

Figure 2. Schematic of the LBA model. The stimulus provides information to four racing accumulators (each corresponding to one of four spatially distinct RDPs); the first accumulator to reach the response threshold determines the response, and thus the decision time. One accumulator corresponds to each possible response, and their average rates of increase (drift rates) are assumed to be determined by the stimulus properties. Response caution determines how much sensory evidence needs to be accumulated before a response is made and captured by the relative distance between the response threshold and the start point. The final response time is the decision processing time (the time taken for the first accumulator to reach the response threshold) plus a constant offset (non decision time).

Since the starting point for the evidence accumulator is a random sample from a uniform distribution on  $(0, A)$ , the amount of evidence that needs to be accumulated to reach the threshold  $b$  is a sample from the uniform distribution  $U(b - A, b)$ , assuming  $b \geq A$ . Since the drift rate for the  $i$ -th accumulator is a random draw from  $N(v_i, s)$ , the distribution function for the time taken for the  $i$ -th accumulator to reach threshold is the given by the ratio of these two, which has the following cumulative distribution function (CDF) (at time  $t > 0$ ):

$$F_i(t) = 1 + \frac{b - A - tv_i}{A} \Phi\left(\frac{b - A - tv_i}{ts}\right) - \frac{b - tv_i}{A} \Phi\left(\frac{b - tv_i}{ts}\right) + \frac{ts}{A} \varphi\left(\frac{b - A - tv_i}{ts}\right) - \frac{ts}{A} \varphi\left(\frac{b - tv_i}{ts}\right) \quad (1)$$

The associated probability density function (PDF) is:

$$f_i(t) = \frac{1}{A} \left[ -v_i \Phi\left(\frac{b - A - tv_i}{ts}\right) + s \varphi\left(\frac{b - A - tv_i}{ts}\right) + v_i \Phi\left(\frac{b - tv_i}{ts}\right) - s \varphi\left(\frac{b - tv_i}{ts}\right) \right] \quad (2)$$

Note that lowercase Greek letters in [Equations 1 and 2](#) refer to PDFs, while the uppercase Greek letters refer to CDFs. For more details regarding these equations and their derivations, see [Brown and Heathcote \(2008\)](#).

We used the LBA for several reasons. First, the parameter estimates are jointly constrained by both accuracy and response time (RT) data (for both correct and incorrect responses), as opposed to using only one dependent measure. Second, the joint use of accuracy and RT data allows the LBA to naturally handle any speed-accuracy tradeoffs that may arise in the data. Finally, the LBA (and other similar models) isolate

specific aspects of cognitive processing that are influenced by various experimental conditions (as captured by the different parameters in the model). For instance, in our cueing experiment, it could be that the cue influences the rate or quality of information extracted from the stimulus (as captured by the drift rate parameter), how much response caution a participant displays (as captured by the distance between the start point and the response threshold parameter), or it may affect nondecision related processes (as captured by the nondecision time parameter).

To evaluate the plausibility of each of these possible models, we fit eight different versions of the LBA model to the data (using all possible combinations of these three parameters to capture the effects of cueing). The parameters were estimated using the method of maximum likelihood (see [Donkin, Brown, Heathcote, & Wagenmakers, 2011](#) for full details of these methods, as well as an extensive discussion of alternative approaches). Initial parameter values for searches were generated two ways: (1) heuristic calculations based on the data and (2) start points determined from the end points of searches for simpler, nested models. Different mean drift rates were estimated for accumulators corresponding to the correct responses (that is, responses that matched the actual location of the target RDP), and the same single value was estimated for all three accumulators corresponding to incorrect responses (responses that did not match the true location of the target RDP). These correct and incorrect drift rates were then averaged across all four accumulators for each subject, respectively. For the purposes of our experiments, we report only the correct drift rates.

The most parsimonious of the eight models that we evaluated was selected using the Bayesian Information Criterion (BIC), a commonly used criterion that evaluates the tradeoff between model complexity and goodness of fit ([Raftery, 1995](#); [Schwarz, 1978](#)):

$$BIC = -2 \cdot (\log lik) + (\log N) \cdot d.$$

where  $lik$  = likelihood,  $N$  = number of data, and  $d$  = number of parameters.

We calculated the group BIC across all subjects for each model design by summing log-likelihoods, sample sizes, and parameter counts. The design with the lowest BIC value was considered the most parsimonious model. We then approximated posterior model probabilities based on the BIC by assuming a fixed effect for subjects. This approach assumed that every subject had an identical structure, such that when we compared model designs (e.g., the model where only drift rate varied versus the model where only response threshold varied), it was assumed that all subjects were described by the same model design. These posterior model probabilities provide support regarding the likelihood of each model design (for more details, see Burnham & Anderson, 2002).

## Results

A one-way repeated measures ANOVA revealed a significant effect of cue validity on accuracy ( $F[7, 49] = 5.140$ ,  $p = 0.0002$ ; Figure 3a). Mean accuracy rates in the neutral condition were slightly higher than in the invalid condition, but not different from the valid condition (see Figure 3a and first column of Table 1). Most notably, accuracy was lowest when the target was offset by  $90^\circ$  or  $120^\circ$  from the attention cue, after which there was a gradual improvement in accuracy (rebound effect; see Discussion). Consistent with this observation, a one-way repeated measures ANOVA on the accuracy rates for only the invalid trials revealed a significant difference between accuracy levels across the different cue-target offsets ( $F[5, 35] = 2.8717$ ,  $p = 0.02$ ).

Similarly, RTs varied significantly as a function of cue condition ( $F[7, 49] = 2.505$ ,  $p = 0.0278$ ; Figure 3b). RTs were significantly faster on valid trials compared to neutral trials, but RTs on valid and invalid trials were of a similar magnitude (see Figure 3b and second column of Table 1). A one-way repeated measures ANOVA on the RTs for only the invalid trials revealed no significant differences between RTs across the different cue-target offsets ( $F[5, 35] = 0.7621$ ,  $p = 0.5832$ ).

The accuracy and RT data present a mixed picture: the accuracy data suggest that attention confers no facilitation for validly cued features, but instead operates primarily by suppressing features dissimilar from the cue. In contrast, the RT data suggest facilitation for the cued feature and little suppression of features dissimilar from the cue. However, there is a speed-accuracy tradeoff occurring: subjects were equally accurate on both valid and neutral trials, but responded significantly faster on valid trials (Figure 3

and first and second columns of Table 1). By using both accuracy and RT data, the LBA model accounts for such tradeoffs and is able to estimate how the cue manipulation selectively influences various latent variables such as the rate of sensory evidence accumulation (drift rate), the amount of information required to make a decision (response threshold), and the time related to nondecisional processes.

Out of the eight tested model designs (where either response caution, drift rate, or nondecision time could stay fixed or vary), the best fitting LBA model—as determined by the BIC—only allowed drift rate to vary between the eight possible cue-target conditions (validly cued targets, neutrally cued targets, and the six possible invalidly cued targets, collapsing across clockwise and counterclockwise offsets). The parameter estimates for response caution and nondecision time for this model were 3.188 and 0.169, respectively (see Figure 4 for the drift rates across the cue conditions). The posterior probability of this model was almost 1, which was more than  $10^{40}$  times more likely than the next best design, in which both drift rate and nondecision time varied (see Methods for more details). Extremely strong support for one alternative like this is characteristic of group-average analyses like ours since such analyses compare extreme hypotheses (i.e., every subject is better described by one particular model compared to another). To confirm that these analyses did not bias our results, we also calculated posterior model probabilities separately for each individual participant and averaged the resulting probabilities; the model where only drift rate varied still had the greatest average posterior probability.

Figure 4 shows the drift rates corresponding to the accumulators that matched the correct response (and all subsequent statistics focus on these drift rates as well, see the LBA model section under Methods for more details). A one-way repeated-measures ANOVA revealed a strong effect of cue condition on drift rates ( $F[7, 49] = 6.793$ ,  $p < 0.0001$ ), and an individual  $t$ -test revealed that drift rates were larger on valid trials compared to neutral trials (Figure 4 and third column of Table 1). In contrast, the drift rates with invalidly cued trials were not significantly different from the drift rates observed on neutrally cued trials (Figure 4 and third column of Table 1). A one-way repeated measures ANOVA on the drift rates associated with just invalidly cued targets revealed a significant difference across the possible offsets ( $F[5, 35] = 5.092$ ;  $p = 0.0013$ ). Thus, drift rates on invalid trials did exhibit a pattern that is analogous to the rebound effect observed in the accuracy data: as the offset between the cued direction and target direction increased, the drift rates corresponding to the correct response decreased up until an offset of  $90^\circ$ , after which they began to rise again.

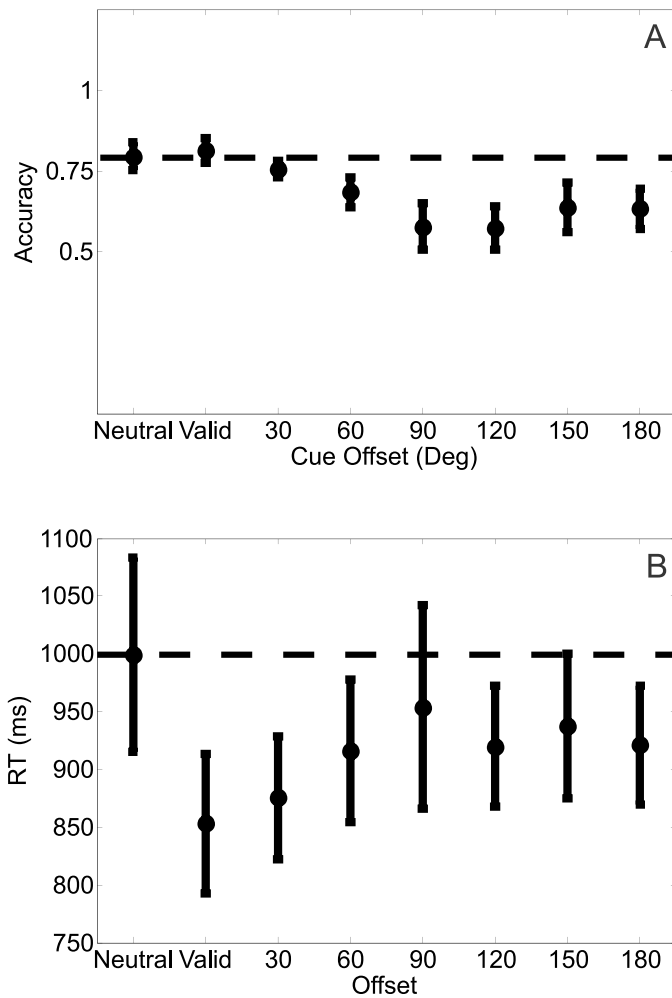


Figure 3. (a) Mean accuracy rates across the different cue conditions for Experiment 1. Mean accuracy rates computed across subjects (ordinate) as a function of the eight possible cue conditions (abscissa). (b) Mean response times on correct trials across the different cued conditions for Experiment 1. Mean response times computed across subjects (ordinate) as a function of the eight possible cue conditions (abscissa). Offsets were collapsed across clockwise and counterclockwise directions. All error bars are  $\pm 1$  SEM, computed after subtracting the mean from each subject.

In Experiment 2, we attempted to amplify the suppressive effects of feature-based attention by creating a variant of the behavioral paradigm in which the distractors competed more effectively with the search target.

## Experiment 2

### Methods

#### Subjects

Thirteen right-handed subjects (five females) were recruited from the University of California, San Diego

Comparison	Accuracy rate	Response time	Drift rate
Neutral vs. valid	$p = 0.9948$	$p = 0.0364^*$	$p = 0.0168^*$
Neutral vs. 30°	$p = 0.995$	$p = 0.085$	$p = 0.9392$
Neutral vs. 60°	$p = 0.1367$	$p = 0.1962$	$p = 0.8191$
Neutral vs. 90°	$p = 0.1003$	$p = 0.7059$	$p = 0.7433$
Neutral vs. 120°	$p = 0.1$	$p = 0.2545$	$p = 0.744$
Neutral vs. 150°	$p = 0.1699$	$p = 0.254$	$p = 0.8631$
Neutral vs. 180°	$p = 0.1$	$p = 0.1895$	$p = 0.1157$
Valid vs. 30°	$p = 0.17$	$p = 0.25$	$p = 0.0566$
Valid vs. 60°	$p = 0.1005$	$p = 0.0847$	$p = 0.0642$
Valid vs. 90°	$p = 0.1168$	$p = 0.254$	$p = 0.0616$
Valid vs. 120°	$p = 0.1005$	$p = 0.19$	$p = 0.062$
Valid vs. 150°	$p = 0.17$	$p = 0.1895$	$p = 0.057$
Valid vs. 180°	$p = 0.101$	$p = 0.0770$	$p = 0.1814$
30° vs. 60°	$p = 0.1862$	$p = 0.019$	$p = 0.5965$
30° vs. 90°	$p = 0.14$	$p = 0.3811$	$p = 0.3192$
30° vs. 120°	$p = 0.1367$	$p = 0.1962$	$p = 0.345$
30° vs. 150°	$p = 0.2625$	$p = 0.0196$	$p = 0.056$
30° vs. 180°	$p = 0.1699$	$p = 0.1305$	$p = 0.062$
60° vs. 90°	$p = 0.2123$	$p = 0.784$	$p = 0.8635$
60° vs. 120°	$p = 0.1368$	$p = 0.9225$	$p = 0.8651$
60° vs. 150°	$p = 0.5676$	$p = 0.7840$	$p = 0.345$
60° vs. 180°	$p = 0.2625$	$p = 0.92$	$p = 0.0617$
90° vs. 120°	$p = 0.3746$	$p = 0.7908$	$p = 0.9392$
90° vs. 150°	$p = 0.995$	$p = 0.791$	$p = 0.25$
90° vs. 180°	$p = 0.4597$	$p = 0.784$	$p = 0.062$
120° vs. 150°	$p = 0.2787$	$p = 0.79$	$p = 0.249$
120° vs. 180°	$p = 0.3084$	$p = 0.9667$	$p = 0.059$
150° vs. 180°	$p = 0.9949$	$p = 0.785$	$p = 0.056$

Table 1. Pair-wise comparisons of mean accuracy rates, mean response times, and mean drift rates between different cued conditions for Experiment 1 ( $n = 8$ ). Offsets were collapsed across clockwise and counterclockwise directions. Please refer to Figure 3 and Figure 4. Note: The reported  $p$ -values here have been corrected for multiple comparisons using a False Discovery Rate procedure.  $*p < 0.05$ ,  $**p < 0.01$ ,  $***p < 0.001$ .

(UCSD, La Jolla, CA) community. All had normal or corrected-to-normal vision. Each subject gave written informed consent per Institutional Review Board requirements at UCSD and completed two 1–1.5 hr sessions in a climate- and noise-controlled subject room. Compensation for participation was \$10.00/hr for the experiment. Data from 1 subject were discarded due to failure to return for the second testing session, so data from 12 subjects were analyzed.

#### Stimuli and task

All methods used in Experiment 2 are similar to those used in Experiment 1 unless noted. In Experiment 2, we also used a four alternative forced choice task, but the single target RDP contained 80% coherent motion, while the distractors contained 40% coherent

motion (Figure 5). The purpose of this manipulation was to magnify competition between distractors and the target, which we anticipated would lead to larger attentional effects compared to Experiment 1. The direction of each distractor RDP was offset from the target direction by either  $\pm 15^\circ$ ,  $\pm 45^\circ$ ,  $\pm 75^\circ$ ,  $\pm 105^\circ$ ,  $\pm 135^\circ$ , or  $\pm 165^\circ$  (pseudorandomly chosen on each trial, with the constraint that each distractor direction was unique). Subjects indicated which RDP contained the high coherence using keys on the number pad to indicate their decision. Invalid cues indicated directions that were offset from the direction of motion of the target RDP anywhere from  $\pm 30^\circ$  to  $\pm 180^\circ$  (in  $30^\circ$  steps) on a trial-by-trial basis. All cues were presented centrally for 1000 ms and the stimulus array was presented for 2000 ms. Subjects were instructed to keep their eyes at fixation throughout the trial and were allowed to make a response any time after the stimulus onset; each trial was self-paced and terminated once subjects provided a response. All subjects were encouraged to respond as quickly and as accurately as possible. Each block contained 48 trials, and in total, the experiment consisted of 20 blocks. Subjects typically completed 4 to 8 blocks on the first day of the experiment (in addition to training) and then returned a second day to complete the remaining blocks. Subjects were allowed to rest between blocks if they chose to do so, and all analyzed data came from subjects who completed all 20 blocks.

We used the same training and staircasing procedures described in Experiment 1 to titrate performance to approximately 75% before data collection in the main task. For the main experiment, the mean contrast level  $\pm$  SEM across the 12 subjects was  $15.21\% \pm 4.3\%$ .

## Results

A one-way repeated measures ANOVA revealed a significant effect of cue-validity on accuracy ( $F[7, 77] = 19.561$ ,  $p < 0.0001$ ; Figure 6a). Accuracy was higher on valid trials compared to neutral trials and generally lower on invalid trials compared to neutral trials (Figure 6a and first column of Table 2a). A one-way repeated measures ANOVA for accuracy rates on only the invalid trials also revealed a highly significant difference ( $F[5, 55] = 11.319$ ,  $p < 0.0001$ ). Most notably, accuracy was lowest at  $90^\circ$  and  $120^\circ$  (Figure 6a and first column of Table 2a), after which there was a gradual improvement (rebound effect, see Discussion).

RTs also varied as a function of cue condition ( $F[7, 77] = 7.44$ ,  $p < 0.0001$ ; Figure 6b). Compared with neutral trials, RTs were significantly faster on valid trials and significantly slower on invalid trials (Figure

6b and second column of Table 2a). A one-way repeated measures ANOVA for RTs on only the invalid trials also revealed a significant difference ( $F[5, 55] = 3.2106$ ,  $p = 0.013$ ).

A one-way repeated measures ANOVA also revealed a significant modulation in the error rate as a function of the directional offset between the cue and an incorrectly selected distractor ( $F[5, 55] = 36.164$ ,  $p < 0.0001$ ; Table 2b and Figure 6c). In particular, subjects selected a distractor whose direction was only  $15^\circ$  away from the invalid cue significantly more often than distractors rotated more than  $105^\circ$  from the invalidly cued direction (Table 2b and Figure 6c).

As in Experiment 1, we found that the best fitting model based on the lowest BIC value was the one where only drift rate varied between the eight possible cue types (collapsing across clockwise and counterclockwise offsets). The parameter estimates for response caution and nondecision time were 20.215 and 0.139, respectively (see Figure 7 for the drift rates across the cue conditions).

The approximate posterior model probability (see Methods for more details) was close to 1, more than  $10^6$  more likely than the next best design in which both drift rate and nondecision time varied. A one-way ANOVA revealed a robust effect of cue-type on drift rates ( $F[7, 77] = 8.281$ ,  $p < 0.0001$ ). Consistent with the raw accuracy rates and RTs, drift rates estimated from valid trials were significantly larger than drift rates estimated from neutral trials. Drift rates were also significantly lower for all invalid offsets compared to neutral trials, with the exception of the  $180^\circ$  offset. A one-way repeated measures ANOVA for drift rates on only the invalid trials revealed a highly significant difference ( $F[5, 55] = 6.7937$ ,  $p < 0.0001$ ). Drift rates showed the same rebound effect evident in the accuracy data: drift rates continued to decrease as the offset between the cue and target increased, up until an offset of  $90^\circ$ , after which they returned to the level observed on neutral trials (Figure 7 and third column of Table 2a).

## Discussion

We utilized two variants of a cueing paradigm to show that goal-directed feature-based attention influences visual performance through both facilitatory and suppressive mechanisms. In Experiment 1, when subjects searched for an oddball motion target, the LBA model revealed increased rates of sensory evidence accumulation for validly cued targets compared to neutral targets (facilitation). In addition, drift rates on invalidly cued trials varied as a function of the cue target offset, with highest drift rates observed for invalid targets that most closely matched the cue.

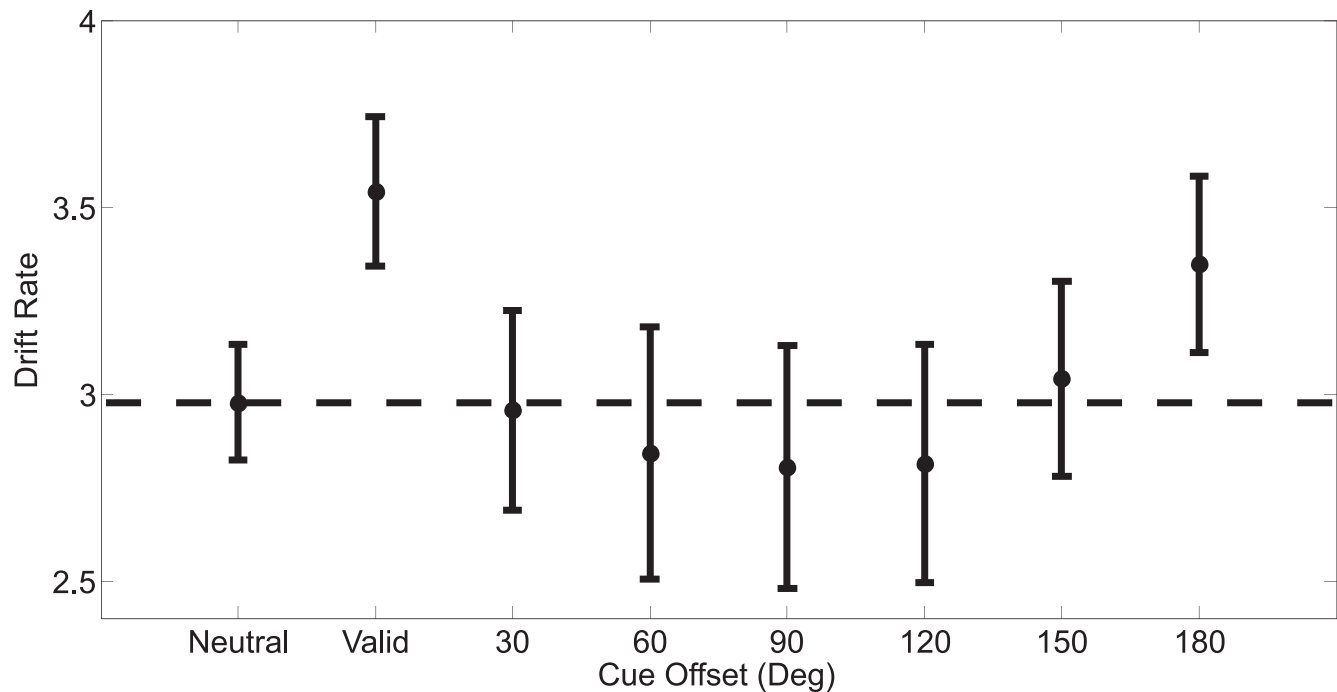


Figure 4. Drift rates for the accumulators corresponding to the correct response on the different cue conditions for [Experiment 1](#). Mean drift rates corresponding to the correct response on each trial computed across subjects (ordinate) as a function of the eight possible cue conditions (abscissa). Offsets were collapsed across clockwise and counterclockwise directions. All error bars are  $\pm 1$  SEM, computed after subtracting the mean from each subject.

However, while these patterns are suggestive, the drift rates on invalid trials were not significantly lower than drift rates on neutral trials. In [Experiment 2](#), two key changes were made in an attempt to amplify attentional enhancement and suppression. First, we increased competition between the target and distractors in an effort to place additional demands on suppressive attentional mechanisms. Second, as a result of the increased difficulty associated with having more salient distractors, the RDPs in [Experiment 2](#) had higher mean contrast levels compared to [Experiment 1](#): 15.21% versus 1.65%. Given that both neurophysiological and psychophysical work suggest that higher contrast levels can yield greater feature-based attentional effects (Hermann, Heeger, & Carrasco, 2012; Martinez-Trujillo & Treue, 2002), it is possible that this increase in contrast might also contribute to more pronounced attentional modulations. Indeed, these manipulations had the intended effect, as an analysis of drift rates revealed extremely robust evidence for both attention-related facilitation and suppression ([Figure 7](#)).

### Rebound effect

In [Experiment 1](#), drift rates corresponding to invalidly cued targets were suggestive of a suppressive effect of feature-based attention ([Figure 4](#) and third column of [Table 1](#)). This pattern, however, was far

more pronounced in [Experiment 2](#), where drift rates corresponding to the invalidly cued targets were significantly lower than those for neutrally cued targets as the offset between the invalid cue and target approached  $90^\circ$  ([Figure 7](#) and third column of [Table 2a](#)). However, as the offset between the invalid cue and target increased from  $90^\circ$  to  $180^\circ$ , the corresponding drift rates also gradually increased, giving rise to a “rebound effect” ([Figure 7](#) and third column of [Table 2a](#)). A similar rebound pattern was also observed in [Experiment 1](#), where an ANOVA conducted on drift rates on invalidly cued targets was significant ([Figure 4](#) and third column of [Table 1](#)).

This nonmonotonic change in drift rate as a function of cue-to-target separation is superficially inconsistent with neurophysiological data showing maximal neural suppression for directions opposite from the attended direction (Martinez-Trujillo & Treue, 2004). Recall that our task only required subjects to identify the quadrant that contained the RDP with the highest motion coherence (among distractors containing 0% motion coherence in [Experiment 1](#) and 40% motion coherence in [Experiment 2](#)). As a result, the observed rebound effect could be related to subjects monitoring orientation signals associated with the axis of motion rather than the direction of motion per se. Indeed, many neurons in areas such as the primary visual cortex will respond robustly to the axis of motion in a manner analogous to a static bar rendered at the same



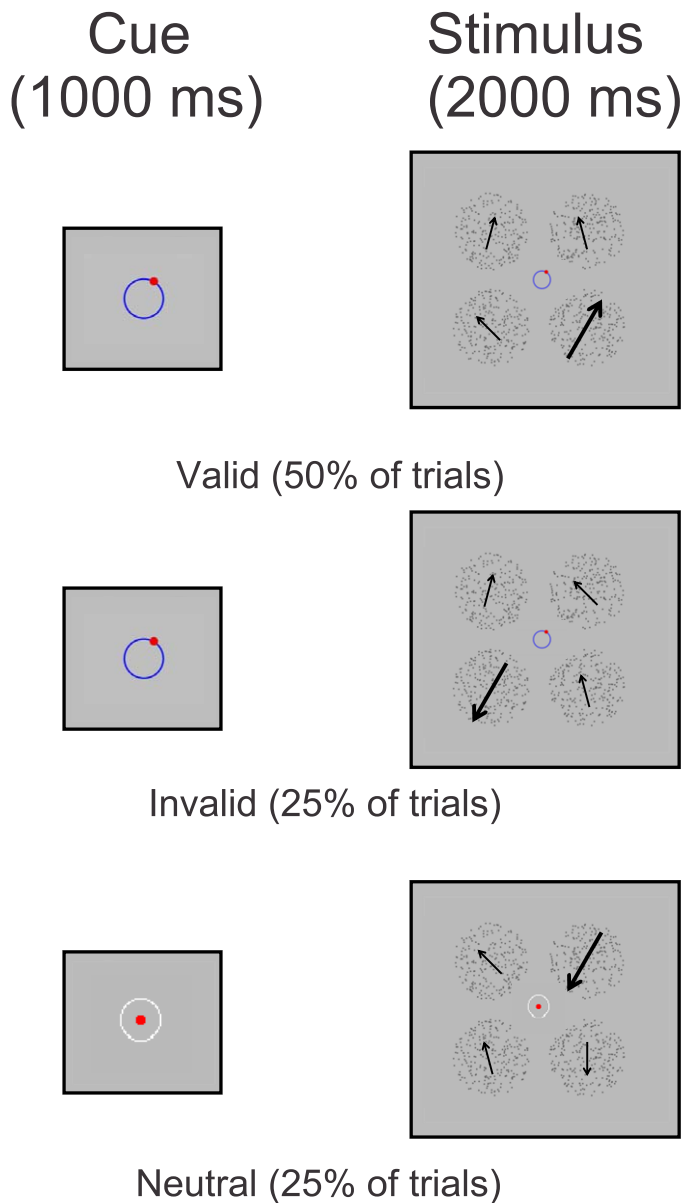


Figure 5. Behavioral paradigm for [Experiment 2](#). At the beginning of each trial there was either a valid cue (50% of the trials) correctly indicating the impending direction of motion, an invalid cue (25% of the trials) incorrectly indicating the impending direction of motion, or a neutral cue (25% of the trials) that contained no directional information whatsoever. Invalid cues indicated directions that were offset from the direction of motion of the target RDP anywhere from  $\pm 30^\circ$  to  $\pm 180^\circ$  on a trial-by-trial basis (determined pseudorandomly within a given block of trials). The target RDP contained 80% motion coherence, while the distractors contained 40% motion coherence, where each distractor direction was offset from the target direction by either  $\pm 15^\circ$ ,  $\pm 45^\circ$ ,  $\pm 75^\circ$ ,  $\pm 105^\circ$ ,  $\pm 135^\circ$ , or  $\pm 165^\circ$  (randomly chosen per trial, where each distractor direction was unique) for eight of the subjects or by  $\pm 18^\circ$ ,  $\pm 36^\circ$ , or  $\pm 72^\circ$  for the remaining four subjects. Note: Cues in the first panel are exaggerated in size for the purposes of clarity.

orientation (Albright, 1984; Conway and Livingstone, 2003; Livingstone, 1998; Livingstone and Conway, 2003). Note, however, that behavioral performance in [Experiment 2](#) on invalid trials with a  $180^\circ$  offset was not as good as performance on valid trials ([Figures 6 and 7](#); [Table 2a](#)). Therefore, signals from motion selective neurons tuned  $180^\circ$  from the cue might very well have been suppressed in motion selective visual areas such as middle temporal (MT), and the partial recovery of performance might be supported by attentional gain targeted towards orientation selective neurons in other areas that are tuned to the axis of motion. In either case, the data suggest that subjects were using the cue to guide search, and clear evidence supporting the suppressive effects of feature-based attention were observed.

### Comparisons with the feature-similarity gain model

Compared to a condition in which only a fixation mark was attended, [Martinez-Trujillo and Treue \(2004\)](#) reported enhanced responses in MT neurons that were tuned to an attended direction of motion and suppressed responses in neurons that were tuned away from the attended direction of motion (see also [Cohen & Maunsell, 2011](#)). These data predict enhanced perceptual sensitivity for attended features as well as a reduction in perceptual sensitivity for features that are maximally separated from the target in feature space (e.g., opposite directions of motion). Consistent with a suppressive component of feature-based attention, [Ling et al. \(2009\)](#) used an equivalent-noise paradigm and a task in which subjects had to discern whether or not a centrally presented RDP contained motion that was clockwise or counterclockwise from one of four reference directions (see also [Baldassi & Verghese, 2005](#)). The coherence (proportion of dots moving in the same direction) of the RDP was systematically adjusted across multiple levels, and the directional offset between the target direction and the reference directions was adjusted to estimate a perceptual sensitivity threshold for each subject. On validly cued trials, attention reduced sensitivity thresholds across all motion coherence levels, suggesting that feature-based attention suppressed neural responses evoked by dots within the RPDs that were moving in uncued directions. This putative suppression of uncued motion directions is consistent with previous neurophysiology studies and with our psychophysical and modeling results. However, the present results further demonstrate that the suppressive effect of feature-based attention can operate across multiple locations in the visual field, as opposed to being restricted to a single spatial location that contains both the cued and the uncued features (as in the variable coherence RDPs used by [Ling et al., \(2009\)](#)).

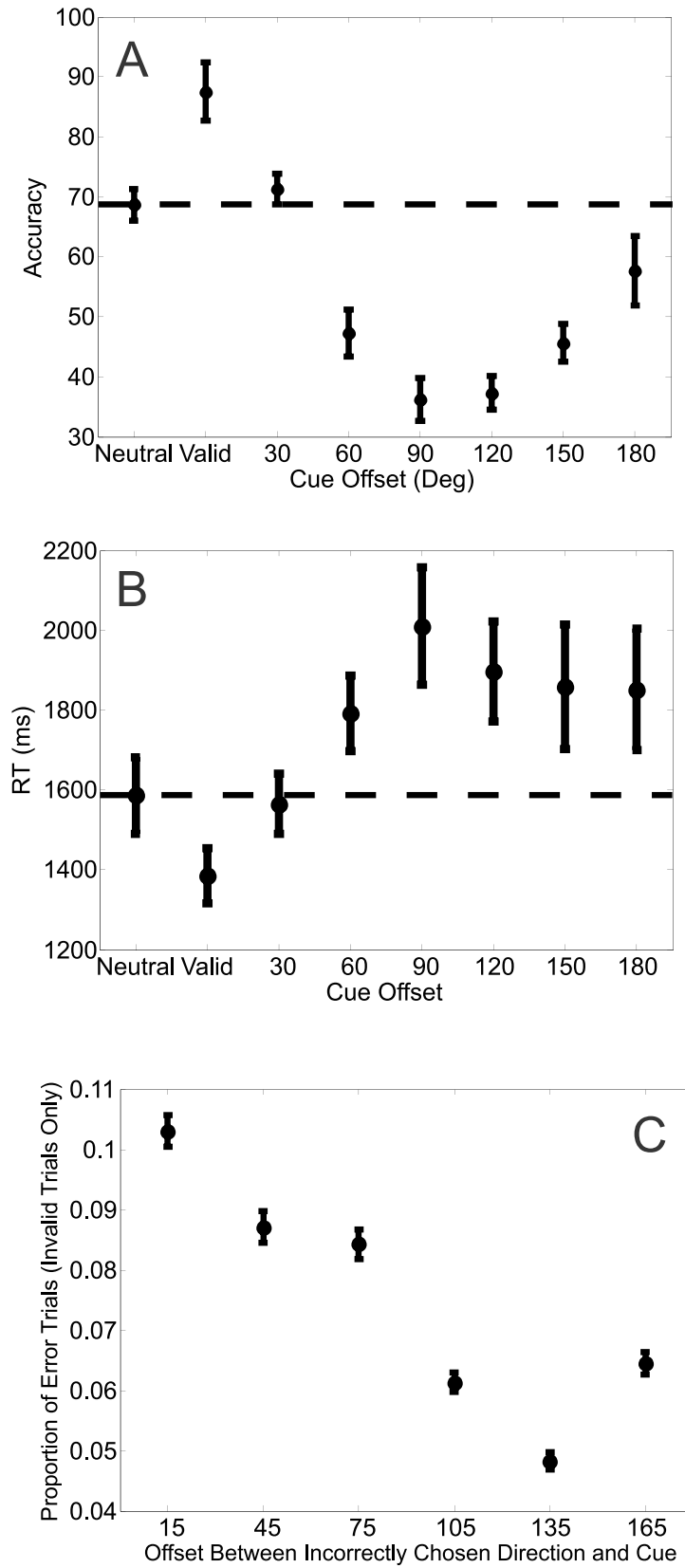


Figure 6. (a) Accuracy rates across the different cue conditions for Experiment 2. Mean accuracy rates computed across subjects (ordinate) as a function of the eight possible cue conditions (abscissa). (b) Mean response times on correct trials across the different cued conditions for Experiment 2. Mean accuracy rates computed across subjects (ordinate) as a function of the eight possible cue conditions

Comparison	Accuracy rate	Response time	Drift rate
Neutral vs. valid	$p = 0.000364^{***}$	$p = 0.0021^{**}$	$p = 0.0056^{**}$
Neutral vs. 30°	$p = 0.3960$	$p = 0.5851$	$p = 0.0409^*$
Neutral vs. 60°	$p = 0.0022^{**}$	$p = 0.052$	$p = 0.0491^*$
Neutral vs. 90°	$p = 0.0004^{***}$	$p = 0.0491^*$	$p = 0.0409^*$
Neutral vs. 120°	$p = 0.00035^{***}$	$p = 0.0037^{**}$	$p = 0.0436^*$
Neutral vs. 150°	$p = 0.0019^{**}$	$p = 0.0031^{**}$	$p = 0.044^*$
Neutral vs. 180°	$p = 0.1656$	$p = 0.01^*$	$p = 0.4928$
Valid vs. 30°	$p = 0.00043^{***}$	$p = 0.052$	$p = 0.0261^*$
Valid vs. 60°	$p = 0.00035^{***}$	$p = 0.0018^{**}$	$p = 0.0325^*$
Valid vs. 90°	$p = 0.0003^{***}$	$p = 0.01^*$	$p = 0.026^*$
Valid vs. 120°	$p = 0.0003^{***}$	$p = 0.0019^{**}$	$p = 0.027^*$
Valid vs. 150°	$p = 0.0004^{***}$	$p = 0.0037^{**}$	$p = 0.026^*$
Valid vs. 180°	$p = 0.0065^{**}$	$p = 0.01^*$	$p = 0.0437$
30° vs. 60°	$p = 0.00037^{***}$	$p = 0.046^*$	$p = 0.3794$
30° vs. 90°	$p = 0.00036^{***}$	$p = 0.052$	$p = 0.0659$
30° vs. 120°	$p = 0.00036^{***}$	$p = 0.0112^*$	$p = 0.1376$
30° vs. 150°	$p = 0.0019^{**}$	$p = 0.0328^*$	$p = 0.5381$
30° vs. 180°	$p = 0.1387$	$p = 0.0835$	$p = 0.0491^*$
60° vs. 90°	$p = 0.0239^*$	$p = 0.3645$	$p = 0.02$
60° vs. 120°	$p = 0.0575$	$p = 0.1426$	$p = 0.041$
60° vs. 150°	$p = 0.7924$	$p = 0.3948$	$p = 0.7489$
60° vs. 180°	$p = 0.3326$	$p = 0.6406$	$p = 0.044^*$
90° vs. 120°	$p = 0.6875$	$p = 0.5851$	$p = 0.4029$
90° vs. 150°	$p = 0.057$	$p = 0.7351$	$p = 0.0473^*$
90° vs. 180°	$p = 0.0275^*$	$p = 0.6283$	$p = 0.03^*$
120° vs. 150°	$p = 0.0565$	$p = 0.3171$	$p = 0.0436^*$
120° vs. 180°	$p = 0.0145^*$	$p = 0.1737$	$p = 0.026^*$
150° vs. 180°	$p = 0.0413^*$	$p = 0.7499$	$p = 0.027^*$

Table 2a. Pair-wise comparisons of mean accuracy rates, mean response times, and drift rates between different cued conditions for Experiment 2 ( $n = 12$ ). Offsets were collapsed across clockwise and counterclockwise directions. Please refer to Figures 6a, 6b, and 7. Note: The reported  $p$ -values here have been corrected for multiple comparisons using a False Discovery Rate procedure.  $*p < 0.05$ ,  $**p < 0.01$ ,  $***p < 0.001$ .

In addition, our data reveal a systematic decline in processing efficiency as a function of the directional offset between the cue and the target. This systematic relationship between the cue-to-target offset and the efficiency of sensory processing is evident both in the pattern of drift rates on invalid trials (Figure 7), and in the pattern of errors made on invalid trials, as subjects in Experiment 2 more often chose a distractor whose direction was similar to the cue compared to a distractor whose direction was far from the cue (Figure 6c).

White and Carrasco (2011) also directly assessed the relationship between feature-based attentional suppression and behavior using a dual-task paradigm. Subjects were asked to indicate whether there was a speed change in a primary RDP (that was shown in one

hemifield) and then asked to discern which of two secondary RDPs shown in the other hemifield contained coherent motion. The direction of coherent motion in the secondary RDP either matched or mismatched (by 180°) the direction of motion of the primary stimulus. As in the present study, performance was enhanced when subjects were given a valid cue that indicated the direction of the primary RDP compared to when they were given a neutral cue. In addition, subjects were more sensitive to coherent motion in the secondary stimulus when the motion in the secondary stimulus matched the cued direction. However, when the direction of the secondary stimulus mismatched the cued direction, performance was not impaired compared to a neutral cue condition. Thus, their overall

(abscissa). (c) Mean proportion of error trials for every offset between the chosen distractor and invalid cue for Experiment 2. Mean proportion of errors as a function of the offset between the direction of the chosen distractor (ordinate) and the invalid cue for that trial (abscissa). Only incorrect trials with invalid cues were used in this analysis. Offsets were collapsed across clockwise and counterclockwise directions. All error bars are  $\pm SEM$ , computed after subtracting the mean from each subject.

### Comparison

15° vs. 45°	$p = 0.4164$
15° vs. 75°	$p = 0.2786$
15° vs. 105°	$p = 0.0015^{**}$
15° vs. 135°	$p = 0.006^{**}$
15° vs. 165°	$p = 0.0321^*$
45° vs. 75°	$p = 0.8433$
45° vs. 105°	$p = 0.1436$
45° vs. 135°	$p = 0.0071^{**}$
45° vs. 165°	$p = 0.084$
75° vs. 105°	$p = 0.1579$
75° vs. 135°	$p = 0.006^{**}$
75° vs. 165°	$p = 0.2217$
105° vs. 135°	$p = 0.2456$
105° vs. 165°	$p = 0.8051$
135° vs. 165°	$p = 0.169$

Table 2b. Pair-wise comparisons of the mean error rate on invalid trials according to the different offsets between the invalid cue and chosen distractor direction ( $n = 12$ ). Offsets were collapsed across clockwise and counterclockwise directions. Please refer to Figure 6c. Note: The reported  $p$ -values here have been corrected for multiple comparisons using a False Discovery Rate procedure. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

pattern of data is consistent with attentional facilitation in the absence of suppression. In contrast, the results from our experiments—particularly Experiment 2—provide strong evidence for both attentional facilitation and suppression. However, our results are not necessarily inconsistent with White and Carrasco’s (2011) findings, as motion in their secondary stimulus either matched the cued direction or was offset by 180° from the cued direction. In both of our experiments, suppression was minimized for directions that were 180° from an invalid cue (the “rebound effect,” Figures 3, 4, 6, and 7). Thus, suppression might simply have been minimized at the 180° offset in their study.

Finally, Tombu and Tsotsos (2008) evaluated a feature-based version of their selective-tuning model, which posits that attention facilitates the processing of attended features, suppresses the processing of immediately adjacent features, and has little impact on the processing of distant features (see also Tsotsos et al. 1995). In their study, subjects had to decide whether the stripes on a grating stimulus were jagged or straight, and the attended orientation was cued on a block-by-block basis. The orientation of the stripes either matched the attended orientation or was offset by 45° (the “similar” condition) or by 90° (the “dissimilar” condition). Accuracy rates were highest when the stripes matched the cued orientation, lowest in the similar condition (45° offset), and intermediate in the dissimilar condition (90° offset). Although this pattern was only observed with “jagged” stripes (and not with straight stripes), their data are consistent with the pattern of suppression and rebound that we report in Experiment 1 (Figures 3 and

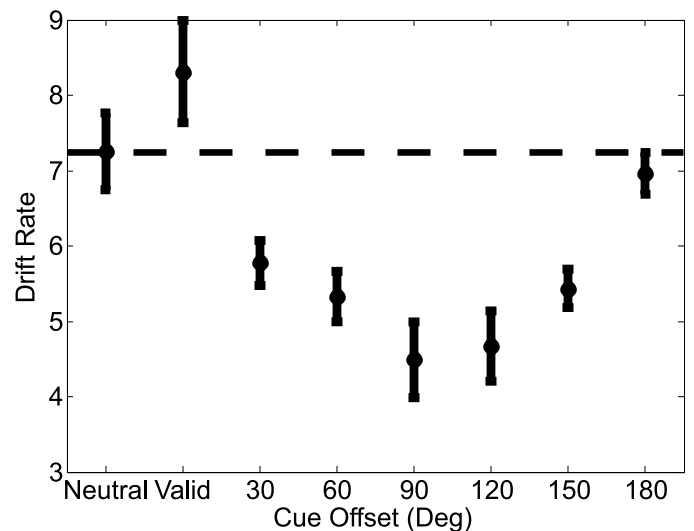


Figure 7. Drift rates for the accumulators corresponding to the correct response on the different cue conditions for Experiment 2. Mean drift rates corresponding to the correct response on each trial computed across subjects (ordinate) as a function of the eight possible cue conditions (abscissa). Offsets were collapsed across clockwise and counterclockwise directions. All error bars are  $\pm 1$  SEM, computed after subtracting the mean from each subject.

4) and Experiment 2 (Figures 6 and 7). Namely, the pattern of suppression was nonmonotonic as the offset between the cued orientation and the presented orientation increased, and offsets farther away from the cued feature were not suppressed as strongly as offsets that were at an intermediate distance from the cued feature value. Thus, it is possible that our results—particularly in Experiment 2—tap into a similar mechanism proposed in Tsotsos et al.’s (1995) selective-tuning model. The present study, however, complements and extends their results by demonstrating enhancement and suppression relative to a neutral cue baseline, by sampling more feature values, and by implementing a quantitative decision model that can better isolate the different latent cognitive factors that are involved in perceptual decision making.

In sum, our results reveal both facilitatory and suppressive effects of feature-based attention that systematically depend on the directional offset of the stimulus and the currently attended direction. These graded attention effects—that primarily influence the rate of sensory evidence accumulation—are generally consistent with the feature-similarity gain model, which predicts increasingly impaired performance for features that are tuned progressively farther away from the cued direction (but see our discussion of the “rebound effect” and the selective tuning model above). To extend these findings in future studies, we can couple our general experimental and analytical approach with paradigms developed by other investigators to examine interactions between suppression and the spatial extent

of feature-based attention (Liu et al., 2011), as well as the impact of feature-based attention on the simultaneous processing of multiple relevant stimuli (Sàenz et al., 2003; White & Carrasco, 2011).

### **Mechanisms of attentional enhancement and suppression: Sensory gain versus selective weighting**

Given the large and growing amount of neurophysiological evidence, it is tempting to ascribe the facilitatory and suppressive behavioral effects observed in our study to modulations of neurons at relatively early stages of sensory processing (Liu et al., 2007; Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Sàenz, Buraças, & Boynton, 2002; Scolarì et al., 2012; Serences, Saproo, Scolarì, Ho, & Muftuler, 2009; Treue & Maunsell, 1996; Treue & Martinez-Trujillo, 1999). However, the attentional enhancement and suppression effects that we observe may not reflect changes in early sensory gain, but instead a selective weighting of sensory responses by downstream decision mechanisms (Baldassi and Verghese, 2002, 2005; Doshier & Lu, 1999; Eckstein, Thomas, Palmer, & Shimozaki, 2000; Law & Gold, 2008, 2009; Palmer, 1995; Palmer, Verghese, & Pavel, 2000). On this account, areas involved in integrating sensory evidence during decision making might overweight the output of direction-selective neural populations tuned to the cued feature, and underweight input from neural populations tuned away from the cued direction. This selective weighting would give rise to enhanced performance in the valid-cue condition and systematically worse performance for targets rotated farther from the cue (Figures 3 and 4 from Experiment 1; Figures 6 and 7 from Experiment 2). Moreover, this type of selective weighting also predicts the systematic pattern of errors observed in Experiment 2, as neurons that respond to distractor directions that are close to the cued direction might more strongly influence decision mechanisms and trigger more frequent incorrect responses (Figure 6c). Finally, the selective weighting account might explain the larger suppressive effects that we observed in Experiment 2 compared to Experiment 1, as the 40% coherent RDP distractors in Experiment 2 are more likely to influence decision mechanisms that differentially weight responses from neural populations that respond to directions that are adjacent to the cued direction.

Thus, based on the current behavioral data alone, we cannot unambiguously determine if the behavioral facilitation on valid trials and the impaired performance on invalid trials is due to sensory enhancement, selective weighting during decision making, or—more likely—to some combination of the two mechanisms.

One potential method to disentangle these alternatives would be to re-run a version of Experiment 2 with fewer offsets and more sessions in order to dramatically increase the amount of data that is collected. With more power, it may be possible to use a modified LBA model to estimate response caution for every possible cue-distractor offset on trials in which a distractor is incorrectly selected in place of the target. Thus, one could test whether or not response caution is lower when distractors are similar to the invalid cue, which might support the idea that the decision criteria are adjusted based on cue-stimulus similarity. However, an alternate, and perhaps more fruitful, approach would be to adapt a version of Experiment 2 to either single unit recording or functional magnetic resonance imaging environments. This would enable measurements of attention-mediated changes in sensory gain throughout the visual cortex and allow one to examine if most of the variability in behavior can be accounted for by only considering the observed changes in sensory gain or if positing an additional mechanism that selectively reweights sensory responses during decision making is needed to fully explain the nature and magnitude of the observed changes in behavior (Pestilli, Carrasco, Heeger, & Gardner, 2011).

### **Linear ballistic accumulator versus signal detection models**

The LBA model is one of many models that utilizes RT and accuracy to examine how experimental manipulations impact latent cognitive factors such as drift rate, decision boundaries, and non-decision times (Brown & Heathcote, 2008; Link & Heath, 1975; Ratcliff, 1978; Ratcliff & Rouder, 1988; Usher & McClelland, 2001; Van Zandt, Colonius, & Proctor, 2000; Wagenmakers, van der Maas, & Grasman, 2007). Other models, such as those based on signal detection theory (SDT), also do an excellent job explaining accuracy data that is obtained in experiments similar to ours (Baldassi & Verghese, 2002, 2005; Eckstein et al., 2000; Palmer, 1995; Palmer et al., 2000). In these SDT models, each element in a visual display elicits a noisy representation within each relevant feature dimension. The observer then combines these representations across all features to obtain a single decision variable, and the stimulus with the maximum value is deemed the most likely to be the target. This approach is particularly adept at explaining behavior in situations where the target is exposed briefly in a data-limited manner, and accuracy is the primary dependent measure (as opposed to RT). However, even though SDT models account for performance on an impressive array of search tasks, sequential sampling models often have an advantage. This is particularly true when a

decision is based on noisy sensory inputs that are continuously present so that the reliability of the final decision variable continuously increases as more evidence is unveiled (Smith & Ratcliff, 2004). In addition, the conception of a perceptual decision as an accumulation process is now well supported based on studies that examine the buildup of firing rates of sensorimotor neurons that are thought to play a key role in mediating basic perceptual decisions (Gold & Shadlen, 2007; Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Leon & Shadlen, 1999; Mazurek, Roitman, Ditterich, & Shadlen, 2003).

### Feature-based attention and changes in neural variability

As discussed above, changes in the rate of sensory evidence accumulation (Figures 4 and 7) can be intuitively linked to changes either in the firing rate of sensory neurons or to changes in the relative weighting of sensory signals by downstream decision mechanisms. However, there is growing evidence that top-down attention can also influence neural variability (Cohen & Maunsell, 2009, 2010, 2011; Cohen & Kohn, 2011; Mitchell, Sundberg, & Reynolds, 2007, 2009). For example, space- and feature-based attention have been shown to reduce the ratio of the variance of individual sensory neurons to their mean firing rate (or the “fano factor”; Mitchell et al., 2009; Cohen & Maunsell, 2011). In turn, a reduction in neural variability should lead to more stable sensory responses across time, thus speeding the process of evidence accumulation during decision making (Churchland, Kiani, Chaudhuri, Wang, Pouget, & Shadlen, 2011). Recently, Rahnev et al. (2011) used a SDT model to demonstrate that such a reduction in neural variability can increase behavioral performance by increasing the signal available for supporting perceptual decisions. Interestingly, this reduction in variability improves performance on average, but also reduces the probability of a high signal response on any given trial, thereby leading to a more conservative bias in behavioral responses (Rahnev et al., 2011). While these results are not directly comparable to the present findings due to differences in the task and the type of model that was employed, they suggest an important role for attention-mediated reductions in neural noise during perceptual decision making. An advantage of sequential sampling models, like the LBA, is that such explanations can be directly investigated. For example, one could explore LBA models in which the parameter governing the variance of the drift rate distributions was free to vary with cueing manipulations. Such models can be difficult to estimate due to the highly correlated posterior distributions for mean drift rate and variance parameters, so

such investigations will require future studies that have many more data points per participant (Donkin, Brown, & Heathcote, 2009; Smith, Ratcliff, & Wolfgang, 2004).

## Conclusions

Here, we provide evidence for both facilitatory and suppressive effects of top-down feature-based attention on human performance that can best be explained by changes in the rate of sensory evidence accumulation, particularly when competition between the target and distractors was high. One critical outstanding issue concerns developing a mechanistic explanation for the observed effects and determining whether feature-based attention mediates behavior primarily via changes in sensory gain, changes in the weighting of sensory evidence by downstream decision mechanisms, or through some combination of the two. Future studies employing neurophysiological or neuroimaging approaches will hopefully dissociate these possibilities and isolate the relative contributions of each mechanism.

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