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Probability Shapes Perceptual Precision: A Study in Orientation Estimation

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Probability is known to affect perceptual estimations, but an understanding of mechanisms is lacking. Moving beyond binary classification tasks, we had naive participants report the orientation of briefly viewed gratings where we systematically manipulated contingent probability. Participants rapidly developed faster and more precise estimations for high-probability tilts. The shapes of their error distributions, as indexed by a kurtosis measure, also showed a distortion from Gaussian. This kurtosis metric was robust, capturing probability effects that were graded, contextual, and varying as a function of stimulus orientation. Our data can be understood as a probability-induced reduction in the variability or "shape" of estimation errors, as would be expected if probability affects the perceptual representations. As probability manipulations are an implicit component of many endogenous cuing paradigms, changes at the perceptual level could account for changes in performance that might have traditionally been ascribed to "attention."

Keywords: attention, kurtosis, orientation estimation, probability, visual perception

The probability of target occurrence influences behavior: We are slower and less accurate at detecting improbable stimuli (Hon, Yap, & Jabar, 2013; Laberge, & Tweedy, 1964; Rich et al., 2008). Probability interacts with perceptual manipulations (e.g., Miller & Pachella, 1973), suggesting a perceptual locus for probability effects. Measuring probability effects has traditionally used detection (Hon et al., 2013; Miller & Pachella, 1973; Laberge & Tweedy, 1964) and search (Rich et al., 2008; Wolfe et al., 2007) tasks where participants specify whether a target is present or absent. Binary decisions results in binary data, and forced choices introduce the possibility of decision-biases (e.g., Menneer, Donnelly, Godwin, & Cave, 2010; Wolfe & Van Wert, 2010).

Direct measures of perception are more informative for how probability affects perceptual processing. In an orientation estimation task, participants briefly view oriented stimuli and reproduce their tilts. Probability effects are produced by manipulating the probability of orientation-location conjunctions, for example, left-tilting can be made likely only on the left side. Employing this method, Anderson (2014) found probable tilts were estimated faster, with more precision, and with a change in the distribution of estimation errors: High-probability tilts were associated with an increased kurtosis. In this article, we extend that finding by demonstrating that these distribution changes occur even with convoluted probability distributions, for example, when the likely target orientation is conditional on a nontarget feature. Other studies suggest that the acuity of orientation perception is anisotropic: Cardinal orientations are better perceived than obliques (Appelle, 1972; Li, Peterson, & Freeman, 2003). The data collected from the reported experiments allow us to explore how orientation anisotropy might be modulated by acquired information on probable features.

Why Kurtosis?

Although it is a typical assumption of experimental data, distributions need not necessarily conform to a normal, or Gaussian, shape: Anderson (2014) demonstrated that probability learning results in kurtosis differences. Gaussians, by definition, have a kurtosis[1] value of three, typically standardized as an *excess* kurtosis of *zero*. We refer to this definition of excess kurtosis for the rest of the article. Figure 1 illustrates the effect of a shift in kurtosis by comparing a Gaussian (gray curve), with a leptokurtic, above zero kurtosis, distribution (black curve) matched on mean and standard deviation. The "peak" of the leptokurtic distribution is higher than that of its counterpart Gaussian, but lacks in "shoulders." Meanwhile, the "tails" of the leptokurtic distribution need not be smaller than the Gaussian's, which explains how kurtosis differences can be seen without corresponding mean error or standard deviation differences.

Where using standard deviation as a measure would tell us that both curves in Figure 1 are equivalent, the kurtosis metric captures these "shape" differences, and provides us with additional information to distinguish between distributions. This could be espe-

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[1] The kurtosis of a distribution is the standardized fourth population moment about the mean. Mathematically, $Kurtosis = \frac{\sum_i (X_i - \overline{X})^4/n}{(\sum_i (X_i - \overline{X})^2/n)^2}$, where n is the number of samples in the distribution, X_i are the individual observations, and $\overline{X}$ is the sample mean (DeCarlo, 1997). *Excess* kurtosis is taken as *Kurtosis – 3*. Gaussians always have an excess kurtosis of *zero*.

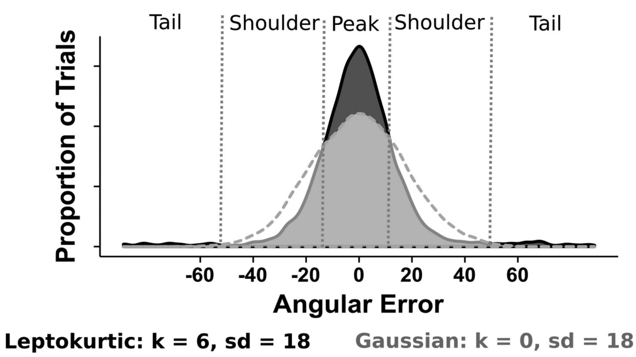

Figure 1. Comparison of a Gaussian (gray) against a matched leptokurtic (black) distribution.

cially meaningful when manipulations reduce some sources of error but not others. For example, in an orientation estimation task, an increase in perceptual acuity should enable what might have been a somewhat precise estimate into a very precise estimate. By contrast, increases in perceptual acuity is less likely to affect larger errors, as they could also stem from nonperceptual sources, for example, from motor errors in responses, distractions, anticipations, and so forth. If it is the case that probability affects perceptual acuity, looking at error distributions might suggest reliable shape changes in the error distribution which might be captured better by a kurtosis metric, rather than something like standard deviation.

Experiment 1a

Experiment 1a was a replication of Anderson (2014) and provided data to examine probability-related differences in the shape of error distributions. It also provided data for looking at potential interplays between probability and orientation biases.

Method

Participants. Twenty undergraduate students from the University of Waterloo (9 females, 11 males) took part in the study. Seventeen participants were right-handed and 3 were left-handed. 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.

Gabors were presented to participants on each trial. These were oriented grayscale sine-wave gratings with a circular Gaussian mask (Figure 2a), with an average measured luminance of 39cd/mm^2. They had a spatial frequency of 4 cycles per degree of visual angle, and were presented on a gray background with a similar luminance of 40cd/mm^2. When viewed from a distance of 60 cm, the Gabors subtended approximately 4° of visual angle both vertically and horizontally. On any given trial, the center of the Gabor was located 4° either to the left or right of the center of the display, which was marked by a black fixation symbol. Lines, used as feedback and for participants to rotate to report their estimations, had a length of 4 visual degrees and always occurred in the same location as the Gabor for that trial.

Spatial Gabors were equally likely to appear on the left or right of the fixation symbol. *Collapsed across these two locations*, any orientation was equally likely. The critical manipulation was the occurrence-rate of the various *probability–location conjunctions*. Half the participants saw the conjunction depicted in Figure 2b: When a Gabor appeared on the left, its orientation was more likely to be left-tilting, but this high-probability tilt was reversed if the Gabor appeared on the right. High-probability orientations accounted for 80% of the trials. The lines in Figure 2b depict the distribution observed by the first participant.

Probability distributions were maintained throughout the experiment. In every set of 20 trials, there were 8 left-tilting Gabors on the left, 2 right-tilting Gabors on the left, 8 right-tilting Gabors on the right, and 2 left-tilting Gabors on the right (or vice versa). Participants were *not* informed about these probability distributions. The location-orientation conjunctions were counterbalanced across participants.

Auditory feedback was given after each trial to maintain motivation. A high pitched sound (http://www.freesound.org/people/HardPCM/sounds/32950/) indicated an error of less than 12°. A lower pitch (http://www.freesound.org/people/tombola/sounds/49219/) indicated an error greater than 12°. Participants were not informed of the error threshold.

Procedure. Participants sat approximately 60 cm from a 32 cm × 24 cm gamma-corrected CRT monitor that refreshed at 89 Hz. Responses were made with a computer keyboard using their dominant hand. The experiments were programmed in Python

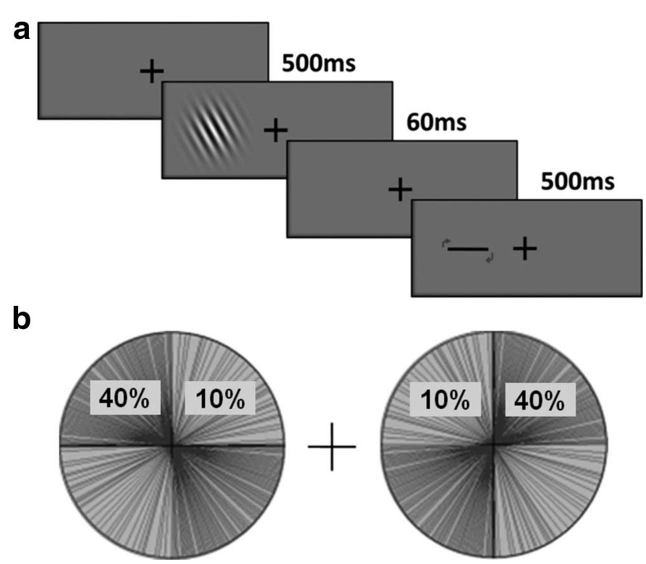

Figure 2. Experimental paradigm and trial distribution. (a) On each trial participants began by looking at the fixation symbol for 500 ms. The spatial Gabor then appeared (left or right) for 60 ms. After a delay period of 500 ms, a horizontal line was drawn onscreen, and participants rotated this line to best match their perception of the orientation of the Gabor. (b) Half the participants saw that when Gabors appear on the left, they tilted left (dark gray: high-probability region), and this was reversed on the right. The other half of the participants saw the opposite pattern. The lines within the colored regions show the actual orientations that the first participant saw.

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 Gabor orientations as accurately 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 questionnaire to examine whether they could explicitly report the probability distribution of the orientations that they had seen. The experiment took approximately 20–25 min.

On each trial, participants were shown the fixation symbol for 500 ms. The spatial Gabor then appeared in one of the two locations for 60 ms, and went off-screen for 500 ms. After this delay period, a horizontal line was drawn on-screen, and participants made their estimations by rotating this line counterclockwise or clockwise by pressing *Z* or *C* on the keyboard. This rotation was at a maximum of 1 angular degree per frame refresh of the monitor. Participants pressed the *X* key to confirm their estimations. The auditory feedback was then given. On the practice trials, a white feedback line with the actual orientation was displayed on top of the participant's response. The visual feedback was not given in the main trials.

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° (anticlockwise error) to +90° (clockwise error). Due to the axial (half circular) nature of orientations, a +91° error wraps back as a −89° error. The excess kurtosis measurement was applied on these sets of angular errors through the use of the R "e1071" package (Dimitriadou et al., 2009). These data were also used to get a measure of bias on the cardinal axes. Vertical-biased estimations, for example, where on a particular trial, participants estimated the orientation more vertically then it should have been, were coded as negative (Figure 3a), whereas horizontal biases were coded as positive (Figure 3b).

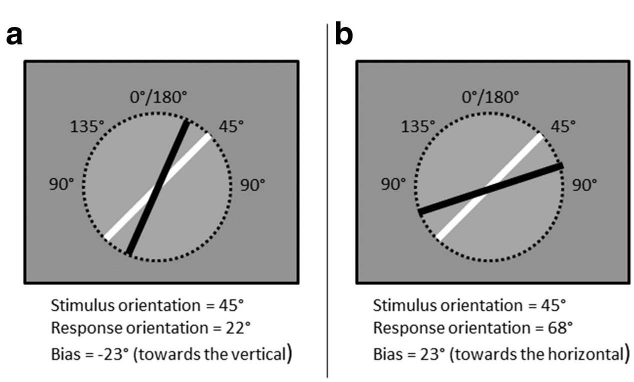

Figure 3. Example of bias. Black lines indicate hypothetical estimations to stimulus orientations (white). In panel a), the estimate is made toward the vertical whereas in panel b) the estimate to the same orientation is biased to the horizontal. The mean bias across these two trials would be zero, and the mean error, taking the average of the absolute angular errors, is 23°.

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, averages of the *absolute values* of the estimation errors were taken. There would be a "0°" bias and "23°" mean error across the trials depicted in Figure 3. Reaction time (RT) for each trial was taken as the time from when the response line appeared to when the orientation was confirmed. Total angular distance moved, time taken to initiate movement (IT), time taken to make movements after initiation (MT), initial rotation direction and number of direction switches (*vacillations*) per trial were also recorded.

Results

Unless otherwise stated, the only data excluded from the analyses were trials in which participants did not make a response within the given 7-s response windows. This only occurred on 0.125% of the trials.

RT analyses. Paired (two-tailed) t tests were carried out between the high and low probability tilts on the various measures (Figure 4). Alpha cutoff for significance testing was the conventional $p = .05$. There was a significant effect of RT, $t(19) = 5.20$, $p < .001$, with high-probability tilts ($M = 1{,}080$ ms, $SD = 250$ ms) estimated faster than low-probability tilts ($M = 1{,}180$ ms, $SD = 270$ ms). Nineteen participants showed this trend, with 1 participant marginally showing the reverse trend. The MT measure revealed a significant effect of probability, $t(19) = 3.65$, $p = .002$, suggesting that high-probability tilts take less time ($M = 890$ ms, $SD = 210$ ms) to estimate than low-probability tilts ($M = 960$ ms, $SD = 220$ ms). This might be because of differences in the total amount of movement made, $t(19) = 3.70$, $p = .02$: Participants made more angular adjustments for low-probability tilts ($M = 58.7°$, $SD = 8.6°$), compared with high-probability tilts ($M = 54.9°$, $SD = 8.2°$). This, in turn, might be due to the different number of times participants vacillate, $t(19) = 4.00$, $p < .001$. Participants vacillate more when responding to low-probability tilts ($M = 0.21$, $SD = 0.11$) than to high-probability tilts ($M = 0.14$, $SD = 0.12$). This difference in movement patterns is unlikely to account for all the RT differences because the IT measure also varied by probability condition, $t(19) = 6.85$, $p < .001$. Participants take less time to initiate movements in the high-probability trials ($M = 210$ ms, $SD = 130$ ms) than in the low-probability trials ($M = 250$ ms, SD = 140 ms).

Angular error analysis. The bias measure revealed that the high-probability tilts were significantly vertically biased, $t(19) = 2.66$, $p = .015$, whereas low-probability tilts were not, $t(19) = 0.57$, $p = .58$. Compared against each other, there was a significant effect of probability on bias, $t(19) = 2.10$, $p = .049$, with high-probability tilts being more vertically biased ($M = -0.99$, $SD = 4.72$) than low-probability tilts ($M = 0.47$, $SD = 4.81$). The mean error measure also reflected a significant effect of probability, $t(19) = 3.08$, $p = .006$, with high-probability tilts associated with an error of smaller magnitude ($M = 12.0°$, $SD = 5.8°$) than low-probability tilts ($M = 13.3°$, $SD = 6.4°$). Of the 20 participants, 17 showed this trend.

Repetition effects analysis. Repetition effects are possible sources of confounds in probability-related studies because high-probability targets are more likely to be repeated, whereas rare

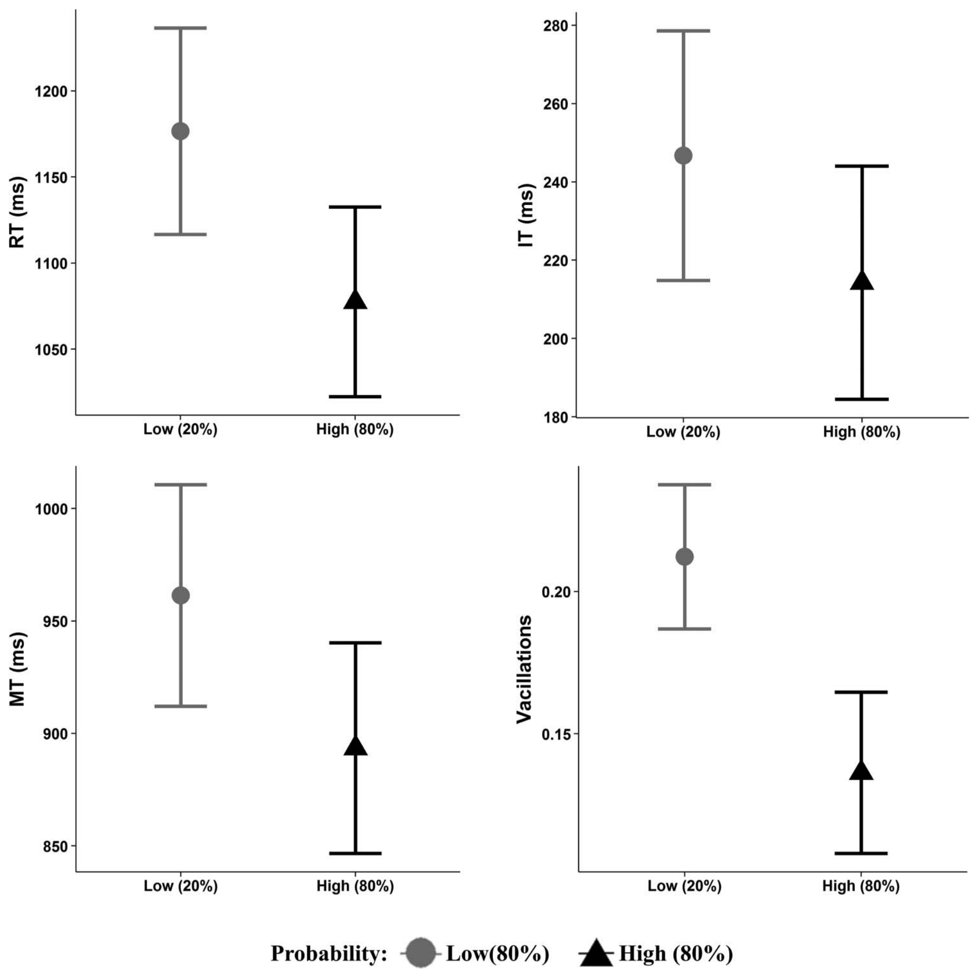

Figure 4. Reaction time and vacillation measures for Experiment 1a. These measures show consistent probability effects (all *p*s < .01) in estimations. Error bars indicate one standard error. RT = time from response line appearance to participants' confirmation; IT = indicates time from appearance to first directional movement; MT = indicates time from movement to confirmation; vacillations = number of direction switches participants made, on average on each trial.

targets are not. If repetitions are driving performance benefits for the high-probability orientation estimations, then we should observe a significant correlation between absolute intertrial differences in orientation and estimation performance. However, neither the errors that participants made ($r < .01$, $p = .449$), nor their RT ($r > -.01$, $p = .637$), demonstrated a significant correlation with the orientation difference measure.

Distribution/kurtosis analysis. The distribution of angular errors made across trials was examined for the low- (Figure 5a) and high-probability (Figure 5b) conditions using the standard deviation and kurtosis as measures. Consistent with the mean angular error measure, the distribution of the errors associated with low-probability tilts (mean $SD = 18.1°$) was significantly higher than that of the high probability tilts (mean $SD = 16.5°$), $t(19) = 2.63$, $p = .016$. However, as Figure 5a and Figure 5b suggests, these distributions are non-Gaussian. Replicating Anderson (2014), there was a significant difference in their kurtoses, $t(19) = 2.11$, $p = .048$. High-probability tilts were associated with a higher kurtosis ($M = 4.86$, $SD = 4.72$), than low-probability tilts ($M = 3.15$, $SD = 4.09$). Of the 20 participants, 14 showed this kurtosis trend, with only one participant clearly showing the opposite trend. The increase in kurtosis is likely the result of the increased "peak" and decreased "shoulders" when comparing the error distributions across probability (Figure 5c), which can be seen in participants' data as well (Figure 5d). The "tails" of the high probability when looking at the aggregate distribution is lower than the low probabilities'. However, large errors are rare (only 3.7% of trials had error of 45° or larger), and estimating the tails is noisy: Even across participants who show increased "peaks" for high probability estimations, the density at the tails is variable (Figure 5c).

Because there were unequal numbers of high versus low probability trials, additional analyses was done to ensure that the kurtosis differences observed were not due to uneven samples. Angular errors for the high-probability orientations and low-probability orientations were separately pooled across participants. 400 "trials" were drawn from each probability pool and the kur-

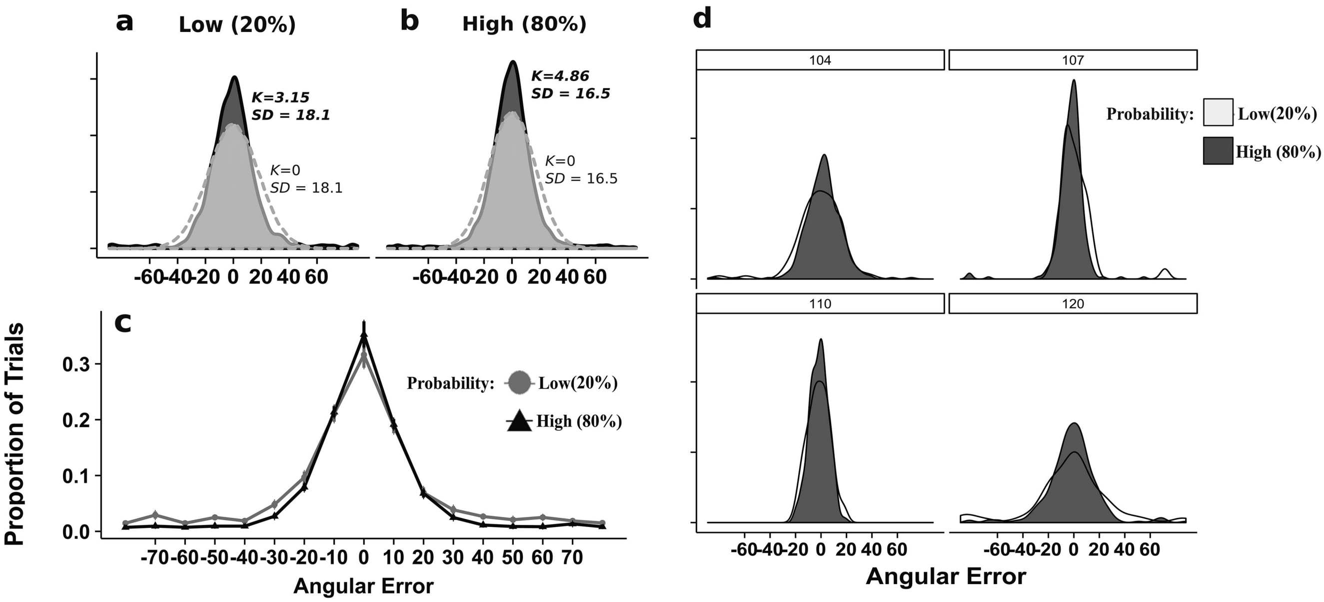

Figure 5. Error distributions across probability conditions. (a) Comparison of actual low-probability distribution to matched Gaussian. (b) Comparison of actual high-probability distribution to Gaussian to matched Gaussian. (c) Aggregate error distributions. Error bars represent one standard deviation. (d) Sample individuals' error distribution for high (dark) versus low (light) probability distributions.

tosis measurement was run on each set. This was repeated 10,000 times and a t test run between the two sets of kurtoses. The t tests on this bootstrapped data consistently revealed a significant effect of probability pool (all ps $< .05$), where the kurtoses associated with high-probability orientations was consistently higher than that for the low-probability ones. The same result persists even if varying the sampling size (e.g., drawing only 100 or 40 "trials" instead of 400). Furthermore, sampling just the final 40 high-probability trials and the final 40 low-probability trials also revealed the same effect on kurtosis, $t(19) = 2.55$, $p = .020$.

Circular statistics. In the above sections, linear statistics were employed, consistent with other studies looking at orientation data (e.g., Anderson, 2014; Anderson & Druker, 2013; Liu & Becker, 2013; Prinzmetal, Amiri, Allen, & Edwards, 1998). Because angular error data occupies an axial space, this "wrap around" might produce increased tails if the variance is large, changing the shape of the distribution and the resultant kurtosis measure. However, this is an unlikely explanation for the differences reported above given the small range of errors actually observed in our experiment. As Figure 5 suggests, the proportion of trials with exaggerated angular errors that approached this wrap-around point was small: The bulk of participants' estimations (96.3%) fell within 45° of angular error.

We ran circular statistical analyses and simulations with circular data. Angular errors were doubled to fit a circular space (Pewsey, Neuhäuser, & Ruxton, 2013), and participants' error data individually fitted with a von Mises (circular normal) distribution through the use of the R "circular" package (Lund & Agostinelli, 2014). Similar to a Gaussian, a von Mises distribution has 2 parameters: a mean and a kappa (analogous to an inverse variance). Across the optimal fits, the *mean* parameter (high-probability: -0.01, low-probability: -0.02) did not significantly vary as a function of probability, $t(19) = 0.23$, $p = .822$. The kappa parameter did significantly differ, $t(19) = 2.66$, $p = .015$ (high-probability: 5.60, low-probability: 4.92).

To exclude kappa differences of the magnitude seen in our data from producing differences in linear statistics as an artifact, we generated surrogate data using the parameters obtained in the previous step and then halved them to transform it back into axial space. The linear kurtosis measure was applied on these fitted distributions. For high-probability orientations, the kurtosis of the fitted distributions ($M = 0.47$, $SD = 0.39$) were significantly less than the actual distributions, $t(19) = 4.15$, $p < .001$. Kurtosis of the fitted low-probability distributions ($M = 0.53$, $SD = 0.45$) were also significantly less than their actual counterparts, $t(19) = 2.88$, $p < .001$. Compared across these optimal fits, there was no significant probability-based difference in kurtosis, $t(19) = 1.22$, $p = .237$. We repeated this analysis 1,000 times to determine its reliability: In only 45 out of the 1000 cases were there significant differences ($p < .05$) in the kurtosis of these von Mises fits: This is likely only due to noise. Furthermore, in *none* of the cases do the kurtoses of the low ($M = 0.43$, 95% confidence interval [CI] of 0.24 to 0.64) and high ($M = 0.38$, 95% CI of 0.20 to 0.59) probability fits approach the kurtosis of the actual data. In sum, circular data distributions with modest kappa measures, such as we measure, cannot in and of themselves produce kurtosis differences.

Time-course analyses. The data were binned into 50-trial bins to examine how quickly the differences in estimation performance developed across the probability conditions. A two-way repeated measures analysis of variance (ANOVA) was run on these binned averages of RT. There was a main effect of probability, $F(1, 19) = 26.28$, $MSE = 28700$, $p < .001$, a main effect of trial bin, $F(7, 133) = 11.82$, $MSE = 73210$, $p < .001$, but no significant two-way interaction, $F(7, 133) = 0.44$, $MSE = 19328$,

p = .877. Post hoc t tests demonstrated a significant difference, $t(19) = 3.93$, $p < .001$, in RT between high (M = 1,157 ms, SD = 338 ms) and low (M = 1,293 ms, SD = 387 ms) probability tilts in the second bin (Trials 51–100). This difference persisted in the third, fourth, fifth and sixth bins (all ps < .05), although not in the final two bins (ps > .05)

A two-way repeated measures ANOVA on the kurtosis measure revealed a main effect of probability, $F(1, 19) = 45.91$, MSE = 8.8, $p < .001$, but no significant main effect of trial bins, $F(7, 133) = 0.90$, MSE = 4.98, p = .51, and no significant two-way interaction, $F(7, 133) = 0.92$, MSE = 4.26, p = .497. Post hoc t tests demonstrated a significant difference, $t(19) = 3.72$, p = .001, in kurtosis between high (M = 0.95, SD = 1.77) and low (M = −0.80, SD = 0.84) probability tilts within the first 50 trials. This difference persisted in all the successive bins (all ps < .05).

Orientation analysis. If probability manipulations improve perceptual precision and thereby increase kurtosis, then other factors that influence precision should also influence kurtosis. We know that orientation anisotropy exists. For example, cardinals are perceived more precisely than oblique orientations (Appelle, 1972). We evaluated how kurtosis tracked stimulus orientation.

Orientations across the 400 trials were grouped up into three orientation bins: One included the 60° of orientations nearest the vertical cardinal, another included the 60° of orientations nearest the horizontal cardinal. The last bin comprised of the remaining 60° of oblique angles. The kurtosis measure was computed for each participant and each combination of condition and bin. A repeated measures ANOVA across the 2 levels of probability and 3 levels of orientation (Figure 6a) revealed a significant main effect of probability, $F(1, 19) = 24.01$, MSE = 9.03 $p < .001$, a significant main effect of orientation, $F(2, 38) = 19.25$, MSE = 9.03, $p < .001$, and a significant two-way interaction, $F(2, 38) = 5.12$, MSE = 8.64, p = .011. The highest kurtosis was seen for near-vertical orientations when they were probable.

To look at the orientation anisotropy in a more fine-grained manner, orientations across the 400 trials were grouped up into bins of 20° instead of 60° (Figure 6b). As before, a repeated measures ANOVA across probability and orientation bin revealed

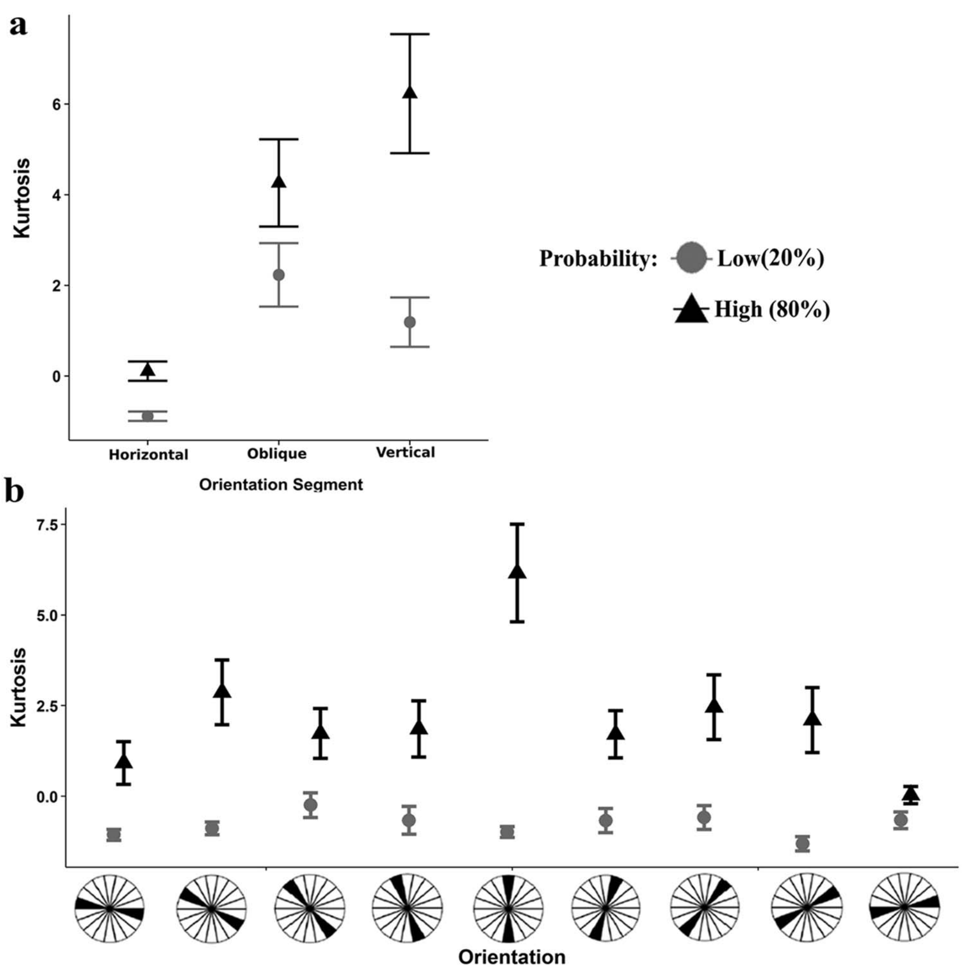

Figure 6. Interaction of probability and orientation in Experiment 1a. (a) Each bin indicates 60° segment classified into either vertical, horizontal, or oblique orientations. (b) A finer-grained orientation analysis: Each bin indicates 20° orientation segments (exemplified by the figures in the x-axis). High-probability tilts are indicated in black. High-probability vertical tilts are associated with the highest kurtosis. Error bars indicate one standard error.

a significant main effect of probability, $F(1, 19) = 91.88$, $MSE = 8.70$, $p < .001$, a significant main effect of orientation, $F(8, 152) = 4.30$, $MSE = 6.41$, $p < .001$, and a significant two-way interaction, $F(8, 152) = 4.34$, $MSE = 7.42$, $p < .001$. One-way ANOVAs were run on each of the two probability conditions separately, both of which revealed a significant quadratic trend for stimulus orientation, (ps $<.05$). As Figure 6b demonstrates, the kurtosis for the high-probability vertical tilts was the highest.

Poststudy questionnaire. None of the 20 participants were able to accurately describe the location-orientation conjunctions.

Discussion

Orientation probability affects participants' estimation performance. Participants were both faster and more precise in estimating probable tilts. These are unlikely due to repetition effects given the lack of correlation between intertrial differences in orientation and performance. Consistent with Anderson (2014), the distribution of estimation errors from high-probability trials also demonstrated increased kurtosis. Near-vertical orientations are also associated with higher kurtosis than other orientations, which, assuming kurtosis is capturing changes in perceptual precision, is consistent with the idea that cardinal orientations might be perceived better (Appelle, 1972). The vertical bias observed suggests that participants perceive orientation as more vertical than it is, despite the default orientation of the response line always being horizontal: It could be that there is something privileged about vertical orientations. Insofar as these orientation anisotropies are reflecting perceptual biases, that probability might modulate them is consistent with the suggestion that probability effects also occur due to changes in perception in response to acquired experience.

Differences in perception across probability conditions can parsimoniously account for both precision and RT effects. Poor precision in the low-probability cases could be due to perceptual information being not as well-encoded as it is for high-probability tilts. Poorer encoding would also be expected to cause uncertainty in participants' estimations, and on low-probability trials, participants take longer to *start* making their estimation, make more vacillations, and are slower to *confirm* their responses. The uncertainty associated with low-probability tilts is likely implicit: Participants do not report seeing any probability distribution, much less provide accurate descriptions.

Experiment 1b

To further examine whether probability effects are implicit, we repeated the design of Experiment 1a, but now had participants explicitly report how *confident* they were of their estimations.

Method

Twenty additional students (9 male, 11 female) took part in Experiment 1b. Nineteen participants used their right hand and one used their left. All participants had normal or corrected-to-normal vision, were not color-blind, and did not have any known auditory deficits.

The procedure was similar to that of Experiment 1a, save for one critical difference: *Before* participants were given the auditory feedback, there was a separate screen where participants were instructed to control a horizontal slider to make a confidence judgment. Using the same three keyboard buttons, participants could move the slider (that always began with a default value of 50), either toward the left ("Completely Unsure," value of 0), or toward the right ("Completely Sure," value of 100). The time participants took to make the confidence judgment was recorded as well.

Results

Estimation task analysis. There was a significant effect of RT, $t(19) = 2.66$, $p = .015$, with high-probability tilts ($M = 1,370$ ms, $SD = 370$ ms) estimated faster than low-probability tilts ($M = 1,430$ ms, $SD = 370$ ms). There was a significant effect of IT, $t(19) = 4.70$, $p < .001$, with less time taken to start estimating high-probability tilts ($M = 230$ ms, $SD = 110$ ms) than low-probability tilts ($M = 260$ ms, $SD = 120$ ms). There was no significant effect of MT, $t(19) = 1.40$, $p = .177$, and no significant effect of vacillations, $t(19) = 1.42$, $p = .172$, though the direction of effects was consistent with Experiment 1a.

For the mean angular error measure, the effect of probability was again significant, $t(19) = 3.53$, $p = .002$, with high-probability tilts being associated with smaller errors ($M = 11.0°$, $SD = 4.1°$) than low-probability tilts ($M = 12.3°$, $SD = 4.7°$). High probability tilts ($M = -1.60$, $SD = 3.58$) were marginally biased toward the vertical, $t(19) = 1.98$, $p = .062$. Low probability tilts ($M = -1.35$, $SD = 3.61$) were not, $t(19) = 1.68$, $p = .109$. There was no significant difference in bias between the probability conditions, $t(19) = 0.514$, $p = .613$.

Examining the kurtosis as in Experiment 1a, the two-way ANOVA across the 2 levels of probability and 9 levels of orientation again revealed a significant main effect of probability, $F(1, 19) = 147.9$, $MSE = 6.3$, $p < .001$, a significant main effect of orientation, $F(8, 152) = 6.3$, $MSE = 10.9$, $p < .001$, and a significant two-way interaction, $F(8, 152) = 3.9$, $MSE = 9.7$, $p < .001$. Similar to Experiment 1a, the probability effect in the kurtosis measure was already present within the 1st 50 trials, $t(19) = 2.36$, $p = .029$.

Confidence analysis. 14 out of 20 participants demonstrated a significant ($p < .05$) correlation between their estimation errors and reported confidence values (*mean* $r = -.35$, $SD = .20$), with smaller confidence being associated with larger errors. Participants only reported low confidence when their performance was especially bad: Taking into account only those trials where the errors was less than 24°, the relation between confidence and error was at chance: Only two participants showed a significant correlation (M $r = -.12$, $SD = .12$), despite these data accounting for 91.5% of the trials. Running a two-tailed paired t test on the confidence reports across the probability conditions revealed no significant difference in either the reported confidence value, $t(19) = 1.13$, $p = .274$, or the time taken to report the confidence, $t(19) = 1.68$, $p = .110$. Confidence reports or time to report confidence did not systematically vary as a function of orientation or as the experiment progressed (all ps $> .05$).

To further evaluate if the kurtosis differences were related to low confidence we binned trials based on confidence percentiles and examined the distribution of angular errors for each confidence bin (Figure 7). Even in the lowest confidence bin,

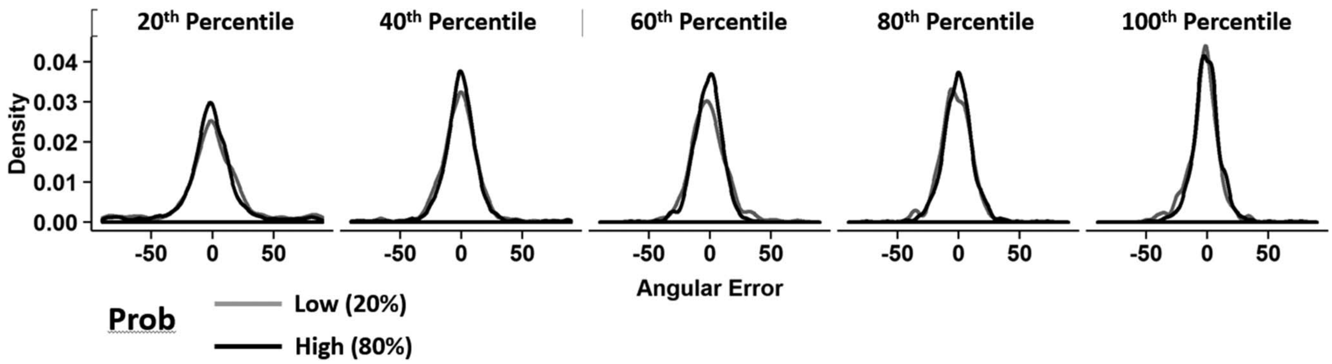

Figure 7. Error distributions by percentile confidence values. High-probability tilts are consistently associated with higher kurtosis than low-probability tilts. No interaction is observed between probability and confidence. Even at low-confidence values (20th percentile), the distribution of errors is not uniform.

the distribution of angular errors was nonuniform: The kurtosis for the high-probability ($M = 4.46$) and low-probability ($M = 1.04$) orientations for these low-confidence estimations was not only significantly different from each other, $t(19) = 3.56$, $p = .001$, but were also *both* significantly ($ps < .001$) different from a uniform distributions' kurtosis of -3. A uniform distribution is what one would expect if participants had been simply guessing.

Poststudy questionnaire. In the questionnaire, none of the 20 participants accurately described the distribution of orientations.

Discussion

The data from Experiment 1b replicates Experiment 1a. Despite being unable to report the probability distributions, participants were faster and more precise in estimating high probability tilts over low probability tilts. Differences in kurtosis were again seen across the probability conditions, and high-probability vertical tilts again had the highest kurtosis. The main departure of this data set from Experiment 1a's was that there was no significant probability-related difference in the time used to make the movements or amount of vacillations. As the trends were in the same direction, this may simply be Type 2 error or it may be that the presence of the confidence scale caused participants to be more deliberate. Regardless, the time taken to initiate movement was significantly different, indicating that these participants were also more uncertain when estimating low-probability tilts.

Although confidence was correlated to precision, this was mainly due to trials with large errors (>24°). Other studies have assumed that guessing results in a uniform distribution of errors (Liu & Becker, 2013; Zhang & Luck, 2008): These studies also involve the presentation of multiple stimuli, with nontarget features likely interfering with the encoding and report of the target (Brady & Alvarez, 2011). In the studies reported here, participants are only exposed to one stimulus at a time, resulting in a strong possibility that at least *some* of the perceptual information would be encoded. The confidence reports obtained in Experiment 1b directly indicates that "guesses" in this context are nonrandom: Even in cases with the lowest reported certainty, estimations are not uniformly distributed. Participants still favor the displayed orientation when they report being uncertain, and still show the probability effect in these instances.

The finding that probability effects on perceptual estimations of orientation are implicit (postquestionnaire) and inaccessible (confidence measure) is in keeping with data on statistical learning. Cosman and Vecera (2014) suggest that capacity-limited working memory representations are not required to acquire statistical information, at least in some cases (cf. Downing, 2000). It has also been suggested that stimulus probabilities can be acquired rapidly and without much effort (Estes, 1964; Hasher & Zacks, 1984). In simple detection studies, approximately 10 target instances are sufficient for the probability effect to be fully realized (Hon et al., 2013). Probability effects in the more complex orientation estimation task also manifest very quickly, being observable both in RT and in precision measures within the first hundred trials despite participants being unable to report the probability distributions at the end of the task.

As in Experiment 1a, Experiment 1b suggested an interaction between probability and orientation: Participants were especially precise in estimating high-probability vertical orientations. This might be an expected outcome if these effects both have their bases in perceptual mechanisms. If probability directly affects perceptual mechanisms without requiring deliberate learning by the participants, it might explain how probability can affect behavior without participants being able to explicitly report a probability difference. However, it has been suggested that contextual probability effects have to be preceded by explicit, deliberative, learning before it can affect task performance, at least in visual search (Cort & Anderson, 2013). To examine how flexible perceptual learning and changes can be in the orientation estimation task, we conducted Experiment 2.

Experiment 2

To clarify whether context-sensitivity for probability exists in the orientation estimation task, we introduced orientation-location conjunctions that were conditional on a nontarget object. Some participants saw left-tilting orientations more frequently on the right side and right-tilting more on the left, but only when the fixation symbol was presented in cyan, and not magenta. All orientations were equiprobable in both possible locations. Learning these conditional relations required the ability to flexibly acquire and utilize contextual probability information that could not be explained away as learning of location-specific probability distributions.

Method

Twenty participants (17 females, 3 males) took part in Experiment 2. They did not take part in the previous experiments. Sixteen participants used their right hand and four used their left. All participants had normal or corrected-to-normal vision, were not color-blind, and did not have any known auditory deficits.

The paradigm used was similar to Experiment 1's, except that the probability distribution was made conditional on the color of the fixation symbol. Half the participants saw the distribution depicted in Figure 8a. When the central fixation symbol was presented in magenta, left-positioned Gabors would be more likely to be left-tiling, but right-tilting would be more likely if the Gabor appeared on the right. This orientation-likelihood reversed when the fixation symbol appeared in cyan. The other half of the participants saw the reverse color-location-orientation mapping. The fixation symbol had a 50% chance to be in magenta or cyan on any given trial. Participants were not instructed on the orientation distribution or about the significance of the color cues.

Forty practice trials were given prior to the main task. The practice trials only consisted of a black fixation symbol and random location-orientation assignments. The same questionnaire was given to participants at the end of the study.

Results

Poststudy questionnaire. No participant explicitly and accurately described the probability distribution presented. No participant accurately guessed the significance of the color cue.

Cue color. Pairwise *t* tests were run across the color cue conditions (cyan or magenta) across both probability conditions. The RT, mean angular error and kurtosis measures revealed no significant effects of fixation spot color (all $ps > .05$). Additionally, trials with repeated color cues (e.g., cyan on Trial 3 and cyan on Trial 4), were contrasted with nonrepeats. There was no significant effect of color repetition on any of the measures used (all $ps > .05$). Therefore, the data were collapsed across cue color and color-probability distribution combinations.

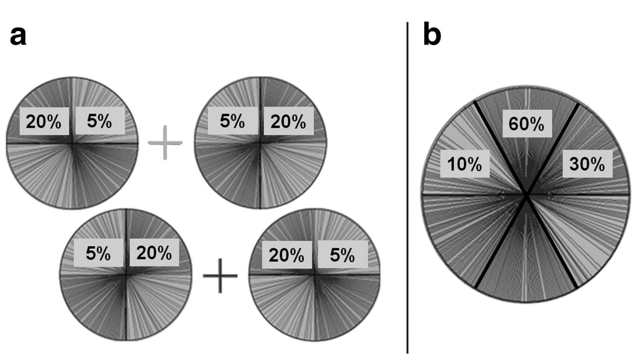

Figure 8. (a) Experiment 2 trial distribution. The fixation symbol randomly changes in color, and the location-orientation conjunction follows this color cue. This color-location-orientation mapping is reversed in half of the participants. (b) Experiment 3 trial distribution. Only centrally located Gabors were displayed. Orientation-segments were counterbalanced across participants.

Estimation data. There was a significant effect of RT, $t(19) = 2.44$, $p = .025$, with high-probability tilts ($M = 1{,}140$ ms, $SD = 230$ ms) faster estimated than low-probability tilts ($M = 1{,}180$ ms, $SD = 260$ ms). Of the 20 participants, 14 participants showed this trend, with the other participants not showing clear differences.

The mean angular error measure did not show a significant probability effect, $t(19) < 1$, $p > .05$, and neither did the standard deviation measure, $t(19) = -1.27$, $p = .220$, but the kurtosis measure did. The two-way ANOVA across the 2 levels of probability and 9 levels of orientation revealed a significant main effect of probability, $F(1, 19) = 133.4$, $MSE = 6.4$, $p < .001$, a significant main effect of orientation, $F(8, 152) = 5.5$, $MSE = 6.2$, $p < .001$, and a significant two-way interaction, $F(8, 152) = 2.5$, $MSE = 6.8$, $p = .014$. As before, one-way ANOVAs were run on each of the two probability conditions separately, both of which revealed a significant quadratic trend for stimulus orientation, ($ps < .05$). The highest kurtosis again goes to the bin consisting of near-vertical orientations, when they are high probability ($M = 5.52$, $SD = 4.85$)

Time-course. To ascertain how fast these probability effects developed, the probability effect was examined across trials. Similar to Experiment 1, probability effects were observable early in the experiment. Within the 1st 50 trials, both the RT measure, $t(19) = 2.58$, $p = .033$, and the kurtosis measure, $t(19) = 2.58$, $p = .018$ showed significant differences across the probability conditions.

Discussion

The results from Experiment 2 largely mirrored those obtained in *Experiment 1* despite the probability distribution being more complex. Participants responded faster to high-probability tilts and these probability effects manifested very quickly. Although the mean accuracy measure did not show a significant difference in precision using standard deviation or mean error measures, the kurtosis and the RT measures demonstrated the same trends seen in the previous experiments. This is the type of case that Figure 1 highlights, where a standard deviation measure fails to capture differences in the shapes of distributions that kurtosis can, and also goes to demonstrate that examining distributions are more informative than examining averages (Prinzmetal et al., 1998). Given that the shape of estimation errors reported here are non-Gaussian (Figure 5), this might explain why kurtosis proves to be a sensitive measure for detecting probability-related differences.

Experiment 2 suggests that the learning and utilization of probability information can be context-dependent. Had participants ignored the color cue, all orientations would seem to be equiprobable at both possible locations. This suggests that the probability effects cannot just depend on the rate of occurrence of orientations at a preferred location alone: It may also depend on contexts that are signaled by another object, in another location. Learning these contexts is implicit (cf. Cort & Anderson, 2013): Participants cannot indicate the significance of the color cue and its relation to the probability distribution. This is in line with the suggestion from Experiment 1 and other previous studies that probability mechanisms in general are implicit.

If probability learning mechanisms are implicit, how sensitive can they be? Studies using simple letter/number detection find graded probability effects: Small differences in probability result in observable changes at the behavioral level (e.g., Miller & Pachella, 1973). Does that level of sensitivity to visual-spatial statistical information extend to more complex probability relations?

Experiment 3

Participants' sensitivity to finer differences in orientation probability was examined in Experiment 3. Instead of having "high" and "low" probability orientations, probabilities were graded. If the implicit mechanisms behind probability effects are sensitive to fine-grained probability differences, this should be observable at the behavioral level.

Method

Thirty-six additional participants (11 males, 25 females) were recruited. Thirty-one participants used their right hand and 5 used their left. All participants had normal or corrected-to-normal vision, were not color-blind, and did not have any known auditory deficits. The paradigm used was similar to the previous ones with two differences. The Gabors now only appeared centrally. Instead of a strict high or low probability, probabilities were segmented into *three* "chunks" and the orientations falling within each region were associated with a probability of either 10%, 30%, or 60% (Figure 8b). The orientation-to-probability associations were counterbalanced across the participants.

Results

Poststudy questionnaire. Four of the 36 participants managed to correctly report an approximate region of the highest probability tilts, for example, "Vertical directions were frequent" or "Things that look like '/' were most common." None indicated that there were three separate probability regions.

Data analyses. One-way repeated measures ANOVA on the RT measure revealed a marginally significant effect of probability, $F(2, 70) = 3.08$, $MSE = 85600$, $p = .050$. Pairwise t tests revealed this was mainly due to the difference between the 30% ($M = 1{,}290$ ms, $SD = 410$ ms) and 10% tilts ($M = 1{,}430$ ms, $SD = 530$ ms), $t(35) = 2.19$, $p = .035$, and between the 10% and the 60% tilts ($M = 1{,}270$ ms, $SD = 430$ ms), $t(35) = 2.05$, $p = .048$, with there being no significant difference between the 30% and 60% tilts, $t(35) < 1$, $p > .05$.

For angular error, one-way repeated measures ANOVA revealed a significant effect of probability, $F(2, 70) = 6.95$, $MSE = 4.63$, $p = .002$. As with the RT measure, pairwise t tests revealed this was mainly due to the difference between the 30% ($M = 8.36°$, $SD = 2.62°$) and 10% tilts ($M = 10.1°$, $SD = 4.54°$), $t(35) = 2.79$, $p = .008$, and between the 10% and the 60% tilts ($M = 8.51°$, $SD = 3.12°$), $t(35) = 3.21$, $p = .003$, with there being no significant difference between the 30% and 60% tilts, $t(35) < 1$, $p > .05$.

The results above suggest that there is a probability effect, but only between the lowest (10%) and the higher (30% and 60%) probabilities. Experiments 1 and 2 suggested a possible interplay between orientation biases and probability effects. As before, orientations were chunked into 20° bins and the kurtosis measurements calculated (Figure 9). A two-way ANOVA on this data revealed a significant main effect of probability, $F(2, 66) = 12.55$, $MSE = 41.8$, $p < .001$, a significant main effect of orientation, $F(2, 66) = 5.118$, $MSE = 41.8$, $p = .009$, and a significant interaction, $F(2, 66) = 3.55$, $MSE = 41.6$, $p = .045$. T tests were carried out to check if there was a graded effect of probability. There was a significant difference between the 30% and 10%, $t(136) = 4.91$, $p < .001$, and between the 10% and the 60%, $t(114) = 5.19$, $p < .001$, and there was now also a significant difference between the 30% and 60% tilts, $t(157) = 2.37$, $p = .019$. Within the 1st 50 trials, there was a difference in both the mean angular error, $t(35) = 2.59$, $p = .014$, and kurtosis measures of precision, $t(35) = 5.6$, $p < .001$, between the highest and lowest probabilities.

Discussion

As in Experiments 1 and 2, high-probability tilts were again estimated faster and more precisely than lower-probability tilts. Although the RT and the mean angular difference measures did not show this in a graded manner, the kurtosis measure did. This is further evidence that examining the shape of error distributions might be more informative than just looking at overall accuracy. Additionally, across all measures, participants do show clear performance differences between a 10% and a 30% tilt probability, suggesting that small probability differences are observable even in complex tasks such as orientation estimations. Additionally, Experiment 3 demonstrated the interaction between tilt-probability and orientation also seen in the previous experiments. As suggested earlier, this would be expected if both the probability effect and orientation effects are perceptually based. In the General Discussion we suggest how these could be tied to the neural bases of orientation perception.

General Discussion

Probability effects are well-documented in simple detection (Hon et al., 2013; Miller & Pachella, 1973; Laberge & Tweedy, 1964) and visual search paradigms (Rich et al., 2008; Wolfe et al., 2007). The experiments reported here, as in Anderson (2014), suggest that there are robust probability effects in perceptual estimations as well: Higher-probability tilts are estimated faster *and* more precisely than are lower-probability tilts (Table 1).

The experiments presented here further examined the characteristics of probability effects in orientation estimation settings. The effects occur without participants being able to explicitly describe the probability distributions, or being more confident of making judgments of one probability class over another. The probability effects develop very quickly, being observable within only 50 to a hundred trials into an experiment. Additionally, these behavioral effects develop even when the probability distributions are complex and utilize context cues. Clearly, probability is doing something to affect the perceptual representation of the orientation. One suggestion is that probability information results in changes to how well the Gabor orientation is perceptually encoded before it goes off-screen.

Because participants are judging a stimulus that is no longer present, memory mechanisms must be involved. They do not,

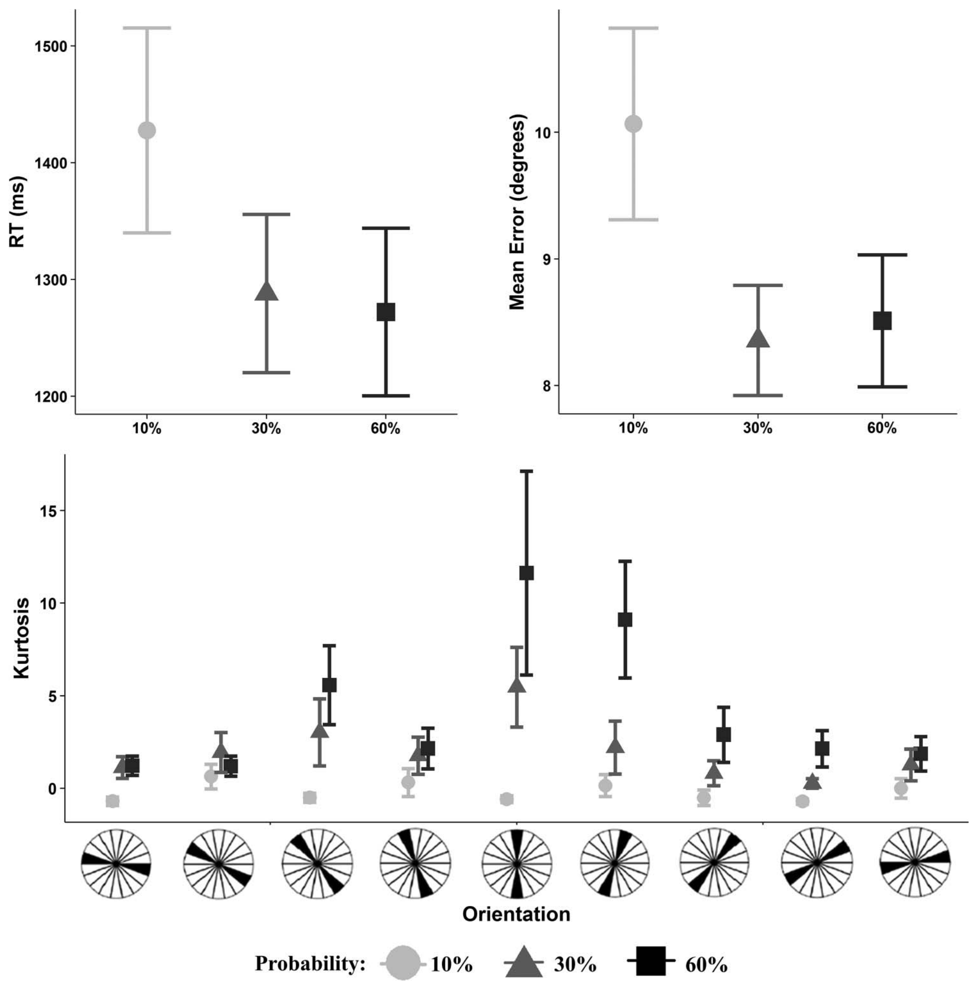

Figure 9. Estimation performance for Experiment 3. The shades of gray corresponds to probability conditions: 10% (lightest), 30%, and 60% (darkest). Error bars indicate one standard error. RT = reaction time.

however, seem to be the basis for such effects. In Anderson and Druker (2013) different delay lengths were used between the Gabor onset and when a response was possible (either 200, 400, and 600 ms). Because performance did not correlate with the length of delay, it does not seem that for the time scales used in these experiments, memory mechanisms are a likely locus for the orientation precision effects.

Could probability effects reflect differences in image persistence? Some participants did report in their questionnaires that the Gabor patches sometimes appeared brighter and for a longer duration, although they did not state which location or orientations were associated with these perceived differences. We deem it unlikely though that afterimages are an important basis for our effects. First, stimulus durations were short (60 ms), and visual

Table 1
Summary of Probability Effects Across Experiments

Measure	Exp.1a (basic)	Exp. 1b (confidence)	Exp. 2 (conditional)	Exp. 3[a] (graded)
Reaction time	$t(19) = 5.20^{***}$	$t(19) = 2.66^{*}$	$t(19) = 2.44^{*}$	$F(2, 70) = 3.08^{*}$
M angular error	$t(19) = 3.08^{**}$	$t(19) = 3.53^{**}$	$t(19) < 1$	$F(2, 70) = 6.95^{**}$
Kurtosis				
Probability	$F(1, 19) = 91.88^{***}$	$F(1, 19) = 147.9^{***}$	$F(1, 19) = 133.4^{***}$	$F(2, 66) = 12.55^{***}$
Interaction	$F(8, 152) = 4.34^{***}$	$F(8, 152) = 3.9^{***}$	$F(8, 152) = 2.5^{*}$	$F(2, 66) = 3.55^{***}$

Note. All significant probability effects: High probability tilts show faster / more precise estimates. Exp. = Experiment.
[a] Comparing across graded probabilities.
$^{*} p < .05$. $^{**} p < .01$. $^{***} p < .001$.

persistence decreases as stimulus duration decreases (Long, 1985). We used a 500-ms delay, and participants took an additional second to complete their estimations. This makes it unlikely that afterimages were present when participants completed their estimations. In addition, the response line appeared at the target location and might actually have served as a mask of sorts. Even if afterimages did persist and in some way had facilitated performance, there is no obvious reason why this persistence should track probability. If it did, we would still need some neural mechanism to explain this effect.

It is conceivable that the lateral geniculate nucleus (LGN), which provides the major input to the primary visual cortex (V1), might be responsive to orientation probability effects: Although weaker than in V1, there are signs of orientation sensitivity in the LGN (Xu, Ichida, Shostak, Bonds, & Casagrande, 2002). "Attention" might also modulate LGN neural activity, specifically relating to orientation perception (Ling, Pratte, & Tong, 2015). Given that probability manipulations could have an "attentional" locus (Hon & Tan, 2013), and that the probability effects reported here resembles the effects of spatial cuing on increasing the speed and precision of orientation estimations (Anderson & Druker, 2013), it is not a stretch to think that probability, like other "attentional" manipulations, might modulate visual processing at its earliest levels.

Compared with the LGN, V1 neuronal populations have a better-documented role in orientation perception (e.g., Ringach, Hawken, & Shapley, 1997; Hubel, Wiesel, & Stryker, 1978). V1 tuning has been implicated as a cause of orientation anisotropy (Li et al., 2003; Furmanski & Engel, 2000), and V1 has also been shown to be modulated by "attentional" manipulations (Tootell et al., 1998). In macaques, orientation tuning of neurons in the V1 region is not static, but instead changes over time (Ringach et al., 1997). In orientation training of rhesus monkeys, only V1 neurons preferring a trained orientation showed tuning changes suggesting specific increases in neuronal sensitivity with exposure (Schoups, Vogels, Qian, & Orban, 2001). Given these findings, how probability affects the perception of orientations might be because of its effects on early visual-processing activity (e.g., in V1 or LGN).

How might probability exert its effect on early visual processing? It is conceivable that neurons' orientation tuning over time varies according to the rate of occurrence of particular orientations. If this is true, then Experiment 2 demonstrates that this occurrence-dependent tuning has to be context-sensitive to nonorientation features. The data also suggests that this tuning adjustment must occur very rapidly, within 100 trials. Schoups et al. (2001) demonstrated orientation tuning changes by having monkeys practice the orientations 2,000–5,000 trials daily for several months.

Instead of neurons being tuned directly, another mechanistic possibility is that probability information weights the relative influence of subpopulations of V1 neurons that already differ in tuning width. There are laminar differences in neural tuning in the V1 cortical area, with orientation-selective cells having a larger bandwidth in layers 4C and 3B (Ringach, Shapley, & Hawken, 2002). Additionally, it has been suggested that people switch between "precise" or "coarse" modes of orientation discrimination depending on how similar or distinct the orientations are (Scolari & Serences, 2010). This, in turn, might be due to differences in reliance on off-channel versus on-channel neurons, which should benefit differently from neural tuning. Relative influence of V1 subpopulations with different tuning might be what allows one to flexibly switch between modes on a trial-by-trial basis, as would be required in Experiment 2.

Regardless of whether the sensitivity changes in feature-processing neurons happens by direct or indirect means, it is particularly elegant as an explanation for probability effects in general because it can be extended to account for probability effects in other nonorientation scenarios. For example, color probability effects might be due to changes in sensitivity in color-processing neurons, presumably in area V4 (Kotake, Morimoto, Okazaki, Fujita, & Tamura, 2009). Although suggestions about a mechanistic link between estimation performance and neural tuning differences are intriguing, it needs further exploration through either neurophysiological or computational techniques.

Another issue of interest is the finding that people are most precise for estimating near-vertical tilts. In Experiments 1 and 2, the boundaries for the high and low probability region respected the vertical. However, the horizontal was also a boundary, but near-horizontal trials did not show any increased precision. These boundaries were also not respected in Experiment 3, which still showed the increased precision for near-vertical tilts. It might be argued that the vertical precision might be because participants start off responding with a horizontal line. However, the Anderson and Druker (2013) study used a vertical start. Reanalyzing that data set (results not shown) shows the same trend: Near-vertical tilts show an increased precision. Better cardinal representations could have been due to participants using the edges of the screen as a guide, but that does not explain why verticals but not horizontals are privileged. Rather than being a task-related artifact, these effects likely reflect preexisting orientation biases (Appelle, 1972), possibly due to differences in V1 neural sensitivity/tuning (Li et al., 2003).

Although detection tasks might be more related to real-world tasks where the increased miss-rates of rare targets are an issue, for example, in security (Wolfe et al., 2007; Lau & Huang, 2010) and in medical screenings (Evans, Tambouret, Evered, Wilbur, & Wolfe, 2011), more direct measures of perception can do more to highlight possible mechanisms underlying the effect. For example, probability effects observed in this and other studies could be described as being "attentional" (Posner, 1980) in nature. Performance benefits due to orientation probability mirrored those obtained from exogenous cuing (Anderson & Druker, 2013), and facilitation effects from cuing are modulated by cue-predictivity: A cue that is only 70% predictive of target locations causes less facilitation than a fully predictive one (Eriksen & Yeh, 1985). Probability effects also interact with attentional manipulations (Hon & Tan, 2013). These findings suggest that acquired information on when stimuli are going to occur does elicit attentional *effects*. However, using "attention" as a *causal* mechanism unnecessarily clouds a deeper understanding of *how* stimulus probabilities affect performance (Anderson, 2011).

Instead, the orientation estimation task used in this study provides us with clues on how probability affects perception. Orientations that are probable are estimated faster and more accurately. Data obtained from the task also allowed us to look at the "shape" of the error distributions more closely via a measure of kurtosis. We find that probability shapes the outcome of perceptual estimations, sometimes in ways that cannot be captured by traditional measures of precision. Probability-related precision increases also seems to compound for orientations that might already be perceptually privileged (e.g., vertical orientations), further suggesting that probability affects perception. The neural mechanism behind such probability effects is uncertain, although it seems likely that acquired information about stimulus probability might affect the sensitivity of the neural populations that code for the relevant perceptual features.

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