "feature expectation" paradigm). Under the Bayesian framework provided by classical signal detection theory, knowledge of the prior probability of occurrence of each category does not increase an observer's ability to distinguish between them, as measured by d'. This is because, despite the probabilistic cue, both features—CW and CCW tilt—remain equally relevant to performing the task, and

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should be given equal weight by an ideal observer (intuitively, the participant can form a judgment that the stimulus is CW either because of evidence for a CW grating is detected, or because evidence for a CCW grating is not detected). Rather, this probabilistic prior information about the likely feature should lead to adjustments in the criterion used for responding (for example, quantified as *c*), biasing participants to respond CW more often than CCW. Feature expectation alone should therefore confer an additive, rather than multiplicative, advantage over the case where no prior information is available, and this is what has classically been observed using conventional signal detection analyses in conjunction with this task (Green & Swets, 1966; Wald & Wolfowitz, 1949).

In the current study we revisit this prediction of the ideal observer model, and subject it to renewed empirical scrutiny. Do expectations about a coming percept enhance the sensitivity of our perceptual decisions? In one obvious sense, the answer is "yes." Many studies of feature-based attention have used variants of a visual search task in which an isolated target (e.g., a grating tilted 5° from vertical) is hidden in an array of distracters (e.g., three gratings with vertical tilt). Cues that provide probabilistic information about the features that will characterize the forthcoming array (e.g., stimuli will probably be close to vertical, rather than horizontal) facilitate performance in this class of task without inducing a response bias, as demonstrated by faster and more accurate searches on "validly" relative to "invalidly" cued trials (Ho, Brown, Abuyo, Ku, & Serences, 2012). Moreover, using this feature search paradigm, when observers are asked to make a fine discrimination judgment, the feature-based cue increases participants' sensitivity to the "off-channel" feature—that is, exaggerated versions of the target feature—that are most diagnostic of the difference between the target and distracters (Navalpakkam & Itti, 2007; Scolari & Serences, 2009). Critically, however, in this class of search task, unlike in the feature probability paradigm introduced above, the advance cues not only indicate what is likely to occur, but also indicate which features are relevant for the decision (e.g., in the current example, vertical, but not horizontal, feature information is decision-relevant, and should be given more weight in the decision). Thus, while feature-based attention clearly enhances the sensitivity of perceptual decisions, it remains unknown how decision sensitivity depends on whether a feature was expected or unexpected—that is, conditionally likely or unlikely—with the task-relevance of that feature controlled for.

Past studies have addressed this question using the framework of signal detection theory (Green & Swets, 1966). Conventional signal detection theory provides useful tools for measuring decision sensitivity in psychophysical tasks, but it suffers from two limitations. Firstly, calculation of d' (sensitivity) and *c* (bias) depend on contingency tables in which stimuli are classified into one of two categories, such as "signal present" and "signal absent." This approach discards sensory information that observers might be using to form a judgment. For example, participants might detect signal-like fluctuations in noise on a signal absent trial, and be correspondingly more likely to respond "present" (i.e., to make a false alarm) than when such fluctuations were absent. Participants' tendency to do this provides an estimate of their sensitivity to the signal, which is overlooked by traditional analysis based on binary trial counts. Secondly, for the same reason, signal detection analyses do not permit separate estimates of sensitivity on low signal energy (i.e., signal absent) and high-energy (i.e., signal present) trials, or indeed on trials that are validly or invalidly signalled by a probabilistic cue. In reference to the latter case, consider a signal detection analysis applied separately to valid and invalid trials in the feature probability paradigm. One cannot simply compute d' separately for those trials on which expectations were fulfilled (valid trials) and those on which they were violated (invalid trials), because an additive change in response bias will lead to a selective increase in hits on valid trials relative to invalid trials, and thus masquerade as a differential change in sensitivity on these trial types. A different approach is required.

Both of these shortcomings can be overcome by using psychophysical reverse correlation (Ahumada, 1996; Neri & Levi, 2006). In a psychophysical reverse correlation analysis, the energy in the stimulus is directly linked to the choices made by the participants, either by computing the excess rate (as a function of response) for a given pixel or feature, or using pixels/features to predict choices under the general linear model (Solomon, 2002). This allows the experimenter to compute how single-trial fluctuations in signal energy relate to behavior (overcoming problem 1), and this can be performed separately (for example) for trials in which stimuli were expected or unexpected (overcoming problem 2). For example, Wyart, Nobre, and Summerfield (2012) recently used this approach to test whether the mere expectation of a stimulus can enhance an observer's ability to detect it. The authors used psychophysical reverse correlation to characterize the decision templates that were employed following cues that signalled whether a vertical grating was likely to be present or absent in noise. They reported that less noisy decision templates were used when the stimulus was expected to be present, rather than expected to be absent, resulting in more sensitive detection judgments. This effect occurred even when spatial attention was controlled for, and the effects of expectation and spatial attention had dissociable influences on high- and low-energy gratings (Wyart et al., 2012). In other words, merely expecting a stimulus to be present heightened detection sensitivity, contrary to the predictions of an ideal observer model.

In the current article, we address a closely related (yet different) question. Consider again the feature expectation paradigm described above. Following a cue alerting the observer to expect a CW grating, the stimulus (once it arrives) can either be CW (i.e., validly cued) or CCW (i.e., invalidly cued). Once again, ideal observer models predict that on the task described above, discrimination sensitivity should be equal on valid and invalid trials, because an ideal observer will have allocated equal weight to CW and CCW angles of orientation. Do human observers indeed do this, or do they use different information to judge (a) that expectations have been satisfied, and (b) that they have been violated? This question remains unanswered, perhaps because it is impossible to address using conventional approaches—that is, by calculating decision theoretic statistics d' and c, for the reasons described above. However, it is possible to use psychophysical reverse correlation to characterize the weight that was given to different features during the decision, independently for validly cue and invalidly cued trials. Here, we adopted this approach, asking whether the fulfilment or violation of expectations changed the way feature information was weighed during perceptual decision-making.

In the present study, thus, we used psychophysical reverse correlation in conjunction with a variant of the feature expectation paradigm, allowing us to assess the weight that expected and unexpected (yet decision-irrelevant) feature information (tilt of a visual grating with respect to vertical) had on fine perceptual discrimination judgments (Figure 1). Probit regression was used to calculate the impact that random fluctuations in stimulus energy at a given orientation had on choice, independently for expected and unexpected gratings that did or did not occur. Aggregating over the resulting coefficients revealed a decision kernel whose height represents an observer's sensitivity to a given position in orientation space. This allowed us to plot and compare the decision kernels for stimuli that were validly or invalidly cued.

To preview our findings, we observed that decision kernels for stimuli with expected features shifted laterally, away from the discrimination boundary, even when spatial attention was controlled for. This ensured a heightened sensitivity to off-channel features—exaggerated versions of the target—that are most informative during fine discrimination judgments, and that has been described before for manipulations of feature attention using the feature search paradigm (Navalpakkam & Itti, 2007; Scolari & Serences, 2009) but not, to our knowledge, for the feature expectation paradigm. In other words, during fine discrimination, visual expectations make observers more sensitive to the most informative features in the visual world, irrespective of the focus of attention.

Methods

Participants

Sixteen healthy human participants with normal or corrected-to-normal vision and no history of neurological or psychiatric illness took part in the experiment. Participants gave informed consent and were compensated £40 for taking part in two experimental sessions of 2 hr each. Research was conducted in accordance with local ethical guidelines. Two participants were excluded after failing to meet required accuracy level during training (see Procedure for details).

Task summary

The task is depicted in Figure 2a. On all trials, participants judged whether one of two gratings occurring on the left or right of the screen was tilted CW or CCW of vertical. The to-be-judged position (left vs. right) was indicated by a colored probe cue that followed the stimuli. Two advance cues provided information about which of the two locations was more likely (66%) to be probed (spatial attention or relevance cue) and whether the grating at either location was more likely (66%) to be tilted CW or CCW (feature expectation or probability cue).

Materials

Stimuli were created and delivered using Psychtoolbox-3 (Brainard, 1997) (www.psychtoolbox.org) for MATLAB (Mathworks, Natick, MA) and were presented on a 17-in. monitor (resolution: 1280×1024; refresh rate: 60 Hz) at a viewing distance of 57 cm. Visual stimuli were two Gabor patches of 2 cycles per degree, with a phase sampled from a uniform random distribution, subtending 4° visual angle, presented simultaneously within pink and blue colored placeholders on the left and right sides of the screen (4° eccentricity). The Gaussian envelope of the Gabor had a standard deviation of 1° of visual angle, leading to a space constant of 1.41°. The contrast of the Gabor patches was fixed within a session (i.e., for individual participants), but varied across participants depending on performance in the initial practice phase. Each Gabor patch was convolved with smooth noise created by passing random pixel values, sampled from a

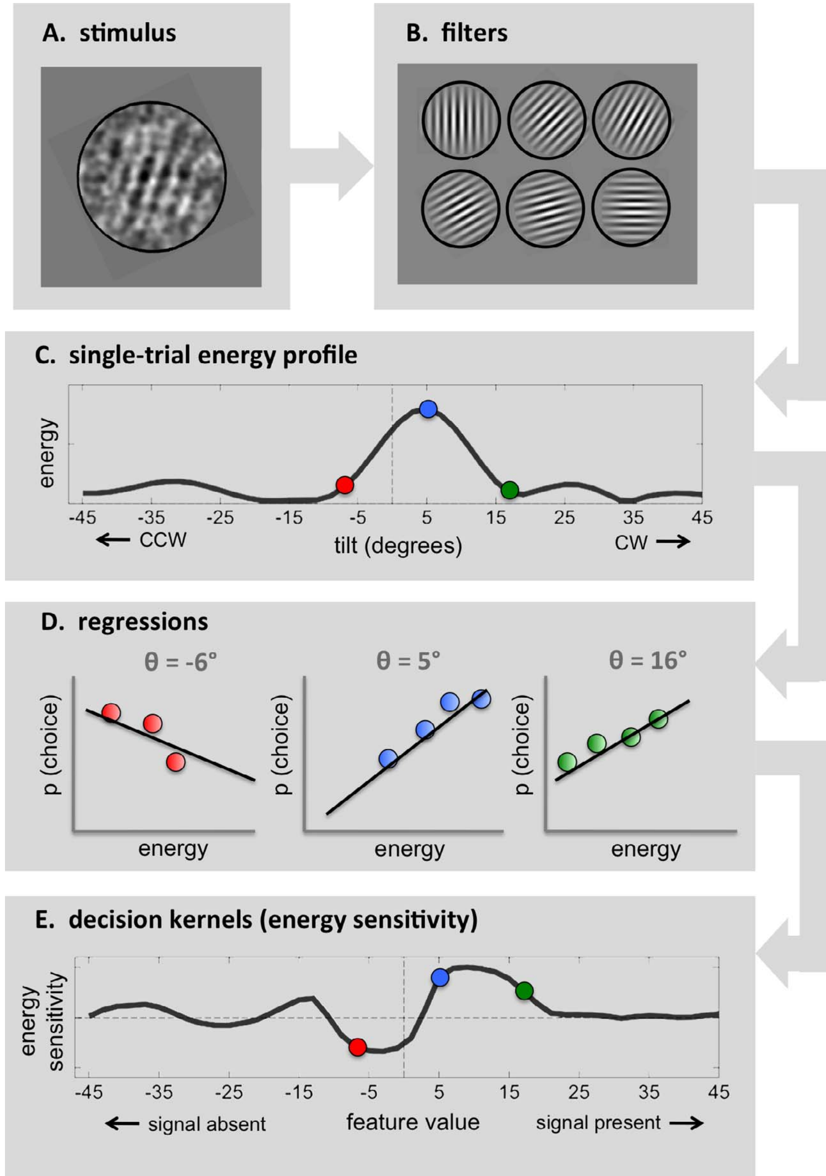

Figure 1. Processing pipeline. An example stimulus (A, target Gabor patch embedded in visual noise) is passed through a pool of Gabor filters with varying orientation (B) to calculate stimulus energy at orientations from $-45°$ to $+45°$ (schematic data). (C) For each attention and expectation category separately, stimulus energy at each orientation was regressed against choice (D) to generate a corresponding beta value (slope of black line), for each orientation. The schematic Figure illustrates this process for three target orientations (red, blue, and green dots in panels C–E). The resulting orientation energy sensitivity profiles were then flipped into frame of reference of stimulus present versus absent (see Methods for details) to generate a decision kernel (E).

Gaussian distribution, through a two-dimensional (2-D) Gaussian smoothing filter. The dimension of this smoothing filter was chosen to maximize the influence of noise on discrimination of the target orientation. This was implemented by maximizing the trial-to-trial variability of the convolution between the smoothed noise and the target signal, resulting in a smoothing of 0.083° of visual angle, and standard deviation of noise contrast of 10%, fixed across subjects and stimuli (see Wyart, Nobre & Summerfield, 2012, for further details). The orientation of each stimulus was sampled uniformly in the range of $-x°$ to $x°$ where x was titrated to provide 69% discrimination accuracy (determined on a subject by subject basis; mean [range] $x = 4.9°$; see below for details) and truncated to ensure that samples never crossed the category (vertical) boundary.

Procedure

Testing comprised two sessions taking place on separate days, each with a duration of approximately

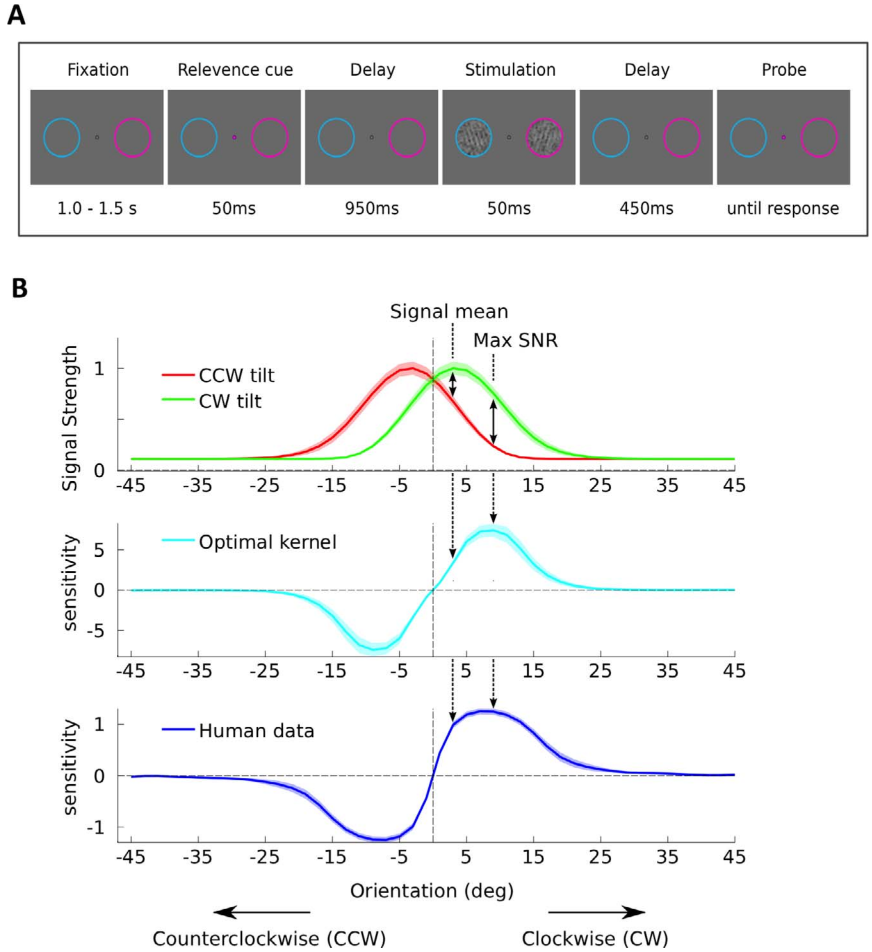

Figure 2. (A) Task structure. Subjects viewed two simultaneously presented noisy Gabor patches in colored placeholders located in their left and right visual fields. They reported the orientation (CW vs. CCW) of one of the Gabors, as indicated by a probe cue. We manipulated signal probability at the 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) Stimulus distributions and sensitivity profiles**.** Top panel: Average stimulus energy for CW and CCW stimuli. Shading indicates variation over participants. Signal mean (peak of energy distribution) and the point of maximum signal to noise ratio are illustrated by vertical dashed lines for the right tilt/clockwise stimuli. Middle panel: Optimal decision kernel, obtained by estimating coefficients from a probit regression model in which signal energy was a predictor of true target category (CW vs. CCW). Bottom panel: Human decision kernel, obtained by estimating coefficients from a probit regression model in which signal energy predicted human choices. Shading indicates standard error of the mean (*SEM*).

2 hr. The first session consisted of training phases in which the participant was gradually introduced to the task, performing the following versions of the task in order: (a) no cueing, (b) relevance cueing only, and (c) relevance and probability cueing. The second session consisted of 768 trials (divided into blocks of 96) of the main task containing both relevance and probability cues. Data from this version of the task is reported in the results section. Both training and test phases began with two blocks (192 trials) in which an adaptive staircase procedure was employed to titrate the mean offset of the stimulus from vertical to 69% (two-up-one-down procedure). This was achieved by either increasing or decreasing the average angular offset from the boundary of the stimulus—that is, the mean of the orientation sampling distribution (see Materials section for stimulus details). This titration procedure converged toward a mean threshold offset value of 3.6° ± 0.6° ($M \pm SEM$).

Feature expectation (probability) cues

Prior to the start of each block, probability cueing instructions were presented, informing the participant about the current probability contingencies (color placeholder – tilt relations). The probability contingencies were fixed within blocks, and set to one of the following two possible contingencies: In 3/8 of blocks

(37.5% trials), the pink placeholder was 0.67 likely to contain a CCW tilt stimulus, and 0.33 likely to contain a CW tilt stimulus, and the blue placeholder was associated with the opposite orientation-color mapping. In a separate 3/8 of blocks (37.5% trials), these probability contingencies were reversed (0.67 CW tilt, and 0.33 CCW tilt for the pink placeholder; 0.67 CCW tilt, and 0.33 CW tilt for the blue placeholder). Finally, in the remaining 1/4 of blocks (25% trials), CCW and CW tilts were equiprobable within both pink and blue placeholders (both Ps $= 0.50$). The spatial locations (left or right of fixation) of the pink and blue placeholders were randomized across trials, resulting in an equal probability of left and right tilts ($P = 0.50$) at both locations, even when biased color-orientation contingencies were used.

Spatial attention (relevance) cues

Each trial from the main task began with the presentation of pink and blue placeholders to the left and right of a fixation point. After a variable delay of between 1000 and 1500 ms, the fixation point changed color, either to pink (37.5% of trials), blue (37.5% of trials), or gray (25% of trials), with a duration of 50 ms. Color cues indicated which stimulus was most likely to be probed with 67% validity (pink: 0.67/0.33 in favor of the pink placeholder; blue: 0.67/0.33 in favor of the blue placeholder). Gray cues indicated that both stimuli were equally likely to be probed.

Imperative stimuli

Subsequently, 1000 ms after presentation of the color (relevance) cue, the two noisy Gabor stimuli were presented for 50 ms inside the colored placeholders, followed after 450 ms by a small central disc (probe cue) whose color indicated whether a discrimination judgment should be made about the Gabor occurring in the pink or blue placeholder. Participants judged whether the probed grating was tilted CCW or CW from vertical (0°). Responses were made via key presses using their left hand (middle finger: CCW tilt; index finger CW tilt; "z" and "x" keys, respectively) when instructed to report the orientation of the stimuli on the left of the screen, and their right hand (index finger: CCW tilt; middle finger CW tilt; "<" and ">" keys, respectively) when instructed to report the right-hand stimuli. An auditory tone presented 250 ms after response (correct: 880 Hz; error: 440 Hz), indicated whether a correct or incorrect response had been made. In the absence of a response, the trial timed out after 3000 ms.

Analysis

Conventional decision theoretic statistics were calculated according to standard formulae (Stanislaw & Todorov, 1999) and compared using analysis of variance (ANOVA). To compute decision kernels, we first computed the noise energy profile for each probed stimulus, by processing through a pool of Gabor filters with varying orientation (ranging from −45° to +45° in steps of 2°) using the following equation:

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

where $E(S|T)$ corresponds to the energy of the stimulus S conditional on the preferred signal T and $< * >$ corresponds to the cross-correlation operator. Computing energy in this manner (rather than via a simple dot product) corrects for any phase differences between target and stimulus. For the main analyses (reported in Figure 3) we calculated energy profiles separately for stimuli for which the signal was CW and CCW, and then the latter were flipped along the left–right axis so that positive-valued stimulus features corresponded to signal presence (rather than CW) and negative-valued stimulus features corresponded to signal absence (note that by contrast Figure 2 is in the native space of CW to CCW). Placing the resulting energy profiles in the frame of reference of signal absent versus present orientation (rather than CCW vs. CW) additionally ensured that any effects observed were unrelated to the relative fraction of signals present or absent on a given side, which would have biased the resulting coefficients.

Subsequently, we estimated decision kernels by regressing energy at each feature bin against binomial choices via a probit function, as follows:

$$p(CW) = \phi[B_o + B_1 \cdot Z[E(S|T)]]$$

where $E(S|T)$ corresponds to the energy of the stimulus S with respect to the template signal T, $Z[\ .\ ]$ to the normal deviate function (mean of the stimulus category of S, standard deviation of the signal-absent energy distribution), and $\Phi[\ .\ ]$ to the cumulative normal function. As for conventional signal detection theory, two parameters are fitted simultaneously: (a) β_0 is independent from the stimulus S and corresponds to the overall bias to respond CW, and (b) 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). For more details about the reverse correlation technique, we refer the reader to an earlier publication (Wyart et al., 2012).

We refer to the profile of energy sensitivities across feature space as a decision kernel. Decision kernels were estimated separately for trials on which the cue correctly indicated that a CW or CCW stimulus would

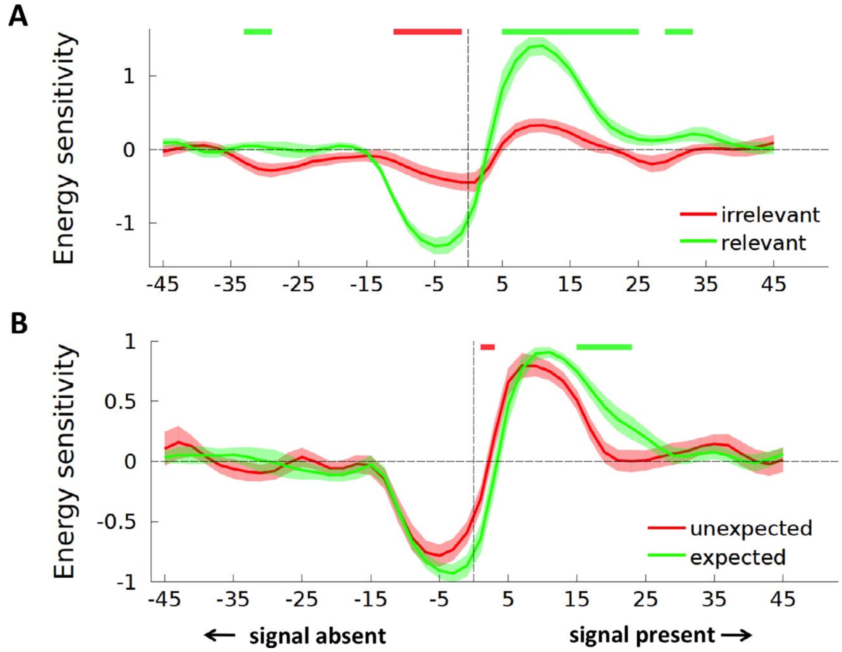

Figure 3. Human decision kernels. (A) Decision kernels for probed stimuli that had been cued as relevant (green) and irrelevant (red) trials. (B) Decision kernels for probed stimuli that were expected (green) and unexpected (red) conditional on the probability cue. The green and red horizontal lines above each panel indicate significance differences between conditions ($P < 0.05$) and the direction of the effect (green, attended > unattended or expected > unexpected; red, unattended > attended or unexpected > expected) The shaded area indicates *SEM*. Note that these data are flipped and folded so that *x*-axis values are in the frame of reference of signal absent versus present (rather than CCW vs. CW).

occur (expected stimuli) and for those where the cue indicated that a CW stimulus was more likely, but a CCW stimulus occurred, or vice versa (unexpected stimuli). Similarly, we computed decision kernels for the probed stimulus under conditions where an advance cue indicated that it was likely to be probed (attended stimuli) or unlikely to be probed (unattended stimuli). Similar kernels were computed for the unprobed grating, to estimate its (distracting) influence on choices. In all cases, coefficients were estimated separately for each participant and compared using ANOVA with Greenhouse-Geisser correction for sphericity.

We also modelled the effects of probability and relevance cues on decision kernels as follows: We calculated the average energy profile for each participant, and transformed it via two parameters: a multiplicative scaling parameter γ and a lateral shift parameter θ. We then searched exhaustively over values of γ (in the range 0 to 2) and θ ($-15°$ to $+15°$) until we found the values that minimized mean-squared error with decision kernels for each condition. The resulting parameters for each condition were compared at the group level using ANOVAs.

Finally, we estimated the theoretical influence of decision kernels on sensitivity by using them to predict the objectively defined tilt on each trial in our experiment. Each subjects' decision kernel was multiplied by the stimulus energy on each trial to provide a theoretical decision variable—that is, revealing the information that should have been available to participants given that strategy. To do this, we reflipped and refolded the decision kernel, to ensure a theoretical decision variable (DV) that ranged from negative (information favoring counterclockwise) to positive (favoring clockwise). Using the distributions of theoretical DVs for objectively CW and CCW trials allowed us to compute receiver operator characteristic (ROC) curves (in bins of 0.25 DV units) and estimate theoretical decision sensitivity (d') for attended and unattended, and expected and unexpected trials, given the observed decision kernels.

Results

Conventional signal detection analyses

We began by analyzing the data in a conventional fashion, estimating how relevance (spatial attention) cues and probability (feature expectation) cues influenced decision theoretic statistics d' (sensitivity) and c (bias). Average values of d' and c are reported for each condition in Table 1. Sensitivity was elevated when the

Relevance cue	Probability cue	d'	Criterion
Irrelevant	Probable	0.60 (0.12)	0.50 (0.11)
Neutral	Probable	0.96 (0.09)	0.29 (0.06)
Relevant	Probable	1.58 (0.14)	0.17 (0.09)
Irrelevant	Neutral	0.47 (0.14)	0.14 (0.10)
Neutral	Neutral	1.08 (0.14)	0.12 (0.09)
Relevant	Neutral	1.57 (0.10)	0.17 (0.07)
Irrelevant	Improbable	0.66 (0.17)	−0.29 (0.20)
Neutral	Improbable	0.99 (0.13)	−0.06 (0.08)
Relevant	Improbable	1.43 (0.13)	0.00 (0.06)

Table 1. Conventional signal detection results. *Notes*: d' and criterion for each relevance and probability condition separately, with standard error of the mean of 14 participants in parentheses.

decision-relevant location had been validly cued as relevant, $F(2, 26) = 19.8$, $p < 0.001$, with no effect of probability ($p = 0.93$) on d' and no interaction ($p = 0.27$) By contrast, criterion c was strongly influenced by the probability cue, $F(2, 26) = 8.34$, $p < 0.008$; in other words, where participants were cued that a CW feature was probable, they were more prone to respond CW than CCW, and vice versa. Although c did not depend on the relevance cue, there was a significant interaction, whereby probability cues had a stronger influence on c for stimuli cued as irrelevant than those cued as relevant, $F(4, 52) = 4.60$, $p < 0.003$. These findings are consistent with previous reports (Rahnev et al., 2011; Wyart et al., 2012) and indicate that (a) the probability manipulation was successful, (b) attention enhances sensitivity, and (c) that participants are more biased by probability at the unattended location.

Decision kernels

Previous studies have reported heightened sensitivity to off-channel features when attention is oriented towards one of two possible task-relevant dimensions (e.g., orientation rather than contrast). In these studies, optimal tuning can be calculated via computational approaches, for example by estimating tuning curves that maximize Fisher information (Navalpakkam & Itti, 2007). In our approach, there is a very simple way to determine the optimal decision kernel: It is that which is obtained by estimating coefficients from a logistic regression model in which the predictor is signal energy and the dependent variable is the true state of the world—that is, whether the probed grating was actually tilted CCW or CW. In Figure 2b (middle panel; cyan), we plot the optimal decision kernel. Although the mean orientation of the signal is offset by the boundary by $\sim 3°$, the point in orientation space that best distinguishes between the two categories, where the signal to noise ratio is maximal, is offset from the boundary by $\sim 9°$.

Decision kernels for stimuli cued as relevant and irrelevant

Next, we computed decision kernels separately for spatially attended or unattended gratings, occurring at locations that had been cued as decision-relevant and decision-irrelevant, respectively (Figure 3a). In both conditions, the decision kernel dipped below zero for the signal absent (by convention, left) side and peaked positively on the signal present (right side), indicating that fluctuations in signal-like noise (i.e., trial-by-trial variation in the resemblance between the stimulus and a CCW- or CW-tilted grating) robustly influenced choices. Notably, fluctuations in noise energy at both the signal-present side (right in Figure 3a) and signal-absent side (left) were predictive of choices; in other words, when a CW-tilted grating was presented, variation in noise energy on the CCW (signal-absent) side partly determined the response, in addition to the strength of the signal on the CW (signal-present side). Most saliently, however, decision kernels for gratings cued as relevant (or attended stimuli) had higher amplitude than those for those cued as irrelevant (unattended stimuli) or those that followed neutral cues (not shown). We assessed this difference statistically by dividing the feature axis into signal absent (left) and signal present (right) sides, and computing the interaction between condition and feature (i.e., distance from the category boundary) for each. Interactions were observed for both the signal-absent side, $F(3.4, 44.5) = 5.94$, $p < 0.001$, and the signal present side, $F(3.9, 51.2) = 4.62$, $p < 0.003$, although the interaction failed to reach significance when the relevant condition was excluded, $F(2.3, 30.3) = 1.00$, $p = 0.453$ and $F(3.5, 46) = 0.917$, $p = 0.389$, respectively, suggesting that there were no reliable differences between the neutral and irrelevant conditions. In other words, spatial attention confers a benefit relative to neutral cues, but invalid cueing carries no additional cost in sensitivity. These findings are consistent with previous reports that attention enhances the sensitivity of discrimination judgments (Carrasco, 2011; Posner et al., 1980), and that it does so by increasing the influence that attended features have on choices (a response-gain enhancement; McAdams & Maunsell, 1999).

Decision kernels for expected and unexpected stimuli

Subsequently, we turned to our main question of interest: How do decision kernels differ for expected

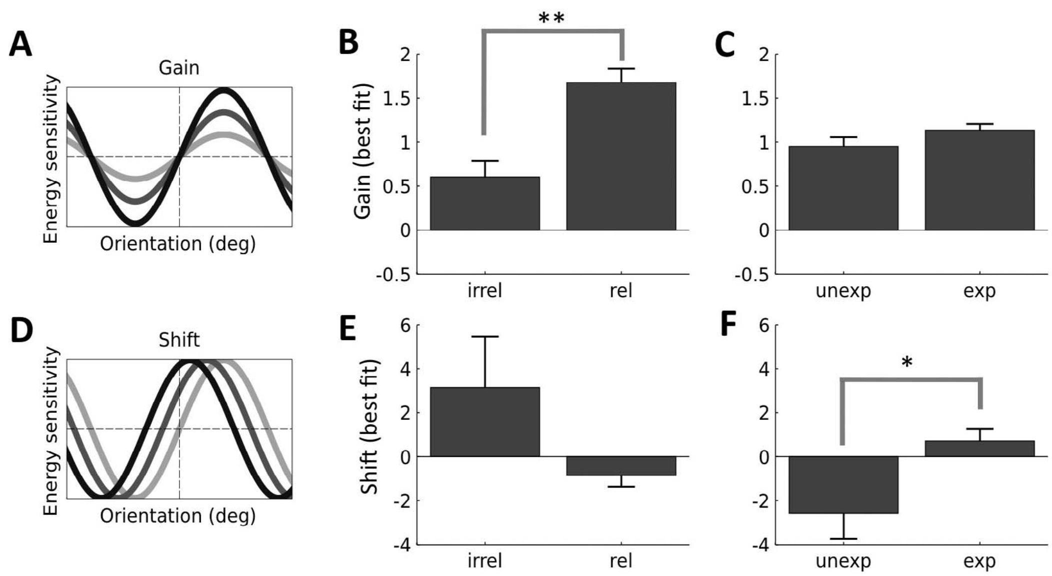

Figure 4. Model fits. Best-fitting γ (gain) and θ (shift) parameter values. (A) Schematic example of the influence of modifying the γ parameter on energy sensitivity profiles. (B) Mean best-fitting γ values for relevant (rel) and irrelevant (irrel) trials separately. (C) Mean best-fitting γ values for expected (exp) and unexpected (unexp) trials separately. (D) Schematic example of the influence of modifying the θ parameter on energy sensitivity profiles. (E–F) Same as (B–C) but for the θ parameter. $^*P < 0.05$; $^{**}P < 0.01$.

and unexpected stimulus features? Here, we divided trials not according to the probability cue per se, but according to whether the grating that occurred was validly cued (e.g., a CW grating following a CW cue; expected) or invalidly cued (a CW grating following a CCW cue; unexpected). Decision kernels for expected and unexpected stimuli are shown in Figure 3b. Here, a different pattern emerged. A reliable interaction was observed for the signal present side, $F(6.3, 81.5) = 2.66$, $p < 0.006$, but not for the signal absent side, $F(3.1, 40.5) = 0.607$, $p = 0.620$. Visual inspection indicated that the effect of feature expectation was to shift the decision kernel to the right—that is, away from the category boundary on the signal present side.

We quantified the effects of feature expectation and spatial attention on decision kernels in two ways. Firstly, we computed t statistics between kernels for attended/unattended and expected/unexpected stimuli at each point in feature space. For expectation, reliable differences of opposite sign were observed on either side of the peak (right, expected > unexpected: 15°–25°, max 19°, $t[13] = 3.07$, $p < 0.004$; left, unexpected > expected, 1°–3°, max 3°, $t[13] = 2.17$, $p < 0.025$). By contrast, the effect of the relevance cue was felt across feature space, from 15° to +35° relative to the category boundary (max 9°, $t[13] = 3.58$, $p < 0.002$). Indeed, the impact of relevance cues was greatest at the peak of the decision kernel, but the expected and unexpected stimuli did not differ at the peak, $t(13) = 0.66$, $p = 0.74$.

Secondly, we (multiplicatively) rescaled and (laterally) shifted the average energy sensitivity profile using two parameters that we termed γ and θ respectively (see Methods). Best-fitting values of γ and θ for each condition were obtained by exhaustive minimization of mean-squared error with respect to the corresponding decision kernel. By repeating this process for each subject individually, we were able compute group-level statistics on these parameters. The spatial relevance cue had a strong impact on γ, suggesting that it was best characterized by a multiplicative rescaling, $t(13) = 3.57$, $p < 0.005$, but not on θ, indicating no lateral shift, $t(13) = 1.74$, $p = 0.11$. In contrast, the feature expectation cue had an effect on θ, $t(13) = 2.61$, $p < 0.025$, but not γ, $t(13) = 1.30$, $p = 0.21$. Mean parameters for each condition are plotted in Figure 4.

The theoretical influence of decision kernels on discrimination sensitivity

Finally, we quantified the theoretical influence of the decision kernels obtained for attended and unattended trials, and expected and unexpected trials, on discrimination sensitivity. To this end, we computed for each trial a theoretical decision variable that quantified the information that would have been available to an observer using each kernel, in the absence of any internal noise. By comparing distributions of this theoretical decision variable for trials on which the stimulus was objectively tilted CCW or CW, we could plot ROC curves that indicated theoretical sensitivity in each condition, given the decision kernel. These ROC curves are shown in Figure 5. Attention enhanced theoretical sensitivity.

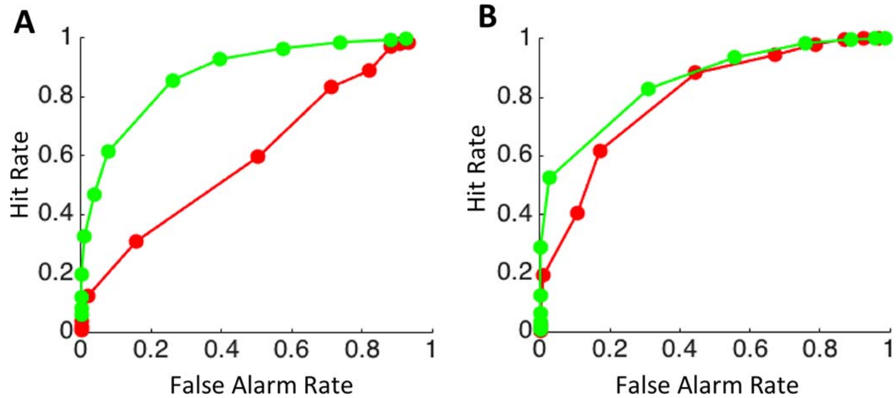

Figure 5. (A): Theoretical ROC curves for the decision kernels obtained under attended (green) and unattended (red) cueing conditions. (B): Theoretical ROC curves obtained using the decision kernels for expected (green) and unexpected (red) trials.

Discussion

Advance knowledge about what is likely to occur in the world (expectation) increases the likelihood of a correct response. However, according to optimal models based on the framework of signal detection theory, expectation does not increase our binary discrimination sensitivity as measured by d'—that is, our ability to tell one stimulus from another. Indeed, the standard approach adopted in signal detection analyses (in which stimuli and responses are sorted into four discrete classes to yield a 2×2 contingency table) precludes the question of how sensitivity differs to expected and unexpected sensory events. Reverse correlation, however, is a powerful technique that allows separate estimates of sensitivity to be computed for different classes of trials—such as signal-present and signal-absent trials in a detection task (Solomon, 2002). Previously, we used reverse correlation to show that during detection, a cue that indicates that a to-be-detected (vertical) Gabor is more likely to be present (rather than absent) is sufficient to enhance sensitivity to noise energy close to 0° (Wyart et al., 2012). In the reverse correlation approach adopted here (and in our previous work) sensitivity is quantified as the slope of the probit function mapping noise energy onto choice—that is, the extent to which an increase in energy (e.g., for a CW stimulus) enhances the probability of a corresponding response (e.g., the report "CW"). Quantifying observers' sensitivity in this way is itself more sensitive (in that it predicts observers' choices better than the binary classification approach), as it capitalizes on the leverage that signal-like variability in noisy stimuli wields over perceptual decisions (Wyart et al., 2012).

Here, we asked whether decision templates change according to whether the stimulus was surprising (invalidly cued) or unsurprising (validly cued), conditioned on an advance cue providing (decision-irrelevant) information about the likely feature. We found that they do. In the first instance, this suggests that decision templates are not fixed, but malleable; the weight given to stimulus information in a choice can vary as a function of whether it was conditionally likely (i.e., expected, or validly cued), or conditionally unlikely (i.e., unexpected, or invalidly cued), given a prior cue. This is a view which, while incompatible with traditional signal detection approaches, accords well with dynamic models of perceptual choice, in which a decision variable evolves nonlinearly over time, through reciprocal interactions between a decision template (or current belief) and sensory evidence (Friston, 2005; Usher & McClelland, 2001; Wang, 2002). In other words, priors about the stimulus are not fixed, but may vary as the sensory information is gradually evaluated. This is also consistent with neural descriptions of the perceptual decision process, which emphasize reciprocal or recurrent interactions between higher and lower stages of processing, giving rise to nonlinear neuronal dynamics during perception and choice (Bastos et al., 2012; Grossberg, 1988; Ullman, 1995).

At least one previous study has observed that decision templates can be altered by experimental variables that are only disclosed to the viewer once a stimulus arrives. During a grating detection task, Solomon (2002; experiment 2) observed different (linear) templates for signal-present and signal-absent trials. Rather than appealing to nonlinear interactions between the stimulus and template, the author suggested that observers were capitalizing on higher order information that differed between signal present and absent trials; indeed, when templates were calculated in a Fourier domain (e.g., independent of the spatial phase of the grating), they were found to be equivalent for the two trial types. However, a similar explanation cannot apply here, because in our experiment, expected and unexpected stimuli were physically identical. Moreover, the stimuli were all of variable phase, as our regression technique calculates the energy via quadrature pairs, obviating the need for a consistent-phase stimulus to disclose decision templates.

We found that decision templates for validly cued (relative to invalidly cued) stimuli differed in a stereotyped fashion. Specifically, when an expected feature occurs (e.g., a CW-tilted grating when CW gratings are conditionally more likely than CCW gratings), the human decision template shifts laterally, to become more sensitive to off-channel information, that is, to an exaggerated version of the target feature (e.g., yet more CW-tilted features). For example, when searching for an isolate tilted by 5° in an array of vertical lines, those neurons coding for orientations at ~10° offer the more diagnostic responses. Note that our data favor a shift rather than a broadening of the template, because significant differences of opposite sign in the observed kernel for expected and unexpected trials were observed near and far from the boundary (Figure 3b, red and green bars). We followed up this analysis by computing theoretical or noise-free sensitivity functions, indexing how well an observer equipped with each decision kernel would distinguish CW- and CCW-tilted stimuli in our experiment. An observer using the decision kernel observed on expected trials would fare better as revealed by the greater area under the ROC curve, and is thus more sensitive (Figure 5).

Previous studies involving fine orientation discrimination have shown that feature-based attention promotes off-channel sensitivity (Navalpakkam & Itti, 2007; Scolari, Byers, & Serences, 2012; Scolari & Serences, 2009). Our study is closely related to this work, but also differs from it in at least two important ways. The first is methodological. Previous behavioral studies have either used a two-step procedure in which tuning is assessed by measuring how one judgment affects another (Jazayeri & Movshon, 2007), or alternatively have established a context on one set of trials, and probed search performance on another (Navalpakkam & Itti, 2007; Scolari & Serences, 2009). One limitation of this approach is that it is unclear, when two different judgments are made, whether they are based on the same information or not, and/or rely on the same underlying computations. The reverse correlation approach described here sidesteps these issues, computing optimal and human decision kernels from the same variability in the noise energy of the stimulus, thereby providing a simple solution for measuring the influence that different features have on choices.

Secondly and more importantly, however, we manipulated the probability of occurrence of a feature (e.g., a CCW vs. CW tilt) in a way that should not lead to adjustments to sensitivity or the decision kernel under an ideal observer model. Previous studies have manipulated feature-based attention in a variety of different ways. Some studies have varied the feature similarity between an attended and an unattended stimulus, without altering the probability of occurrence of either (Martinez-Trujillo & Treue, 2004; Saenz, Buracas, & Boynton, 2002). These studies have provided evidence that attending to one feature (e.g., vertical motion) can increase the gain for neurons that prefer that feature outside of the spatially attended zone. However, unlike in our study, this approach does not manipulate the probability of occurrence of stimulus information, and thus presumably does not change the observers' visual expectations. Moreover, like previous studies, we found that probability cues have the greatest impact on spatially unattended stimuli (Rahnev et al., 2011), a finding that is incompatible with traditional feature-based attention models.

Other studies of feature-based attention have employed variants of a search paradigm, in which observers identify an array element that is characterized by a deviant feature. For example, Ho et al. (2012) provided a cue that specified the likely direction of motion of a forthcoming target random dot motion field that had to be identified from among three distracter random dot motions on the basis of its discrepant motion direction, reporting a cost to performance when the cue was invalid and the discrepancy to the presented target direction was large. A similar task was used by Scolari and Serences (2009). Although this comparison of performance on valid and invalid trials closely resembles the approach taken here, it is important to note that in this search paradigm, advance cues disclose which feature is most likely to be relevant for the decision (e.g., vertical vs. horizontal motion). Thus, unlike in our binary discrimination paradigm, in this paradigm the cues allow an ideal observer to give more weight to expected information and incur a sensitivity benefit on validly cued trials. This is not the case in our binary discrimination task, where the expected and unexpected feature are both equally relevant to the decision, and should be given equal weight by an ideal observer. Thus, our task shows that the observers' sensitivity is altered by cues that confer information about what is probable, independent of what is relevant, a distinction that we have previously referred to as "expectation" versus "attention." Nevertheless, the relationship between visual expectation and feature-based attention remains rather murky (Summerfield & Egner, 2009), and it is likely that our effects overlap at least partially with those mechanisms previously described by researchers investigating optimal shifts in tuning as a result of feature-based cues (Scolari & Serences, 2009). Our work thus builds on, and extends, these earlier findings.

Why should we be more sensitive to expected information? Neural information processing resources are limited, and the brain has evolved to process preferentially that information that is most diagnostic for accurate decisions and adaptive behavior (Simoncelli, 2003). Where the statistics of the environment vary, an efficient solution is to devote resources to those events that are likely to occur, so that they are detected and discriminated with higher fidelity, irrespective of whether they fall within the focus of attention or not (Barlow, 1961). Adapting the gain of information processing to various portions of an image as a function of whether they are surprising or expected is a sensible mechanism for allocating limited resources, and may constitute a general principle for human decision-making across perceptual and economic domains (Summerfield & Tsetsos, 2015).

In conclusion, thus, where stimuli are expected during fine discriminations, our decision kernel shifts, allowing us to capitalize on off-channel features that are most informative about stimuli category. This finding fits into an emerging picture by which the sensitivity of information processing adapts to suit the range and distribution of features in the sensory world. For example, during both psychophysical judgment and sequential integration, more probable features are processed with higher gain, a phenomenon that is reflected in increased encoding of informative features in parametrically varying neural activity (Cheadle et al., 2014; de Gardelle & Summerfield, 2011; Michael, de Gardelle, Nevado-Holgado, & Summerfield, 2013; Wyart et al., 2012).

Keywords: psychophysics, spatial attention, visual expectation, reverse correlation methods

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Corresponding author: Christopher Summerfield.
Email: christopher.summerfield@psy.ox.ac.uk.
Address: Department of Experimental Psychology, University of Oxford, Oxford, UK.

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