

# Not All Probabilities Are Equivalent: Evidence From Orientation Versus Spatial Probability Learning

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Frequently targets are detected faster, probable locations searched earlier, and likely orientations estimated more precisely. Are these all consequences of a single, domain-general “attentional” effect? To examine this issue, participants were shown brief instances of spatial gratings, and were tasked to draw their location and orientation. Unknown to participants, either the location or orientation probability of these gratings were manipulated. While orientation probability affected the precision of orientation reports, spatial probability did not. Further, utilising lowered stimulus contrast (via a staircase procedure) and a combination of behavioral precision and confidence self-report, we clustered trials with perceived stimuli from trials where the target was not detected: Spatial probability only modulated the likelihood of stimulus detection, but not did not modulate perceptual precision. Even when no physical attentional cues are present, acquired probabilistic information on space versus orientation leads to separable ‘attention-like’ effects on behaviour. We discuss how this could be linked to distinct underlying neural mechanisms.

## **Public Significance Statement**

We are sensitive to environmental information. Objects that preferentially appear in certain locations are found faster. Objects that preferentially contain particular features (e.g., specific colors or patterns) are perceived better. Attention research suggests that “attending” to space differs from “attending” to features. We asked whether, by extension, spatial learning is different from feature learning. Undergraduates were shown gratings (striped patches) and asked to both locate and draw how tilted they were. Participants were not informed that the gratings were more likely to be located in particular places or to have particular tilts. Gratings were detected more often when they appeared in popular places. However, despite this detection advantage, there was no benefit to showing how tilted they were. Only objects with probable orientations were drawn more precisely. These results suggest that although we are sensitive to both spatial and feature information, they affect our perceptual abilities in different ways.

*Keywords:* attention, orientation, space, probability, visual perception

We are sensitive to structure in the history of sensory signals. This structure can take, broadly speaking, two forms: dependencies across time and biases in prevalence. Although it is hard to deduce from the terms, higher order statistical structures such as temporal dependency are typically researched under the heading of *statistical learning* (Turk-Browne, 2012). In contrast, manipulations of the frequency or prevalence of an event commonly leads to *probability* or *frequency learning* (Hasher & Zacks, 1984; Kelly & Martin, 1994). The work reported here is concerned with whether probability learning is, to some degree, object-generic and

responds not simply to absolute frequencies, but to the conjunctions, or co-occurrences, of object features and characteristics.

When we learn about the probability of a target, are all aspects of our perceptions and judgments regarding that target affected similarly? By making a range of orientations more likely in some locations and less likely in others, the aggregate probability of a target’s orientation and location can be kept uniform. Using such a manipulation, Jabar and Anderson (2015) demonstrated that the orientations of probable conjunctions are estimated faster, with more confidence, and with greater precision than stimulus conjunctions with lower probability. But as Jabar and Anderson only looked at orientation probability and its impact on orientation precision, a question remains open: How generic is the probability effect? If it had been measured, would spatial location estimation have also been affected, as an object general effect implies? Would manipulations of spatial probability result in the same changes as with manipulations of orientation probability?

Our interest in this question is motivated by an effort to better understand the psychological processes and neural mechanisms that inform perceptual judgments, as complex statistical relation-

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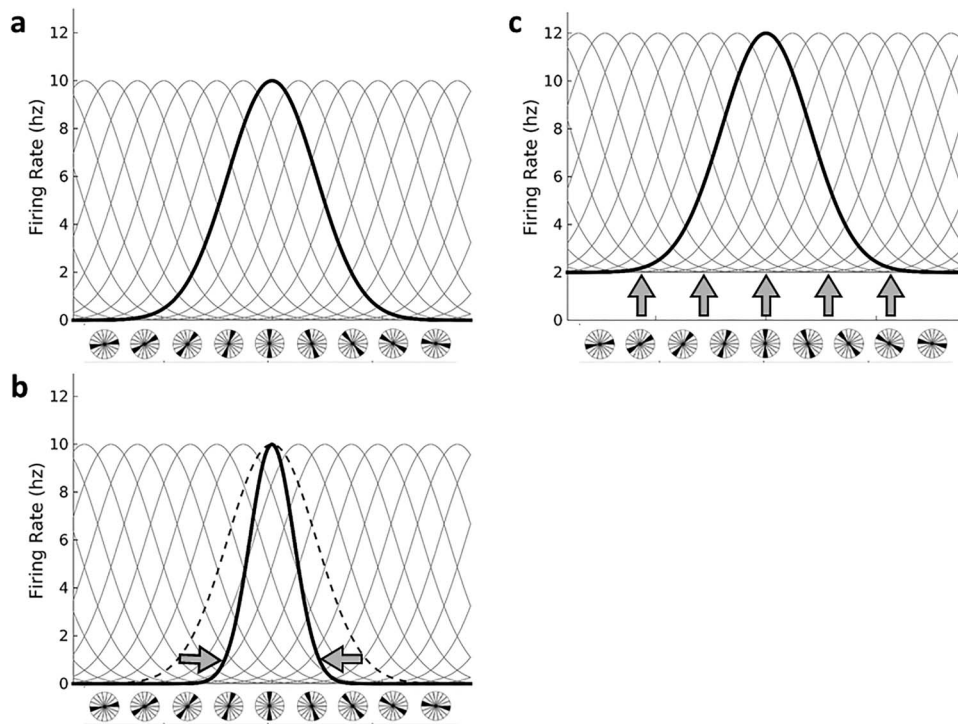
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ships among the objects that we view are common and affect behavior (Chun & Jiang, 2003). Similarly, probability relationships overlap with attentional processes (Hon & Tan, 2013). When the validity of exogenous cues are manipulated, their effectiveness is known to vary monotonically (Eriksen & Yeh, 1985; Hughes, 1984). Similar probability effects have also been observed in perceptual estimation tasks, in which probable tilts are estimated more quickly and more precisely (Anderson, 2014). When the probability that a target will appear at a particular location is adjusted, reaction time (RT) changes (e.g., Gekas, Seitz, & Seriès, 2015; Geng & Behrmann, 2005; Vincent, 2011; Walthew & Gilchrist, 2006). Jiang, Sha, and Remington (2015) used a T-among-L search display with the target appearing 3 times more likely in one particular quadrant. The targets in the probable location were detected significantly faster. Spatial probability effects are also obtainable when the probability distribution is made more complex and varying across space continuously (Druker & Anderson, 2010).

Because probability and attentional manipulations produce similar effects, dissociations observed in the attention literature might replicate within the probability domain. One common dissociation in attentional paradigms is between spatial and feature-based attention (Carrasco, 2011; Fink, Dolan, Halligan, Marshall, & Frith, 1997; Ling, Jehee, & Pestilli, 2015; Yantis & Serences, 2003), such as having different time courses (Liu, Stevens, & Carrasco, 2007). Another dissociation is in terms of neural mechanisms. Both spatial and feature cues affect early visual processing, but in

different ways. Several groups have found spatial cueing effects on early visual processing (Luck & Ford, 1998), including the primary visual cortex (V1; Liu, Pestilli, & Carrasco, 2005; Tootell et al., 1998). Gandhi, Heeger, and Boynton (1999) had participants in a scanner view moving gratings that appeared in one of two possible locations (left vs. right). By manipulating a spatial cue, an “attentional” modulation of the BOLD signal was found in the contralateral V1 cortex. Brefczynski and DeYoe (1999) similarly found retinotopic mapping of (covert) attention-related activation in V1. Electrode recordings in animal models suggest a similar locus (Sharma et al., 2015). Other studies suggest that spatial attentional effects might be found even earlier in the visual processing hierarchy, such as at the level of the lateral geniculate nucleus (Ling, Pratte, & Tong, 2015; Schneider & Kastner, 2009) and superior colliculus (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Muller, Philiastides, & Newsome, 2004; Schneider & Kastner, 2009).

Although both object-based (Roelfsema, Lamme, & Spekreijse, 1998) and space-based (e.g., Gandhi et al., 1999) attention modulate activity in the primary visual cortex (e.g., Saenz, Buracas, & Boynton, 2002), it has further been suggested that feature-based attention affects neural tuning (Ling, Liu, & Carrasco, 2009; Martinez-Trujillo & Treue, 2004; Paltoglou & Neri, 2012) for the particular neurons selective for the attended target feature (e.g., Figure 1b); deploying attention to a location increases the firing rate of all neurons coding for a particular location (Figure 1c), even when no stimulus is subsequently shown (Kastner, Pinsk, De



**Figure 1.** Depiction of gain versus tuning. (a) The default tuning curves of a population of orientation-selective neurons. Y-axis: firing rate. X-axis: orientation shown within the population’s receptive field. The bold line represents the tuning curve of a vertical-prefering neuron. (b) Tuning curves if the vertical-prefering neuron is selectively tuned. (c) Tuning curves after a baseline gain increase. Note that no orientation is particularly privileged in this instance.

Weerd, Desimone, & Ungerleider, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Paltoglou & Neri, 2012).

Because of the similarity between probability and attention manipulations experimentally, common neural mechanisms could be involved. Perhaps spatial probability is gain-based, whereas feature probability is tuning-based. This dissociation in neural mechanisms is predictive of dissociable behavioral outcomes. It has been suggested that optimal tuning functions of sensory neurons are context- and environmental-specific rather than being universal (e.g., Dean, Harper, & McAlpine, 2005; Hosoya, Baccus, & Meister, 2005), and therefore that adaptive-tuning (e.g., Figure 1b) is required for optimal performance of the sensory system (Yaeli & Meir, 2010). If feature probability affects V1 tuning, then it potentially explains why orientation precision could be improved by orientation probability (Anderson, 2014; Jabar & Anderson, 2015): The probable (trained) orientations are simply better perceptually encoded, because the relevant neurons now being more optimally tuned (Summerfield & Egner, 2009). By contrast, an additive gain without associated tuning (e.g., Figure 1c) might not lead to optimal perceptual encoding because the signal-to-noise ratio remains constant. If spatial probability is gain-based, orientation precision should remain unaffected across high- and low-probability locales. However, the ability to detect target occurrences might improve, as average firing of the neural population would be increased.

To reprise, we investigate how manipulations of spatial and orientation probabilities affect their *joint* reporting, measured by both speed and accuracy. This allows us to determine how generic probability effects are at the level of a particular target. In addition, given the similarities between attentional tasks and probability tasks, we can evaluate the outcome of these experiments with an eye toward comparing attentional and probability effects. Experiment 1 begins by testing whether our previous findings that orientation probability increases orientation precision are robust to the change in procedure that required each participant to report location and orientation on every trial, and in which participants used a mouse instead of a computer keyboard (Anderson, 2014; Jabar & Anderson, 2015). Experiment 2 was similar, but manipulated spatial probability. Experiment 3 was a defense against ceiling effects for spatial localization, and used a preliminary staircase procedure to find a stimulus contrast that made locating the stimulus challenging. The upshot of these experiments is primarily that the two probability manipulations decompose, as they do for attention, and that spatial probability affects primarily target *detection*, whereas orientation probability primarily mediates changes in discrimination *precision*.

### Experiment 1

Experiment 1 served to test whether the probability effects on orientation judgments reported in Jabar and Anderson (2015) were replicable when the response method was changed. Rather than the keyboard-based response used before, participants reported both a location and an orientation on every trial using a mouse. After a brief presentation of a single oriented Gabor, participants first localized where they perceived the center of the Gabor to have been by clicking on it with a computer mouse. They then moved the mouse away from this anchor point to “draw” an orientation (finalized with another mouse click).

### Method

**Participants.** Twenty-one undergraduate students from the University of Waterloo (13 females, eight males) took part in the study. Eighteen participants were right-handed. The three left-handed participants were told that they could move the mouse to their left hand if they wanted, but they opted to use their right hand. All participants had normal or corrected-to-normal vision, and did not declare any auditory deficits. This study was approved by the institute’s Office of Research Ethics.

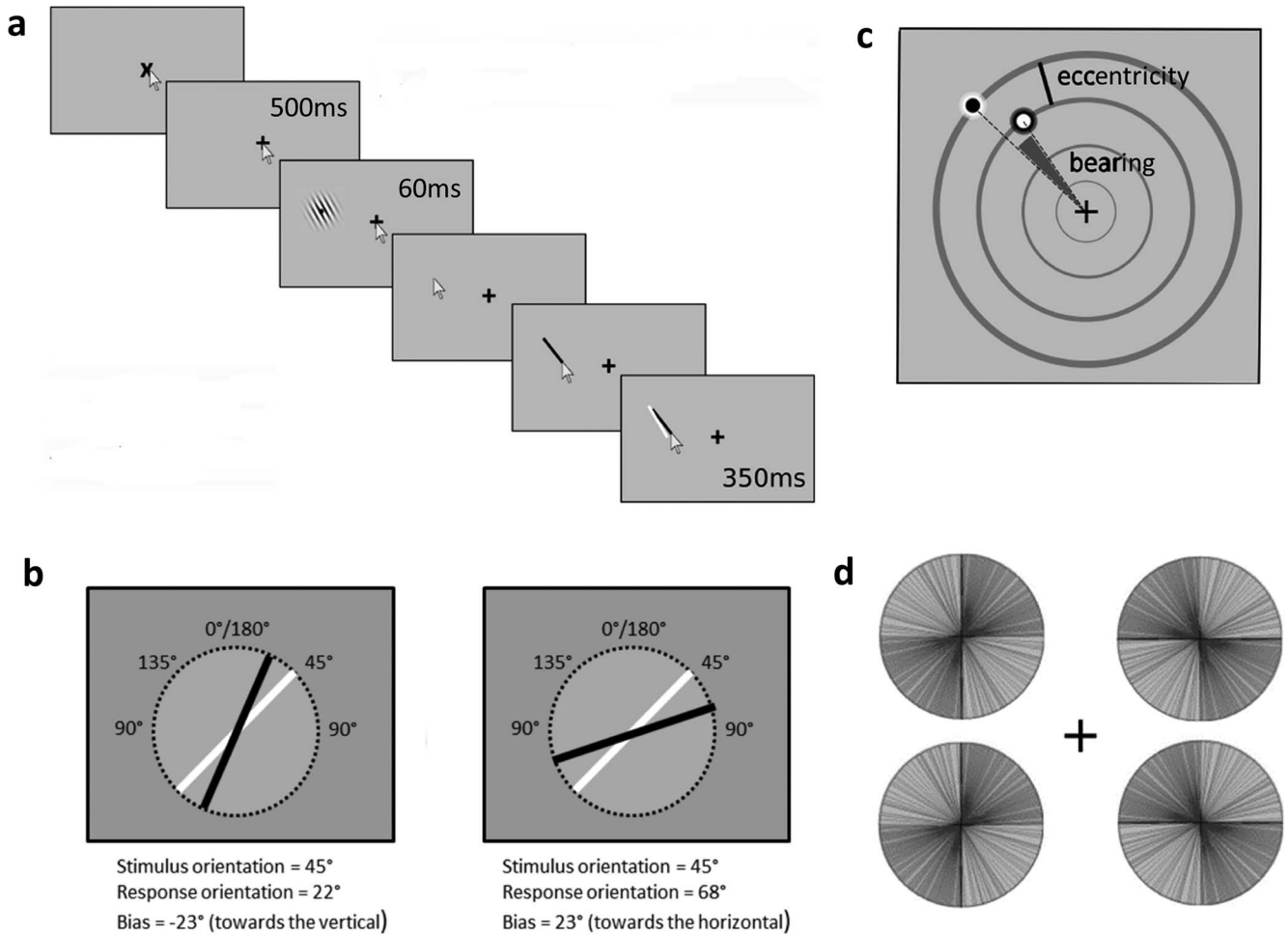
**Stimuli.** The center of the display was marked by a black fixation symbol subtending approximately  $1.2^\circ$  in both axes. Spatial gratings were presented to participants on each trial. These were oriented grayscale sine-wave gratings with a circular mask (Figure 2a), with an average measured luminance of  $39 \text{ cd/mm}^2$ . They had a spatial frequency of 3.16 cycles per degree of visual angle, and were presented on a gray background with a similar luminance of  $40 \text{ cd/mm}^2$ . When viewed from a distance of 60 cm, the gratings subtended approximately  $2.5^\circ$  of visual angle. The center of the grating was displaced  $4^\circ$  either to the left or right of the center of the display and  $4^\circ$  up or down; thus, they fell at the corners of a virtual square. The center of the grating was marked with a small black dot to aid participants in their location reports. Lines, used as feedback, always occurred in the same location as the grating for that trial and matched its diameter.

Because the effects of repetition are a possible confound when examining probability effects (see Hale, 1969), we manipulated the occurrence rate of the various *probability-location conjunctions*. Collapsed across the four equiprobable locations, all orientations were equally likely. Repeats of orientation are therefore as likely to occur for “low-probability tilts” as they are for “high-probability” ones. Further, the possible orientations were continuous, reducing the odds of an exact repeat. Half of the participants saw the conjunction depicted in Figure 2d: When a grating appeared on the top left or bottom left, its orientation was more likely to be left-tilting, but this high-probability tilt was reversed if the grating appeared on the top right or bottom right.

Probability distributions were maintained throughout the experiment. In every set of 20 trials, all four locations appeared 5 times each, and there were four occurrences of one set of orientations (high-probability: 80%), and one occurrence of the other set (low-probability: 20%). The lines in Figure 2d depict the distribution observed by the first participant. The location-orientation conjunctions were counterbalanced across participants. Participants were *not* informed about these probability distributions.

Auditory feedback was given after each trial to maintain motivation. A high-pitched sound (<http://www.freesound.org/people/HardPCM/sounds/32950/>) indicated an orientation error of less than  $12^\circ$  and a spatial (Euclidean) error within  $0.5^\circ$ . The orientation error threshold was the same as in Jabar and Anderson (2015). The spatial error threshold was chosen after pilots tests, such that participants crossed the spatial threshold about as often as they did the orientation threshold (about 85% of the time). Any error beyond these cutoffs caused a lower pitch sound to be played (<http://www.freesound.org/people/tombola/sounds/49219/>). Participants were not explicitly informed of the error threshold.

**Procedure.** Participants sat approximately 60 cm from a  $32 \text{ cm} \times 24 \text{ cm}$  gamma-corrected CRT monitor that refreshed at 89 Hz. Responses were made with an optical mouse. The position of



**Figure 2.** Paradigm and precision measurements. (a) General paradigm used for all experiments reported. Participants initiated trials by clicking on the central fixation symbol. After a delay of 500 ms, a spatial grating (with a central dark spot) appeared for a brief 60 ms. Participants then moved the mouse to click on where they thought the center of the grating was. After this click they moved the mouse a way to draw a line that best represented the orientation of the grating, and then gave a second click to confirm the orientation estimate. Visual and auditory feedback was then provided. (b) Example of how orientation angular errors are calculated. White lines: Actual orientation. Black lines: Estimated orientation. Note that between the example trials, the bias will be zero, but the median absolute error would be 23°. (c) Example of how spatial eccentricity and bearing errors are calculated. White marker: Actual location. Black marker: Estimated location. (d) Orientation probability distribution used in Experiment 1. Note that all dark lines/symbols correspond to high-probability trials, whereas light lines/symbols correspond to low-probability trials.

the on-screen mouse cursor was recorded every frame of the experiment. All experiments were programmed in Python using the PsychoPy library (Peirce, 2009). Participants were instructed to fixate at the center of the screen.

Prior to the task, participants were instructed to make their estimations of the location, and then the orientation, of the gratings as precisely as they could. They were *not* told that they needed to be fast. Participants were given 40 practice trials in which the orientations occurred uniformly. These data were not included in the analysis. The main task consisted of 400 trials, which were sectioned into two blocks. Participants were given the option to take a break in between the blocks. At the end of the computerized task, participants were given a short, open-ended

questionnaire to examine whether they could explicitly report the spatial and orientation distribution of the gratings that they had seen. The experiment took approximately 20 to 25 min to complete.

Participants initiated each trial by clicking on the central fixation symbol, which changed from an “x” to “+” to indicate that the trial had started. Participants were shown the “+” fixation symbol for 500 ms after this initial click. The grating then appeared in one of the four locations for 60 ms (five frame refreshes). Participants were then free to move the mouse. They first had to click at the center of the location where they perceived the grating to have appeared. After this, participants could move the mouse away from the location of the grating in any direction and a line would appear



that followed the mouse and grew to the diameter of the grating. After the participant had drawn a line that reproduced the orientation of the grating, they made another click. The auditory feedback was then given, along with a white feedback line representing the actual grating displayed.

**Postexperiment questionnaire.** After the 400 trials and before participants were debriefed, participants were given a short questionnaire consisting of the following five open-ended questions:

1. Did anything about the experimental task stand out to you?
2. Please describe any strategies you may have used.
3. Did you feel that you perceived some stimuli better or differently than others, or in certain cases? Did you notice any change over time in your experience?
4. Do you think that some orientations are more likely at certain times? If yes, please elaborate.
5. Do you think that some locations are more likely at certain times? If yes, please elaborate.

**Analysis procedure.** All data analyses were conducted using the R statistical software package (R Core Team, 2012). Angular errors for each trial were calculated as the difference between the Gabor orientation and the orientation of the participants' estimates. Possible angular errors ranged from  $-90^\circ$  (anticlockwise error) to  $+90^\circ$  (clockwise error). Because of the axial (half circular) nature of orientations, a  $+91^\circ$  error wraps back as a  $-89^\circ$  error. These data were also used to get a measure of bias on the cardinal axes. Vertical-biased estimations, when participants estimated the orientation more vertically than it should have been, were coded as negative. Horizontal biases were coded as positive (Figure 2b).

Angular error analyses were done on both the *bias* and the *mean error* measures. The bias measurement gives the average of these signed errors across trials, such that a nonbiased participant should approach a mean of "0" bias. To look at the mean error made, the median of the *absolute values* of the estimation errors were taken. As an example of these calculations, there would be a  $0^\circ$  bias and  $23^\circ$  magnitude of angular error across the trials depicted in Figure 2b.

Spatial error was broken down into the two polar axes: eccentricity and bearing (Figure 2c). Because the targets were always equidistant from the fixation, people were highly precise for this measure, and no manipulation affected it. Therefore, we do not focus on the eccentricity error analyses. Spatial bearing error was the main measure of spatial precision, and was calculated in an analogous way to how orientation errors were measured. Spatial bearing errors occupied a circular instead of an axial space.

RT for each trial was decomposed into three components. Initiation time (iRT) was the time taken from the grating onset to when a participant first moved the mouse. The time between initiation and the click indicating location was labeled the *sRT*. Time from this click to the click indicating orientation was labeled the *oRT*. Total distance moved in both the spatial estimation and orientation estimation phases were also recorded.

Responses were quick and fluid, and appeared automatic. Therefore, we excluded trials in which participants reacted very slowly (iRT > 1,000 ms; 0.2% of trials). In addition, excluded were trials for which the Euclidean distance between the response and the central fixation was less than  $2^\circ$  (2% of trials). This was so that precision metrics did not include trials in which participants either accidentally clicked again on the fixation symbol, or in which participants purposely clicked the central location again because they did not know the actual location. Alpha cutoff for all significance testing was the conventional  $p = .05$ .

## Results

We examined the effects of orientation probability on RT, on orientation precision, and on spatial precision. Results from Experiment 1 largely aligned with the results of our previous studies. Slight effects on RT were observed. More importantly, orientation probability affected orientation precision, and these effects manifested quickly. Orientation probability did not affect spatial precision.

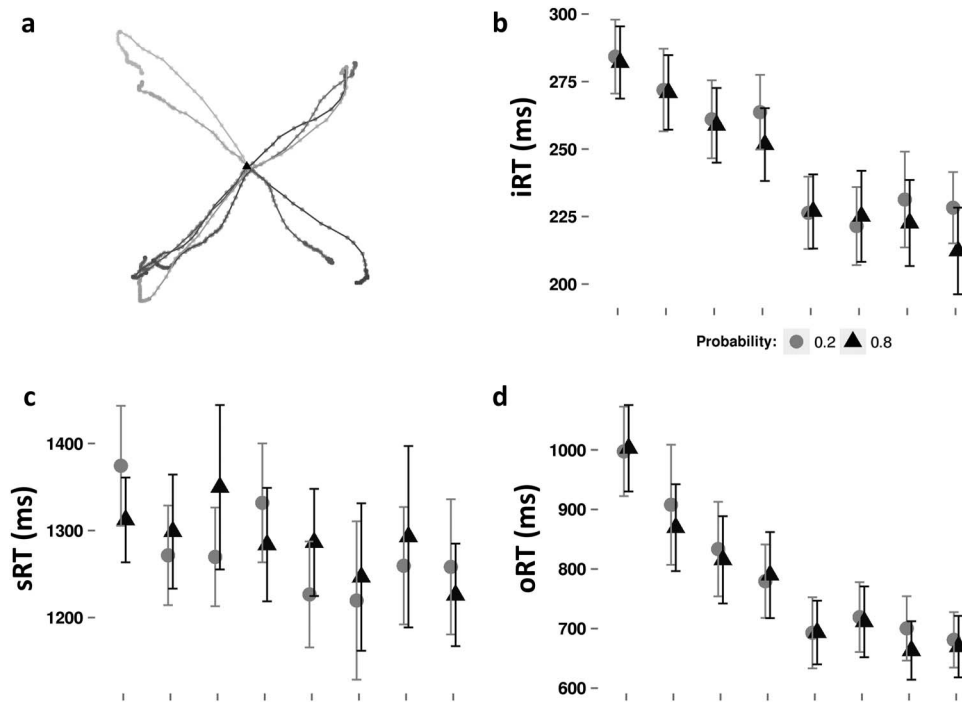
**RT analyses.** The 400 trials were binned into 50-trial blocks to look at effects of time on the experiment. A two-way fully within ANOVA was carried on these data. For the iRT measure (Figure 3a), there was a main effect of probability,  $F(1, 19) = 5.74$ , mean squared error (MSE) = 381,  $p = .027$ , a main effect of trial bin,  $F(7, 139) = 18.86$ ,  $MSE = 1,330$ ,  $p < .001$ , but no significant two-way interaction,  $F(7, 139) = 0.50$ ,  $MSE = 546$ ,  $p = .830$ . In general, the difference in iRT between high ( $M = 246$  ms) and low ( $M = 249$  ms) probability was small, although quite consistent across the trial blocks (Figure 3a). These initiations are not only fast, they also tend to be accurate, with 77% of them falling within a  $45^\circ$  bearing of the actual stimulus bearing (Figure 3b).

The same analysis on sRT (Figure 3c) suggested no main effect of probability,  $F(1, 19) = 0.18$ ,  $MSE = 14,152$ ,  $p = .680$ , no main effect of trial bin,  $F(7, 139) = 1.09$ ,  $MSE = 48924$ ,  $p = .376$ , and no significant two-way interaction,  $F(7, 139) = 0.95$ ,  $MSE = 27,287$ ,  $p = .473$ . The analysis on oRT (Figure 3d) suggested a marginal main effect of probability,  $F(1, 19) = 4.04$ ,  $MSE = 5,348$ ,  $p = .059$ , a main effect of trial bin,  $F(7, 139) = 16.73$ ,  $MSE = 32,568$ ,  $p < .001$ , but no significant two-way interaction,  $F(7, 139) = 0.39$ ,  $MSE = 8,903$ ,  $p = .905$ .

In sum, the iRT measures proved to be the most robust. Initiating movements to gratings with a probable orientation were made slightly faster. Drawing the orientation was also marginally faster. Orientation probability had no apparent effect on the time taken to complete the spatial localization postinitiation.

**Orientation (angular) error analysis.** Paired two-tailed  $t$  tests were run on the bias measure. This revealed that the high-probability tilts were significantly vertically biased,  $t(20) = 2.47$ ,  $p = .023$ , whereas low-probability tilts were not,  $t(20) = 0.56$ ,  $p = .58$ . Compared against each other, there was a significant effect of probability on bias,  $t(20) = 3.44$ ,  $p = .003$ , with high-probability tilts being more vertically biased ( $M = -1.13$ ,  $SD = 2.09$ ) than low-probability tilts ( $M = 0.32$ ,  $SD = 2.59$ ). Bias was not affected by stimulus location: Across possible comparisons, all  $ps > .05$ .

The error distributions from high- versus low-probability trials also differ (Figure 4a): The median absolute error measure suggests a significant effect of probability,  $t(20) = 5.44$ ,  $p < .001$ ,



**Figure 3.** Reaction time (RT) data from Experiment 1. (a) Sample mouse movement during the initiation and spatial estimation phase. Note how initial movements from center are ballistic, and then they slow down (spacing between markers indicates 1 frame: 11 ms) as the mouse is adjusted toward the stimulus locations. (b) Initiation time (iRT) across experimental trials (each bin represents 50 trials). (c) Time from initiation to spatial localization (sRT) across experimental trials. (d) Time from spatial localization to completion of orientation estimate (oRT). Note: Dark markers represent high-probability trials; light markers represent low-probability trials.

with high-probability tilts associated with an error of smaller magnitude ( $M = 7.07^\circ$ ,  $SD = 1.99^\circ$ ) than low-probability tilts ( $M = 8.09^\circ$ ,  $SD = 1.73^\circ$ ). Of the 20 participants, 19 showed this trend, with the two showing the opposite trend also being the worst performers (Figure 4b). This strong trend also remains if the error distributions are bias-corrected,  $t(20) = 6.03$ ,  $p < .001$ . Partitioning these data into 50-trial bins also suggest demonstrates that precision effects are observable even within the first bin,  $t(20) = 2.61$ ,  $p = .017$ . Although the significance fluctuates in later bins, high-probability orientations were always more precisely estimated (Figure 4c). Taken individually, this orientation probability effect on precision is also significant in all four locations ( $ps < .05$ ).

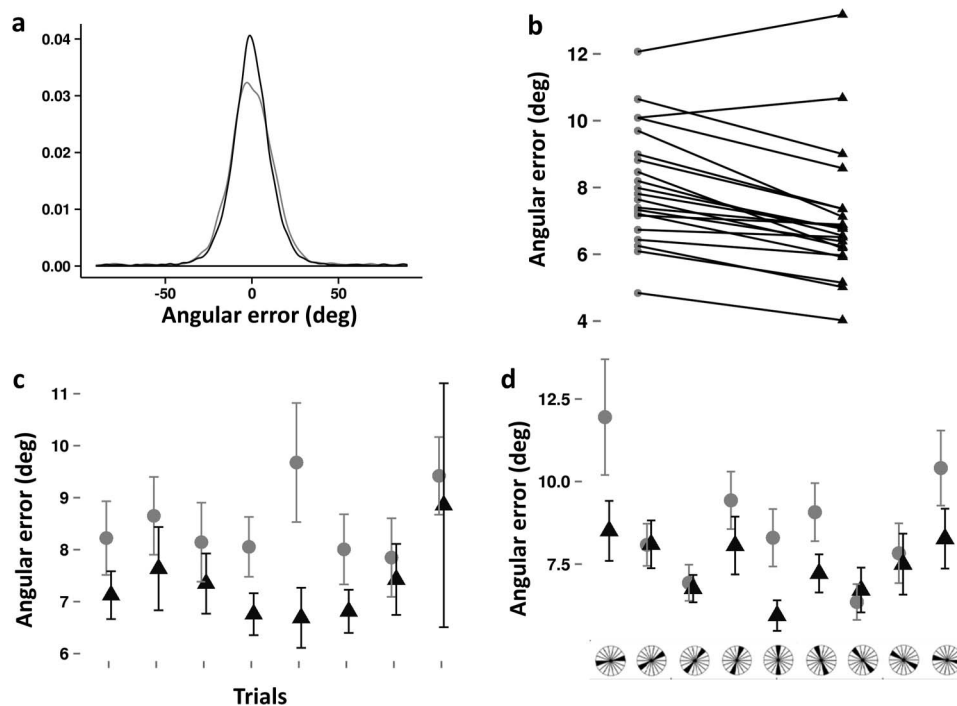
**Orientation anisotropy analysis.** Possible orientations were binned into  $20^\circ$  segments and angular error was looked at for each bin (Figure 4d). A two-way ANOVA revealed that there was a significant main effect of probability,  $F(1, 20) = 24.39$ ,  $MSE = 6.10$ ,  $p < .001$ . There was a main effect of orientation bin,  $F(8, 160) = 3.59$ ,  $MSE = 17.06$ ,  $p < .001$ . There was also a significant interaction,  $F(8, 160) = 2.45$ ,  $MSE = 7.18$ ,  $p = .016$ . Size of the orientation probability effect (low–high probability) in the bin containing the near verticals was greater than in the ones containing the  $45^\circ$  and  $135^\circ$  obliques ( $ps < .05$ ), but not the one containing the near-horizontals ( $p > .05$ ). The mean absolute angular error was smallest in the vertical bin compared with the oblique and horizontal bins ( $ps < .05$ ). In sum, probability effects were

largest at the cardinals, but vertical orientations were most precisely represented overall.

**Standard deviation and kurtosis.** In Jabar and Anderson (2015), we argued that a mixture of perceptual and nonperceptual effects of probability would lead to changes in error distribution shapes (e.g., Figure 4a) that could be quantified by the kurtosis.

We find that although there is a trend for kurtosis to be higher for high-probability tilts ( $M = 3.73$ ,  $SD = 4.37$ ) than for low-probability tilts ( $M = 2.44$ ,  $SD = 4.26$ ), the difference is not significant,  $t(20) = 1.33$ ,  $p = .197$ . However, the kurtoses are significantly above zero for high-,  $t(20) = 3.91$ ,  $p < .001$ , and low-probability,  $t(20) = 2.62$ ,  $p = .016$ , orientations. Because normal (Gaussian) distributions have an excess kurtosis of zero, these data confirm that the error distributions are not normally distributed.

**Repetition effects analysis.** Repetition effects are possible sources of confounds in probability-related studies because high-probability targets are more likely to be repeated (Hale, 1969), whereas rare targets are not. If repetitions or sequences are driving performance benefits for the high-probability orientation estimations (e.g., Fischer & Whitney, 2014), then we might observe a significant correlation between absolute intertrial differences in orientation and estimation performance (small changes lead to small errors; large changes lead to large errors). In fact, the correlation is negligible ( $r < .01$ ,  $p = .507$ ). Comparing the extremes—for example, trials in which the intertrial difference was



**Figure 4.** Experiment 1 orientation precision. (a) Orientation error distribution. Negative indicates an anti-clockwise error; positive is a clockwise error. The darker lines represent the distribution for high-probability trials. (b) By-subject median absolute errors across probability. Note that 19 of 21 cases show a decrease in error (increase in precision) for the high-probability trials (dark markers). (c) Median absolute errors as a function of experiment trials. Each bin represents 50 trials. (d) Median absolute errors by orientation segments, indicated by figures on the x-axis.

10° or less (mean angular error = 9.6°) versus those that were 80° or larger ( $M = 9.3^\circ$ )—also reveals no significant effect ( $t < 1, p = .541$ ). Lastly, ignoring trials with small (10°) intertrial differences, the effect of orientation probability on orientation precision still holds,  $t(20) = 3.25, p = .004$ . The effect of repeating locations (approximately 25% of the trials) versus nonrepeats was not found to significantly affect either orientation precision or the size of the orientation probability effect ( $ps > .05$ ).

**Spatial error analysis.** Participants demonstrated precise bearing reports: 77% of the estimates were made within 3° of the actual bearing (Figure 5a). This spatial bearing error was not significantly different between high- ( $M = 2.79, SD = 0.59$ ) and low-probability ( $M = 2.84, SD = 0.63$ ) orientations,  $t(20) = 0.39, p = .702$ . These were also no significant linear correlation between bearing error and orientation error for either high-probability trials,  $r = .41, p = .065$ , or low-probability trials,  $r = .08, p = .722$ .

As mentioned in the Method section, because targets always appeared equidistant from the central fixation, the spatial eccentricity error was at floor (high-probability = 0.55°; low-probability = 0.54°). Neither this measure nor the mean Euclidian distance between estimated and actual location were significant across orientation probability ( $ps > .05$ ). As with orientation probability, repeating versus nonrepeats of locations was not found to significantly affect spatial precision,  $t(20) = 0.51, p = .615$ .

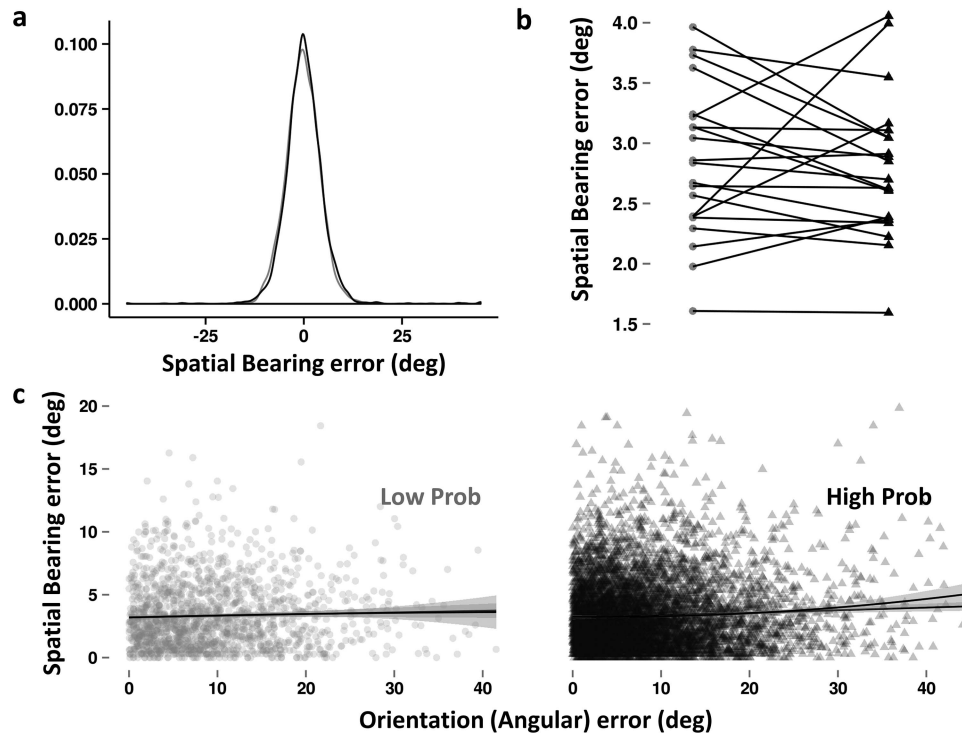
**Postexperiment questionnaire.** Although a majority of participants demonstrated behavioral differences contingent on orien-

tation probability, consistent with Jabar and Anderson (2015), none correctly indicated the orientation probability distribution.

## Discussion

Experiment 1 largely replicated the findings from Jabar and Anderson (2015). Probable orientations were estimated more precisely, despite participants showing no signs of explicit awareness of the distribution. The orientation anisotropy seen previously was also replicated: Near-vertical tilts were most precisely represented, especially when they were probable (Figure 4c). It is important to note that in prior publications with this task, the response line was always presented at a static fixed orientation, but in this experiment, there was no response line until participants initiated their response. Thus, these effects are not because of anchoring. Anisotropy represents an innate perceptual bias (Appelle, 1972), possibly because of V1 neurons tuning (Li, Peterson, & Freeman, 2003).

Compared with our previous paradigm using the keyboard responses (e.g., Jabar & Anderson, 2015), participants in this experiment were more precise in their orientation estimation while the size of the orientation probability effect was similar. This is despite having to process the spatial dimension and report it *before* making the orientation estimation. Having to process the spatial information does not impede the orientation reports implying some separability of the two estimation processes.



*Figure 5.* Experiment 1 spatial precision. (a) Distribution of spatial bearing error. Negative indicates an anticlockwise error; positive indicates a clockwise error. The darker lines represent the distribution for high-probability trials. (b) Median absolute spatial bearing errors by-subject. Dark markers represent high-probability trials, light markers represent low-probability trials. (c) Scatterplot of spatial bearing error versus orientation angular errors. Straight lines indicate best fit line; curved lines indicate the best fit quadratic.

Kurtosis does not seem to capture the differences in orientation error distribution between high- and low-probability conditions here (Figure 4a) as well as it did in Jabar and Anderson (2015), although the trend is still here. This is most likely because of the change in response method: Whereas the previous experiments had participants use a keyboard to rotate a response line, participants in this set of experiments had to draw the orientations. Although the distributions are still non-normal—excess kurtoses are above zero—reduced nonperceptual error might have led to less deviations from normality. For these reasons, we use the median absolute error as the metric for precision here.

In addition to being reported more precisely, responses to high-probability tilts were also initiated more quickly. Spatial RT did not vary as a function of probability, perhaps because it reflects time required to make precise motor movements rather than reflect time to detect. Although orientation probability affected orientation precision, it did not influence spatial precision. This is consistent with the hypothesis that spatial and orientation effects are separable, similar to spatial and feature attentional effects.

Results from Experiment 1 are in line with the suggestion that feature probability, similar to feature-based “attention,” affects neural tuning. The second part of the hypothesis is that spatial probability, like spatial attention, is linked to neural gain. If true, there should be no spatial probability effects on orientation precision, because a gain mechanism (e.g., Figure 1c) would predict that orientation-selective neurons would be stable over the range of orientations.

## Experiment 2

Using the same paradigm, Experiment 2 examined the effects of spatial probability instead of orientation probability. If the gain hypothesis is true, orientation precision should not be affected by spatial probability. If the dimension-specific hypothesis is true, unlike in Experiment 1, we should also expect to observe probability effects on spatial precision.

### Method

**Participants.** Two additional sets of participants were recruited. Twenty undergraduate students (18 females, two males) took part in Experiment 2a. Nineteen participants were right-handed. Twenty undergraduate (11 females, nine males) took part in Experiment 2b. Seventeen participants were right-handed. All participants used their right hand, had normal or corrected-to-normal vision, and did not declare any auditory deficits. These experiments were approved by the University of Waterloo’s Office of Research Ethics.

**Stimuli and procedure.** The procedure for Experiment 2a was the same as before. The only difference was that orientation was kept equiprobable at each location, and spatial probability was manipulated. Two locations on opposite corners were made more probable than the other two. These locations were counterbalanced across participants. Probabilities were maintained in 20-trial blocks. In each set of 20 trials, eight appeared in one location and another eight appeared in the opposing corner (high-probability =



80%). The remaining 4 were split across the other 2 locations (low-probability = 20%). As before, participants were not informed about these distributions. They were only instructed to be as precise as they could for both the orientation and spatial estimations.

In Experiment 2b, instead of having four discrete locations, the gratings appeared anywhere in a ring around the central fixation, with the same eccentricity as the other experiments. Instead of biasing two locations, two quadrants were biased. Figure 6 depicts a sample distribution of where participants end up locating the gratings, for both Experiment 2a and 2b.

## Results

**RT analysis.** As with Experiment 1, the RT data from both sets of Experiment 2 were split into iRT, sRT, and oRT. None of these showed significant effects of spatial probability in either experiment ( $ps > .05$ ).

**Orientation error analysis.** For Experiment 2a, in both high- ( $M = -1.25$ ,  $SD = 2.24$ ) and low-probability ( $M = -1.11$ ,  $SD = 2.23$ ) locales, there was a significant vertical bias ( $ps < .05$ ) in orientation estimation. However, probability did not modulate this bias,  $t(19) = 0.33$ ,  $p = .742$ . For Experiment 2b, although both high- ( $M = -0.48$ ,  $SD = 1.90$ ) and low-probability ( $M = -0.35$ ,  $SD = 1.91$ ) had the same trend toward vertical bias, this was not significant ( $ps > .05$ ), and there was no significant difference across the probability conditions,  $t(19) = 0.47$ ,  $p = .641$ .

The median absolute angular error measure was not significantly different across high- ( $M = 7.75$ ,  $SD = 2.12$ ) and low-probability ( $M = 7.96$ ,  $SD = 2.46$ ) locales in Experiment 2a (Figure 7a),  $t(19) = 0.81$ ,  $p = .426$ . This was the same in Experiment 2b (Figure 7b): There was no significant difference across high- ( $M = 7.63$ ,  $SD = 1.38$ ) and low-probability ( $M = 7.35$ ,  $SD = 1.33$ ) locales in orientation precision,  $t(19) = 1.14$ ,  $p = .270$ . There was also no significant difference in orientation precision across the experiments, for both probability conditions ( $ps > .05$ ).

**Spatial error analysis.** The median absolute spatial bearing error was also not significantly different across high- ( $M = 2.91$ ,

$SD = 0.93$ ) and low-probability ( $M = 3.05$ ,  $SD = 0.92$ ) locales in Experiment 2a (Figure 7c),  $t(19) = 0.70$ ,  $p = .491$ . This was the same in Experiment 2b (Figure 7d): There was no significant difference across high- ( $M = 2.93$ ,  $SD = 0.69$ ) and low-probability ( $M = 3.04$ ,  $SD = 0.81$ ) locales in orientation precision,  $t(19) = 0.79$ ,  $p = .439$ . There was also no significant difference in orientation precision across the experiments, for both probability conditions ( $ps > .05$ ), even if comparing with Experiment 1 ( $ps > .05$ ). As with Experiment 1, repeating versus nonrepeats of locations was not found to significantly affect spatial precision,  $t(20) = 0.86$ ,  $p = .400$  in Experiment 2a. Because locations were continuously distributed in Experiment 2b, quadrants of space were compared. There are two high-probability location quadrants for each participant. Trials in which there was a switch from one high-probability quadrant to another (40% of trials) were compared with when there was a repeat in the same quadrant (40%). There was no effect of repeated quadrants in either orientation or spatial precision ( $ps > .05$ ).

**Postexperiment questionnaire.** Three of the participants in each experiment correctly indicated the spatial probability distribution.

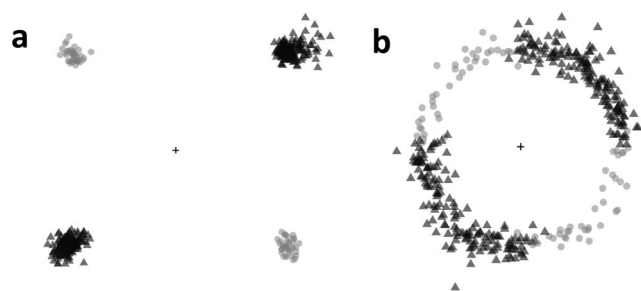
## Discussion

Experiment 2 suggests that the effects of *spatial* probability are different from the effects of *orientation* probability (e.g., Experiment 1; Anderson, 2014; Jabar & Anderson, 2015), orientation judgments are more precise, but when some *locations* are more probable, the precision of orientation estimations at the probable locations is unchanged. In addition, spatial probability did not affect spatial precision. The spatial precision in both Experiments 2a and 2b matched that from Experiment 1: The findings are incompatible with the idea of probability causing a domain-general “attentional” effect. The findings also pose trouble for domain-specificity hypothesis, as that would have predicted that spatial probability would have improved spatial precision.

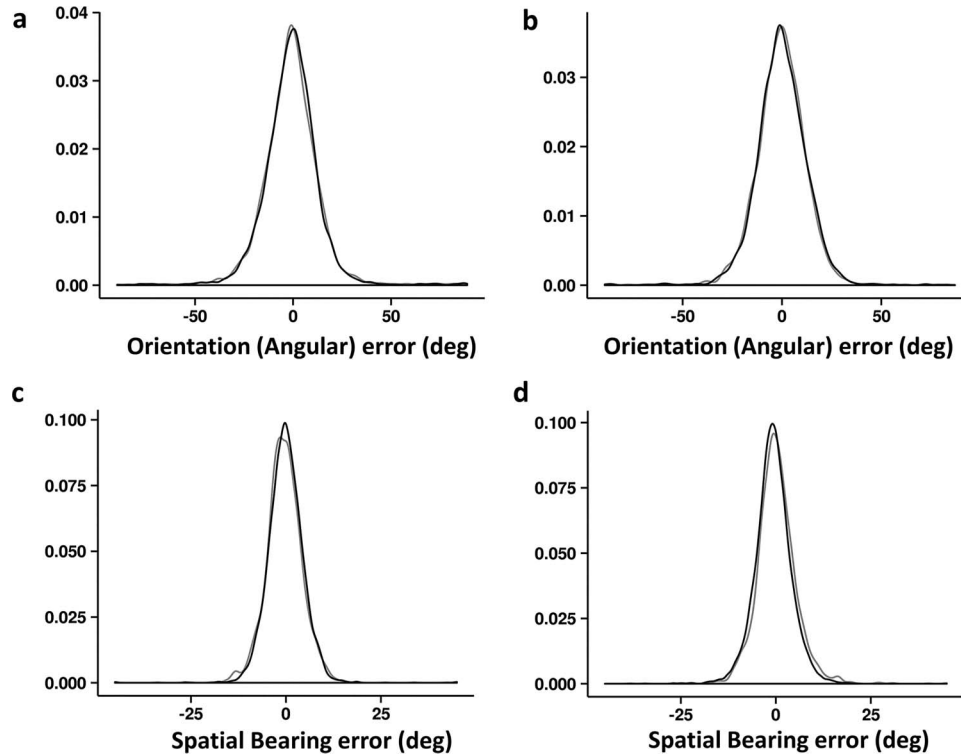
Perhaps the spatial estimation task was too easy? This is not the case for Experiment 2b, in which spatial uncertainty was substantial. However, to further probe this account, we ran Experiment 3, in which we reduced contrast to make the estimation task harder. Because spatial probability has been shown to affect detection (e.g., Jiang et al., 2015; Vincent, 2011; Walthew & Gilchrist, 2006), we also designed Experiment 3 to obtain a measurement of detection rate in addition to precision. This was specifically to show that the effects of spatial probability are on detection, but *not* on precision.

## Experiment 3

Experiment 3 introduced two main modifications. First, we employed a “3 down, 1 up” staircase procedure to bring detection down to approximately 80% (Leek, 2001) and remove the possibility of a ceiling effect on performance. The second modification was the inclusion of a confidence report at the end of each trial. If participants fail to detect the target, they will guess, and they will report lower confidence. Guessing results in uniformly distributed errors. Using the combination of confidence self-reports and behavioral precision, we can separate guess trials from the detected



**Figure 6.** Experiment 2 probability distribution. (a) For Experiment 2a, targets appear in only one of four discrete locations. The markers indicate where the first participant ended up clicking in response to these four locations. Dark triangle markers indicate target in high-probability locales. Two *discrete* locations are biased. (b) For Experiment 2b, targets appear in any bearing, with the same eccentricity from the fixation. Two quadrants are biased. Note that the probable locations are counterbalanced across subjects for both experiments.



**Figure 7.** Experiment 2 error distributions. (a) Orientation errors for Experiment 2a. (b) Orientation errors for Experiment 2b. (c) Spatial errors for Experiment 2a. (d) Spatial errors for Experiment 2b. Note that in each panel, there are two distributions: high (dark) and low probability (light). There is a very high level of overlap between the two in all cases.

trials and better decompose measured imprecision: How much of spatial probability effect is in the change in perceptual estimation precision per se, and how much is in the change in the proportion of trials the target is undetected and participants guess?

## Method

**Participants.** Twenty-one additional undergraduate students (13 females, eight males) took part in Experiment 3. Nineteen participants were right-handed. All participants used their right hand, had normal or corrected-to-normal vision, and did not declare any auditory deficits. These experiments were approved by the University of Waterloo's Office of Research Ethics.

**Stimuli and procedure.** Prior to the main task, a "3 down, 1 up" staircase procedure was done to determine what contrast led to an 80% detection rate (absolute bearing error  $< 22.5^\circ$ ). These trials were qualitatively similar to those used later, but spatial and orientation probabilities were uniform. The first 10 trials were designated as practice and contrast was not altered regardless of performance. Average luminance of the grating was not affected by the contrast reductions (always maintained at  $39 \text{ cd/mm}^2$ ).

There were 400 test trials. Spatial probability was manipulated as in Experiment 2b. After the spatial and orientation estimations, but before the feedback, participants were asked to indicate a response to the question "How confident are you that you saw the stimulus?". The continuous scale ranged from 0 to 100, but had descriptive labels at three points: 0 (*definitely did not see*), 50

(*maybe I saw*), 100 (*definitely saw*). Specifically, this measure was aimed at figuring out when participants perceived or did not perceive the stimulus, and not whether the participant was confident about their responses.

## Results

**Staircase and confidence.** Sample staircase results are shown in Figure 8a. There was a spread of values participants ended up with, but it was mostly in the 4% to 8% range ( $Mdn = 6\%$ ; Figure 8b).

There was a significant effect of spatial probability on reported confidence,  $t(20) = 2.97$ ,  $p = .008$ . Participants reported being more confident of detecting the grating in high-probability locales ( $M = 60.2$ ,  $SD = 17.1$ ) than in low-probability locales ( $M = 57.6$ ,  $SD = 17.9$ ). Separating the data into 50-trial bins, we find that high-probability locales were associated with higher confidence reports at all bins.

Samples of the distributions of confidence reports given by the participants are shown in Figure 9a. There is bimodality: Most of the reports tend to be high, but some are near zero. Because participants were asked to rate how confident they were that they saw the stimulus, the peaks could correspond to *detected* (high-confidence) versus *nondetected* (low-confidence) trials. What is clear is that different participants use the confidence scale differently: Using arbitrary cutoffs on the raw values to classify the detected trials would be problematic.

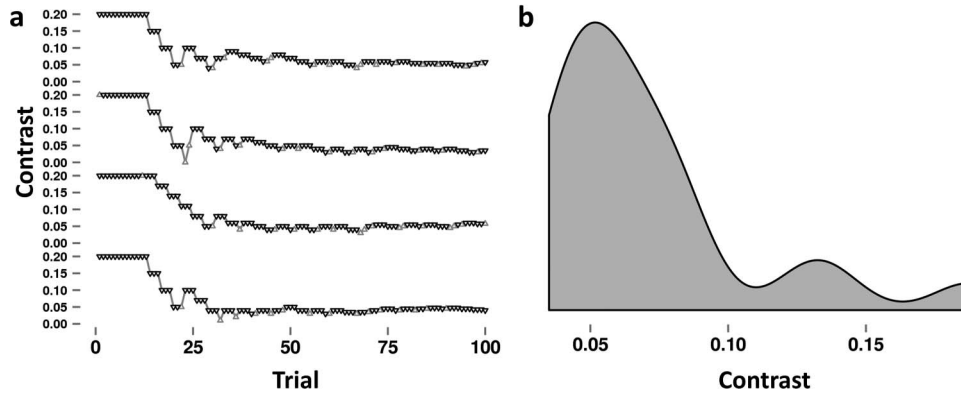


Figure 8. Experiment 3 staircase procedure. (a) Sample staircasing of stimulus contrast using spatial bearing error using the “3 down, 1 up procedure.” Each panel represents data from one participant. Light markers represent the points where participants crossed the error threshold. The first 10 trials were for practice and were not staircased. (b) Distribution of threshold contrasts found by the staircase procedure. Contrast was calculated as the luminance difference between the brightest and darkest “band” of the grating divided by the sum.

**Expectation-maximization clustering.** Instead of using raw confidence values as cutoffs, we looked at the two-dimensional distribution of spatial errors and confidence. Because the confidence scale was explicitly related to participants’ ability to *detect* the stim-

ulus, what we expected was that when reported confidence is high, participants detect/perceive the stimulus and therefore should have high spatial precision (smaller bearing errors). When reported confidence is low, participants likely failed to detect the stimulus and

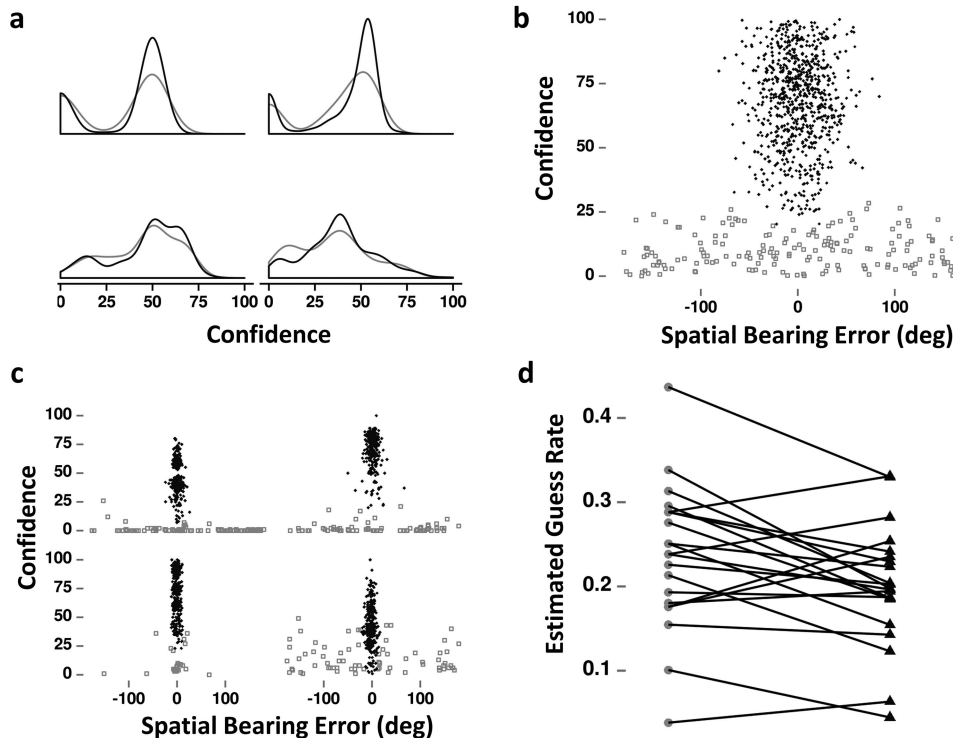


Figure 9. Experiment 3 guesses versus detections. (a) Sample distribution of confidence reports by probability condition (high probability is depicted with the darker lines). Each panel represents data from one participant. (b) Expected error by confidence distribution. At low confidence, participants should make uniform errors (indicating guessing), whereas at high confidence, the same participant should make precise spatial estimations. (c) Sample of clustering using the expectation-maximization (EM) technique. The darker markers represent trials that were most likely detected/perceived. (d) Guess rates by subject, based on the results of the EM clustering. Dark triangle markers indicate the guess rates for high-probability locales; light circular markers indicate the guess rates for low-probability locales.

therefore made random guesses, leading to a fairly uniform distribution of spatial errors. Essentially, the two-dimensional distribution of spatial errors and confidence should end up as an inverted “T” shape (Figure 9b). We can cluster these points into guesses versus detection. We used these expected clusters as a starting parameter to cluster participants’ data, although the proportions, centers and size of the clusters were free to vary. This expectation-maximization clustering was done using the EMCluster R package (Chen & Maitra, 2015).

Sample participants’ two-dimensional distributions are depicted in Figure 9c. The expected inverted “T” shape is apparent, and the clustering fits with our expectations. After clustering each participants’ full data set, we separated them into high- and low-probability trials, and looked at the proportion of trials in each condition that belong in the “guess” (low reported confidence with random spatial error) cluster (Figure 9d). Out of the 21 participants, 15 showed decreased guessing rates, that is, better detection, for high- ( $M = 20.5\%$ ) versus low-probability ( $M = 23.7\%$ ) locales. This difference was significant across participants,  $t(20) = 2.19$ ,  $p = .041$ . Note that the exact initial/expected values used for the clustering (Figure 9b) have slight effects on the exact values of the guessing rates. To confirm that our results were not dependent on starting values for the optimization, we ran each clustering procedure 1,000 times, slightly jittering the expected clusters. All tests consistently indicated that there was a significant 3% to 4% difference in guessing rate between probability conditions. The guessing rates also hovered around the 20% to 25% range, which is what we expected given the use of the “3 down, 1 up” procedure (Leek, 2001). We compared this procedure with visually clustered data and ended up with similar results.

As a check of the clustering method, a mixture model was also used to estimate the proportion of perceived versus guessed trials. Similar to the method used by Zhang and Luck (2008), the spatial bearing error data from each participant were fitted with a mix of uniform and Gaussian, in which the three parameters—proportion ( $\lambda$ ), mean, and variance mean of the Gaussian component—were free to vary. Proportion of the uniform was just 1 minus  $\lambda$  and thus was not a free parameter. The idea here is that the uniform distribution represents the guessed trials, and therefore the  $\lambda$  parameter should match the results of the clustering analysis. The mixture model suggested that participants perceived the grating ( $\lambda$ ) 84.2% ( $SD = 4.7\%$ ) of the time in the high-probability trials, but only 80.5% of the time ( $SD = 6.1\%$ ) in the low-probability condition, with there being a significant,  $t(20) = 2.20$ ,  $p = .034$ , difference between the two. However, there was no difference in either the mean or variance of the mixture models across high- and low-spatial-probability trials ( $ps > .05$ ). Both the clustering and mixture models therefore are in agreement that spatial probability modulate guess/detection rates, but not the precision with which estimations are made. The guess rates (high = 15.8%, low = 19.5%) estimated from the mixture model also significantly correlated ( $ps < .05$ ) with the guess rates from the clustering model, for both high- ( $r = .771$ ) and low-probability ( $r = .723$ ) data, further suggesting convergence between the two methodologies at the level of individual subjects.

**RT analysis.** The iRT was faster for perceived ( $M = 387$  ms) than for guessed ( $M = 685$  ms) trials,  $t(20) = 7.06$ ,  $p < .001$ . The sRT was not different between perceived ( $M = 1,564$  ms) and guessed ( $M = 1,686$  ms) trials,  $t(20) = 0.94$ ,  $p = .353$ . However, the oRT was slower for perceived ( $M = 866$  ms) than for guessed

( $M = 669$  ms) trials,  $t(20) = 2.29$ ,  $p = .028$ . It is possible that participants were caught off guard during the spatial localization phase of the experiment if they did not detect the stimuli, leading to longer iRTs, but clicked randomly for their orientation judgments leading to faster oRTs.

Looking only at perceived trials, there was still an effect of spatial probability on iRT: Targets appearing in high-probability locales ( $M = 386$  ms,  $SD = 57$  ms) were reacted to faster than for those appearing in low-probability locales ( $M = 393$  ms,  $SD = 63$  ms),  $t(20) = 2.60$ ,  $p = .017$ .

**Precision analyses.** Orientation errors were much larger for the guess trials ( $M = 34.4$ ) than the perceived ones ( $M = 10.1$ ),  $t(20) = 13.4$ ,  $p < .001$ . This amount of error highlights that we should only take into account trials that were clustered as “detected” or “perceived” when we are interested in perceptual precision.

Orientation error for the perceived trials was not any better for the high- ( $M = 7.75$ ,  $SD = 1.52$ ) versus the low-probability ( $M = 7.56$ ,  $SD = 2.12$ ) conditions,  $t(20) = 0.72$ ,  $p = .482$ . The orientation bias was not significantly different from zero for either probability condition ( $ps > .05$ ).

Spatial error for the perceived trials was also not any better for the high- ( $M = 3.91$ ,  $SD = 0.90$ ) versus the low-probability ( $M = 3.95$ ,  $SD = 1.20$ ) conditions,  $t(20) = 0.72$ ,  $p = .482$ . However, compared with Experiment 2b, in which stimuli were displayed with higher contrast, spatial error in Experiment 3 was increased,  $t(20) = 4.70$ ,  $p < .001$ , so we did achieve an indication that spatial precision can be affected by contrast manipulations. In comparison, orientation precision was not affected across these experiments,  $t(20) = 0.466$ ,  $p = .642$ .

To address a lack of statistical power as a potential concern over the lack of precision effects in the spatial probability tasks, the data from Experiment 2a, 2b, and the perceived trials of Experiment 3 were pulled and placed into a Bayesian comparison (high vs. low spatial probability) through the use of the BayesFactor R package (Morey, Rouder, & Jamil, 2015), treating the 61 participants as a random factor. The Bayes factor (BF) obtained from comparing the spatial bearing error was 0.063 ( $\pm 1.31\%$ ). The BF obtained from comparing the orientation error was 0.029 ( $\pm 2.28\%$ ). These numbers support the hypothesis that spatial probability has no effect on either spatial or orientation precision.

As a comparison, data from the 21 participants in Experiment 1 were also looked at. The BF from comparing the spatial error was 0.116 ( $\pm 22.86\%$ ), whereas the BF obtained from comparing the orientation error was 378.755 ( $\pm 0.81\%$ ). These numbers support the hypothesis that although orientation probability does not affect spatial precision, it very clearly affects orientation precision.

**Repetition analysis.** Because there was an effect of spatial probability on detection rates, the effects of repeated locations were looked at for the guessed or nonperceived trials. Particularly, for the high-probability locales, the proportion of trials from repeated location ( $M = 40.2\%$ ) compared with trials followed by the other high-probability quadrant ( $M = 40.1\%$ ) was not significantly different,  $t(20) = 0.065$ ,  $p = .949$ , suggesting that repetitions are not driving the probability effect on guess rates.

**Postexperiment questionnaire.** Of the 21 participants, three correctly indicated the spatial probability distributions.



## Discussion

Experiment 3 replicated Experiment 2. For trials in which the grating was perceived, spatial probability affected neither spatial nor orientation precision, but initiation times were faster for the high-probability locales.

Reducing contrast did reduce spatial precision, and precludes the possibility that the absence of an effect in Experiments 2a and 2b were because of a ceiling effect. Although spatial probability did not affect spatial precision, it did affect detection: Although detection rates on average were about 80%—a rate predicted by the type of staircase procedure employed—detection rates were lower when the grating appeared in the low-probability locale compared with the high-probability locales. This lower guess rate for high-probability locales was not because of repeats in location (Geng & Behrmann, 2005), suggesting that spatial probability effects in this case are not because of sequential dependencies (cf. Walthew & Gilchrist, 2006), perhaps because locations were continuously distributed. In addition, even for trials in which the stimulus was perceived, the iRT was still significantly faster for high-probability locales, consistent with the idea that spatial probability affects detection. Given the size of these detection effects, is difficult to get an estimate of how quickly the changes in detection as a result of spatial probability occurs. However, reported confidence was higher (trendwise) for high-probability locales throughout the experiment, even within the first 50 trials. It is likely that spatial probability learning, like orientation probability learning, occurs very quickly.

In sum, the three experiments outlined in this article consistently indicate that although orientation probability affects orientation precision, spatial probability only affected target detection. In the following section, we discuss the implications of these findings.

## General Discussion

The goal of these experiments was to evaluate how generic the effects of probability manipulations are. For this assessment, we used a fairly typical visual discrimination task. Does manipulating the probability of where a target will appear (or whether it bears a probable feature) affect the speed and accuracy with which the target can be located, and does it also affect the fineness with which features can be discriminated? A second goal was, given the overlap at the level of task structure and experimental procedures, to infer whether probability effects and attentional effects are likely to index common underlying psychological processes or neural bases.

The principal result was that probability cues, whether spatial or featural, shorten RT, just as do conventional cues in spatial and feature attention experiments (Hon, Yap, & Jabar, 2013; Laberge & Tweedy, 1964; Miller & Pachella, 1973). Because of our experimental procedure, we were able to decompose these speed effects into initiation and movement components. The speed-up was most apparent for movement initiation. This was true for both orientation (Experiment 1) and spatial probability (Experiment 3). The effect was larger for spatial probability, but perhaps this was because of the increased difficulty associated with a reduction in contrast. The most obvious reason for this improvement was better target detection (Fecteau, Korjoukov, & Roelfsema, 2009; Geng, & Behrmann, 2005; Jiang et al., 2015; Rich et al., 2008; Vincent, 2011; Walthew & Gilchrist, 2006; Wolfe et al., 2007).

In Jabar and Anderson (2015), participants were shown a dial after each Gabor, and asked to rotate it using keyboard buttons, to best represent the orientation they saw. By manipulating feature (orientation) probability, it was found that the initiation time (time taken to initiate an anticlockwise or clockwise dial rotation) required was decreased for probable tilts. Orientation precision was also improved. These results were replicated in Experiment 1 of the current study, despite the changes to the response method. As with feature probability, initiation time (time taken to move the mouse away from central fixation) was also affected by spatial probability. However, in Experiments 2a, 2b, and 3, spatial probability did not affect orientation precision, even while spatial probability improved detection (Experiment 3). Consistent with the studies outlined in the introduction, both spatial and feature probability manipulations create effects that are “attention-like.” However, this study also clearly indicates a difference between the two.

Instead of a general “probability effect,” we should be concerned with probability *effects* (plural). Given that the task is not one of forced choice, there is less opportunity for probability effects to be mediated at the level of a decision process (Wolfe & Van Wert, 2010), and one might think that decision effects would more likely affect judgment time than initiation time. Motor (or response) biases are also unlikely to explain the results as the effects of feature probability were location-contingent. All movements were equiprobable and all angles were shown equally often. Thus, we are led to propose that the most parsimonious explanation is that the basis for the orientation probability effect is perceptual (Dykes & Pascal, 1981), perhaps at the level of orientation tuning in early visual areas. On the other hand, spatial probability affected neither the precision of spatial errors nor orientation estimation errors. This decomposition of spatial and orientation probability effects maps nicely on to the decomposition of attention into spatial and feature-specific varieties (e.g., Carrasco, 2011), and leads us to conjecture common mechanisms for probability and attention.

We suggest that a plausible locus for the shared effects of spatial and feature probability and spatial and feature attention is at the level of early visual processing, where attention has been noted to have consistent effects (Brefczynski & DeYoe, 1999; Gandhi et al., 1999; Liu et al., 2005; Sharma et al., 2015; Tootell et al., 1998). The basis for these effects are broadly of two types (Martinez-Trujillo & Treue, 2004; Saenz et al., 2002): first, sharpening of neuronal tuning function in early sensory neurons, and second, increasing the gain of neuronal firing curves for early sensory neurons.

Feature attention has been suggested to be primarily driven by the first mechanism, changes in neuronal tuning curve width (Paltoglou & Neri, 2012). V1 neurons show changes in tuning functions with an increased experience of particular orientations (Ringach, Hawken, & Shapley, 1997; Schoups, Vogels, Qian, & Orban, 2001). By contrast, spatial attention’s effects are primarily accompanied by increases in neuron firing generally, a phenomenon referred to as *response gain* (Kastner & Ungerleider, 2000; Ling et al., 2009; Figure 1c). Our suggestion that feature probability effects are also mediated by neuronal tuning effects is consistent with recent work on statistical decision theory (Eckstein, Peterson, Pham, & Droll, 2009). Probabilistic information

for features might tune relevant perceptual channels, which then affects decision making.

The analogy between categories of attentional cues and probability manipulations is provisional. There are differences as well. Chief among them is the temporal dynamics. Probability learning is acquired across trials, whereas spatial cuing is typically a brief trial-specific signal. In addition, cues provide a nonspecific preparatory signal that is absent in pure probability learning, resulting in different effects. For example, although spatial *cuing* might affect orientation estimation (Anderson & Druker, 2013), spatial *probability* might not.

In summary, the main empirical result in this article is that probability effects, like attention, can dissociate between feature and spatial biases. Feature probability affects precision, whereas spatial probability only affects detection. Based on these findings, and previous work on the mechanisms underlying attentional cuing, we argue that there are conceptual and mechanistic links between probability and attention, chiefly that they may both affect perceptual processing by similar neural mechanisms. Cues and probability provide participants with information about *what* stimuli might appear, and *where* they might appear (Anderson, 2011). This information leads to biases in early perceptual systems that show a common reliance on adjusting the gain and tuning of sensory neuronal populations.

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