# Orienting to probable stimuli increases speed, precision, and kurtosis. A study in perceptual estimation.

by

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Running Head: Orienting to Probability

## **Author Declaration**

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners. I understand that my thesis may be made electronically available to the public.

Running Head: Orienting to Probability

#### **Abstract**

Stimulus probabilities affect detection performance. Rare targets, even in security or medical screenings, are missed more often than frequent ones. To minimize such probability-related costs, there is a need to understand how probability effects develop and how they might interact with perceptual processes. A previous experiment demonstrated that estimates of Gabor orientations were more precise on trials where the Gabor location was exogenously cued. Exogenous cues might be biasing perceptual processing towards the features in the cued location, and enhancing the perceptual representations of the target. Here, the same "attentional" effects were replicated without the use of explicit cues. Instead, different location-orientation conjunctions occurred with different probabilities. Across different probability distributions, it was consistently observed that participants rapidly developed faster and more precise estimations for higher-probability tilts. This occurred despite participants not being instructed on the underlying probability distributions, despite participants not being able to indicate confidence differences (Experiment 1b), despite the probability distribution being complex (Experiment 2), and despite probability differences being fine-grained (Experiment 3). High-probability tilts were also consistently associated with a distribution of angular errors that were more kurtotic than for low-probability tilts. Mixture model analyses suggested that these kurtosis differences reflect a mix of 'precise' and 'coarse' estimations, with high-probability tilts being associated with more of the former. Additionally, near-vertical orientations were associated with an increased kurtosis, particularly when vertical tilts were probable. Similar to mechanisms underlying perceptual biases, these findings suggest that acquired information might be affecting neural sensitivity to result in better-encoded perceptual representations for high-probability tilts.

## Acknowledgements

This work was done under the exceptional supervision of Dr. Britt Anderson, whose expertise and experience in the topic was essential in the research that went into this thesis. I'd also like to especially thank my fellow lab member Alex Filipowicz, whose interest in this research has been a major motivation in making this work what it is. Gratitude also goes to lab member Christie Haskell for her invaluable technical expertise, and to undergraduate research assistant Sarah Gibbon for her help on collecting the data for the confidence measure experiment. Part of this thesis was presented at Vision Science Society (VSS) 2014. This research is supported by NSERC grant 114545.

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#### Introduction

The frequency of occurrence of stimuli affects detection performance in many real-word tasks. Rare targets are less likely to be detected, even in security (Wolfe et al., 2007, Lau & Huang, 2010), and in medical (Evans et al., 2011) screenings, resulting in severe detectionrelated costs. To minimize this, there is a need to understand the cause of such probability effects. Numerous studies implicate probability as affecting the mechanisms that governs perception (Biederman & Zachary, 1970; Dykes & Pascal, 1981; Lau & Huang, 2010). This idea is supported by studies finding that probability manipulations interact with low-level perceptual manipulations, such as stimulus contrast (e.g. Miller & Pachella, 1973). However, given that labbased studies of this phenomena mainly utilize simple symbol or feature detection (Hon, Yap & Jabar, 2013; Miller & Pachella, 1973; Laberge, & Tweedy, 1964), or visual search (Rich et al., 2008; Wolfe et al., 2007), accuracy measures boil down to some averaging of binary responses: On any single trial, participants are only required to indicate whether a target is present (or absent). On the other hand, if stimulus probability was truly affecting the perceptual processing pathways in some fashion, then more direct measurements on how participants perceive objects of differing prevalence could aid in elucidating the nature of the effect.

Such measurements might be obtained from an orientation estimation task, where participants view an oriented stimulus, and are then asked to reproduce its tilt. A continuous measure of angular errors – the difference between the estimate and the presented orientation – can be obtained on a trial-by-trial basis. Exogenous cuing can be studied in such tasks by having a single Gabor patch (Methods, *Experiment 1a*) appear on either the left or right, and having the same or different location cued. Data from this task mirrors the classic Posner (1980) findings:

Participants are both faster and more precise in estimating the orientation of a Gabor when its location was cued (Anderson & Druker, 2013). The same Posner-described "attentional shift" pattern can be obtained without the use of exogenous cues by having regularities in the distribution of spatial-orientations. Left-tilting spatial Gabors could be made more likely to occur on the left, but right-tilting made more likely on the right. These location-orientation conjunctions can be counterbalanced across participants. Using this method, Anderson (submitted) found that participants were both faster and more precise in estimating the high-probability tilts over the low-probability ones. High-probability tilts were also associated with a distribution of angular errors that had an increased kurtosis over the one for low-probability tilts.

This paper seeks to extend those findings on orientation probability. Although the idea of inferring mechanisms based on the distribution of responses is not without precedent (see Prinzmetal, 1997), there is a need to further examine *how* these kurtosis differences might come about in response to probability differences. The kurtosis of a distribution is the standardized fourth population moment about the mean. Mathematically, it can be represented as:

$$Kurtosis = \frac{\Sigma_i (X_i - \bar{X})^4 / n}{(\Sigma_i (X_i - \bar{X})^2 / n)^2}$$

where n is the number of samples in the distribution,  $X_i$  are the individual observations, and  $\bar{X}$  is the sample mean (DeCarlo, 1997). The kurtosis of normal distributions – or gaussians – is always constant regardless of their mean or variance: they have a kurtosis of three (typically standardized as an *excess* kurtosis of zero). While it is common to assume distributions to be normal, the error distributions from Anderson's estimation task are *not*. However, kurtosis differences can arise as a result of differences in the *mixing* of gaussians. Mathematically, if a

distribution is made up of gaussian components differing in variances, kurtosis differences can be induced by differences in the mixing proportions of those gaussians (*Figure 1*).

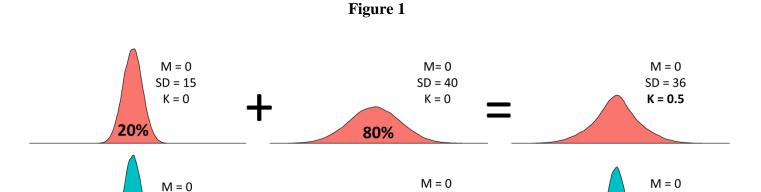
Kurtosis differences in the estimation task could be reflecting some difference in component mixing between probability distributions. Mixture models have been used in memory research to account for differences in performance. For instance, to examine data from a colour recall task, Zhang & Luck (2008) used a mixture model on the distribution of colour judgement errors participants made. This enabled them to disentangle trials where the item to be reported was in memory, from guess trials where the item was not in memory. Similarly, a mixture model could uncover systematic differences in trial types across high and low-probability tilt estimations.

Referring to  $Figure\ I$ , if the green mixture is analysed, the optimal fit should indicate a mix of 80% narrow gaussians (M=0, SD=15) and 20% of a wide gaussian (M=0, SD=40). The red mixture fit should indicate the same components, but the reverse proportions (20% narrow and 80% wide). If the error distributions of high-probability tilts are indeed associated with a higher kurtosis, computationally, it could be the direct result of there being a higher proportion of gaussians with a small variance contributing to the high-probability error distribution, compared to the low-probability distribution. Hypothetically, systematic differences in the mixing of these two components could represent differences in the proportions of 'precise' trials where the stimulus information was well-encoded (resulting in a smaller variance), versus 'coarse' trials (larger variance) where the information was not as well-encoded.

SD = 15

K= 0

80%



20%

SD = 40

K = 0

SD = 22

K = 3.5

Figure 1. Example of component mixing. Different mixing proportions of narrow gaussians (column 1) and wide gaussians (column 2) identical in means (M) and standard deviations (SD) can result in mixed distributions (column 3) with fundamentally different values of excess kurtosis (K). The Anderson study suggested that the distribution associated with low-probabilities is associated with a lower kurtosis, while the one for high-probabilities is associated with a higher kurtosis. If true, a mixture model should suggest that the high-probability distribution might be due to a greater mix of narrow gaussians than wide gaussians (blue scenario) to result in a high kurtosis, while the opposite might be true for low-probabilities (red scenario).

Note: Gaussians always have an excess kurtosis of zero.

The Anderson study also differed from traditional detection tasks in the complexity of the probability distribution used. Probability was based on *conjunctions* of location and orientations (e.g., left-titling more likely only on the left side, etc.), yet participants showed clear probability effects. What are the limits of participants' ability to acquire probability information? This was examined in *Experiment 2* by introducing *conditional* feature conjunctions. For example, left-titling was more likely only on the left side, but only when the fixation symbol was cyan. Probability information of such complex conjunctions would likely be too demanding for participants to deliberately use, let alone learn. Instead, finding probability effects in such an instance would support the idea that the learning of spatial-featural configurations can occur without the need for explicit processing (Chun & Jiang, 1998; Cosman & Vecera, 2014).

If probability learning is implicit, it is of interest to examine how sensitive the learning mechanisms can be. Are changes induced by exposure to probability information all-or-none, or can they be varied in a graded manner? Probability studies utilizing symbol detection suggest the later: There is a degree of fine-grained sensitivity to probability information, since small differences in stimulus probability can result in observable changes at the behavioural level (Hon & Jabar, submitted; Miller & Pachella, 1973). If probability effects across tasks are due to the same fundamental mechanisms, this sensitivity should be observable in orientation estimations as well. This was examined in *Experiment 3*.

What might those fundamental mechanisms be? A common account of probability effects is that, because they are more expected, higher probability targets enjoy a perceptual advantage (Biederman & Zachary, 1970; Miller & Pachella, 1973; Orenstein, 1970; Dykes & Pascal, 1981). While probability has to affect perception at some level, studies have reported mixed results

about the interaction between probability and low-level perception (De Jong & Sanders, 1986; Miller & Pachella, 1976; Pachella & Miller, 1976). Perceptual manipulations used in such studies typically involve contrast reduction or reducing discriminability of the target through the use of flankers (see Orenstein, 1970). However, people – and non-human animals – do have clear perceptual biases in their orientation judgements: Across a range of tasks, e.g., discrimination, detection, recognition, etc., observers tend perceive cardinal directions (vertical and horizontal) more precisely than oblique orientations (Appelle, 1972). Neurophysiological investigations into the "oblique effect" have suggested that orientation-selective simple V1 neurons have different tuning widths based on what their preferred direction is (Li, Peterson & Freeman, 2003), at least in cats. Human cortical V1 activation differences are also observable in fMRI, when comparing perceptions of cardinal versus oblique orientations (Furmanski & Engel, 2000). This oblique effect can be reduced by aligning the oblique stimuli to cardinal direction through head-tilting (Higgins & Stultz, 1948), supporting the idea of a locus in retinotopically-aligned V1 neurons.

In an orientation estimation task, these orientation biases and their possible interactions with orientation probability could be concurrently studied, which could point towards a neural locus of probability effects. As seen in *Figure 2*, the tuning curve of an orientation-selective neuron would indicate how sensitive it is to orientations deviating from its preferred direction. The broader the tuning curve is, the greater the range of orientations it will be sensitive to. If orientation effects are the result of sensitivity differences across orientations, then a finding that probability effects differ as a function of orientation might further suggest possible mechanisms for probability effects: It could fundamentally also be due to sensitivity changes to neurons relevant to processing of the target features.

Figure 2

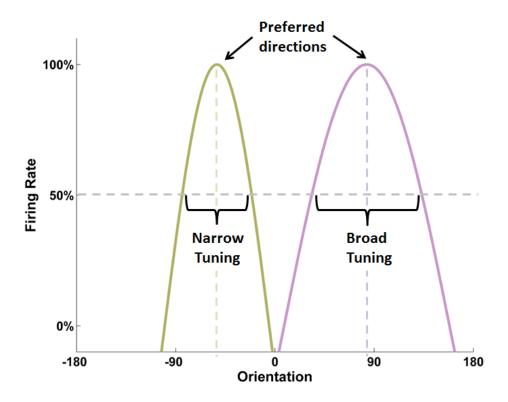


Figure 2. Example of tuning curves in orientation-selective neurons. Neurons with broader tuning curves (purple) fire to a greater range of possible stimulus orientations deviating from its preferred direction.

#### **Experiment 1a**

Experiment 1a was a replication of Anderson's study on probability cuing. Not only was this to serve as a foundation for the later experiments, but it was also intended as a means to probe the orientation probability effect with additional analyses. Given Anderson's findings, it was expected that participants would demonstrate faster and more precise estimations for the higher-probability tilts. These tilts should also be associated with an error distribution that demonstrated increased kurtosis over the one for low-probability tilts. The mixture hypothesis (Figure 1) should suggest that the higher-probability distribution would be comprised of more narrow gaussians than in the lower-probability distribution. By subjecting the error distributions from the orientation estimation task to a mixture model analysis, this hypothesis was examined.

Data from orientation estimation tasks also allows us to probe the issue of whether there are systematic biases in orientation. If probability affects how sensitive participants become to the different tilts, this might interact with pre-existing sensitivities to certain tilts (e.g., to cardinal directions). Since the "oblique effect" has been suggested, in part, to be due to neural tuning differences, variations in probability effects across orientations might indicate a similar locus: Orientation probability could be affecting the tuning functions of orientation-selective V1 neurons. This potential interaction was probed for in *Experiment 1a*, and was replicated in the three experiments that follow.

#### Methods

#### **Participants**

Twenty undergraduate students from the University of Waterloo (9 females, 11 males) took part in the study in exchange for credits in their psychology classes. 17 participants were right-handed and 3 were left-handed. All participants had normal or corrected-to-normal vision, were not colour-blind, and did not declare any auditory deficits. This study was approved by the Departmental Ethics Review Committee (ORE #19255).

#### Stimuli

Oriented spatial Gabors were presented to participants on each trial. These were grayscale sine-wave gratings with a circular gaussian mask (see *Figure 3*). The Gabors had a spatial frequency of 4 cycles per degree of visual angle, and were presented on a grey background. When viewed from a distance of 60cm, the Gabors subtended approximately 4 degrees of visual angle both vertically and horizontally. On any given trial, the center of the Gabor was located 4 degrees either to the left or right of the centre 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.

Figure 3

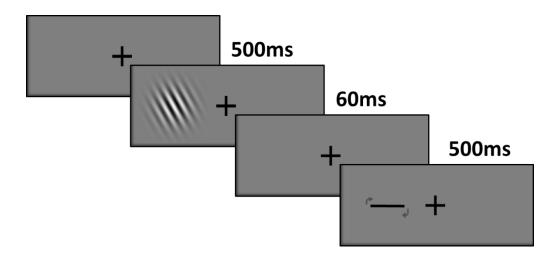


Figure 3. Experiment paradigm. On each trial of the task, participants began by looking at the fixation symbol for 500ms. The spatial Gabor then appears in one of the two locations (left or right) for 60ms, and then went off-screen. After a delay period of 500ms, a horizontal line is drawn onscreen, and participants are to rotate this line to best match their perception of the orientation of the Gabor.

Spatial Gabors were equally likely to appear on the left or right of the fixation symbol. Across these two locations, any orientation was equally likely. The critical manipulation was the occurrence-rate of the various probability-location conjunctions. For instance, half the participants saw the conjunction depicted in *Figure 4*: When a Gabor appeared on the left, its orientation was more likely (80% of the time) to be left-tilting, but this high-probability tilt is reversed if the Gabor appeared on the right. The lines in *Figure 4* 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. Participants were *not* informed about these probability distributions. The location-orientation conjunctions were counterbalanced across participants.

Auditory feedback was given at the end of each trial to encourage participants to be accurate. A high pitched sound (<a href="http://www.freesound.org/people/HardPCM/sounds/32950/">http://www.freesound.org/people/HardPCM/sounds/32950/</a>) indicated they were at or below an error threshold (12 degrees), while a lower pitched sound (<a href="http://www.freesound.org/people/tombola/sounds/49219/">http://www.freesound.org/people/tombola/sounds/49219/</a>) indicated that they were above this threshold. Participants were not explicitly told what this threshold was.

Figure 4

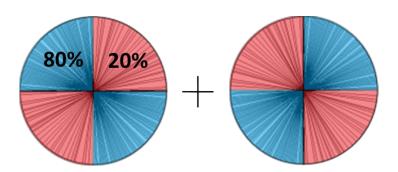


Figure 4. Experiment 1 trial distribution. Half the participants saw that 80% of the time, when Gabors appear on the left, it will have a left-tilting orientation (blue: high-probability region), and reversed on the right. The other half of the participants saw the opposite pattern. The lines within the coloured regions show the actual orientations that the first participant saw.

Procedure

Participants sat approximately 60 cm from a 32 cm x 24 cm gamma-corrected CRT monitor that refreshed at 89Hz. Responses were made with a computer keyboard using their dominant hand. The experiments were programmed in Python using the PsychoPy library (Peirce, 2009). Participants were instructed to look at the center of the screen throughout the experiment. Eye movements were not recorded.

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 occur completely randomly. An experimenter was present for these practice trials. The main task consisted of 400 trials, which were sectioned into two blocks. Participants were given the option to take a break inbetween the blocks. At the end of the computerised task, participants were given a short questionnaire (see *Appendix A*) to examine whether they could explicitly report the probability distribution of the orientations that they saw. The experiment took approximately 20-25 minutes.

On each trial, participants were shown the fixation symbol for 500ms. The spatial Gabor then appeared in one of the two locations for 60ms, and went off-screen for 500ms. After this delay period, a horizontal line was drawn on-screen, and participants made their estimations by rotating this line counter-clockwise 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.

#### Results

All data analyses were conducted using the *R* statistical software package (*R* Development Core, 2012). Mixture model analyses were done using the "*mixtools*" *R* package (Benaglia et al., 2009). Angular errors for each trial were calculated as the difference between the Gabor orientation and the orientation of the participants' estimates. The excess kurtosis measurement was applied on these sets of angular errors through the use of the *R* "*e1071*" package. Because angular errors can range from -90 to 90 degrees, a non-biased estimation would have a mean of zero. Vertical-biased estimations, e.g., where on a particular trial, participants estimated the orientation more vertically then it should have been, were coded as negative. The bias measurement gives the average of these angular errors across trials.

To estimate the magnitude of the errors made, the mean angular error measure was taken as the average of the *absolute* value of the angular errors. 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. Unless otherwise stated, the only data excluded from the analyses were trials in which participants did not make a response within the given seven-second 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. Alpha cut-off 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 = 1080 ms, p < .001)SD = 250 ms) estimated faster than low-probability tilts (M = 1180 ms, SD = 270 ms). 19 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 highprobability 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 = 0.02): Participants made more angular adjustments for lowprobability tilts (M = 58.7 deg, SD = 8.6 deg), as compared to high-probability tilts (M = 54.9deg, SD = 8.2 deg). 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 since 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).

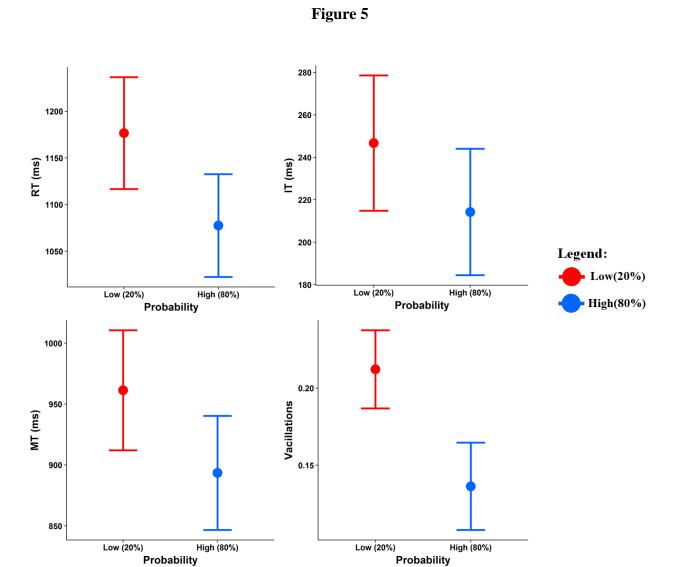


Figure 5. Reaction time and vacillation measures for Experiment 1a. RT indicates time from response line appearance to participants' confirmation. IT indicates time from appearance to first directional movement. MT indicates time from movement to confirmation. Vacillations indicate number of direction switches participants made, on average on each trial. These measures show consistent probability effects (all ps < .01) in estimations. Error bars indicate one standard error.

Angular Error Analysis

The high-probability tilts were significantly vertical-biased (t(19) = 2.66, p = 0.015), whereas low-probability tilts were not, (t(19) = 0.57, p = 0.58). Compared against each other, there was a significant effect of probability on bias, (t(19) = 2.10, p = 0.049), with high-probability tilts being more vertical-biased (M = -0.99, SD = 4.72) than low-probability tilts (M = 0.47, SD = 4.81). The mean angular error measure also reflected a significant effect of probability, (t(19) = 3.08, p = .006), with high-probability tilts associated with smaller errors (M = 12.0 deg, SD = 5.8 deg) than low-probability tilts (M = 13.3 deg, SD = 6.4 deg). Of the 20 participants, 17 showed this trend.

# Figure 6

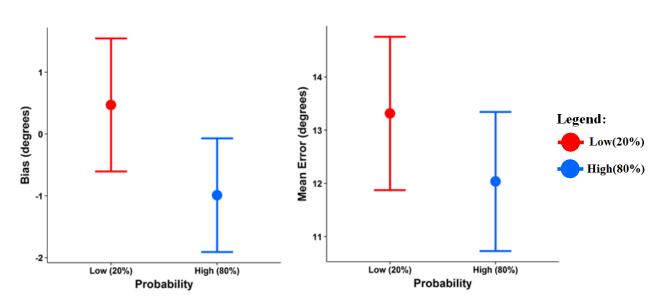


Figure 6. Angular error measures for Experiment 1a. A negative bias indicates an overestimation towards the vertical meridian. Both measures show probability effects (ps < .05). Error bars indicate one standard error.

Kurtosis Analysis

The distribution of angular errors made across trials was examined for each probability condition. *Figure 7a* shows the proportion of trials as a function of the extent of the error made (binned into increments of 10 degrees of error). A greater proportion of the high-probability trials were estimated with near-perfect precision, as compared to low-probability trials. For trials with larger errors, the proportion of high-probability trials was less than for low-probability trials. These differences in the peak and shoulders of the two distributions can be captured as a difference in their kurtoses, (t(19) = 2.11, p = .048). High-probability tilts are 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 trend, with only one participant clearly showing the opposite trend.

Because there were unequal numbers of high vs. low probability trials, additional analyses was done to ensure that the kurtosis differences observed were not due to uneven samples. Bootstrapping analyses suggested that a smaller sample size, e.g., selecting 10 or 40 instead of 400 data points from the same distribution does not systematically result in a smaller or larger kurtosis (all ps > .05). Furthermore, sampling just the final 40 high-probability trials and the final 40 low-probability trials still revealed the same effect on kurtosis (t(19) = 2.55, p < .05).

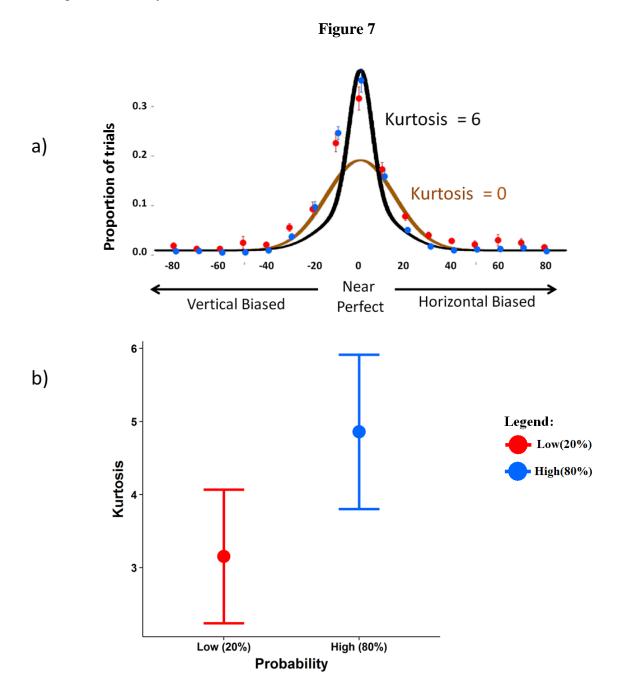


Figure 7. Kurtosis measure for Experiment 1a. Panel (a) shows the distribution of angular errors for high (blue) versus low (red) probability trials. Panel (b) shows that excess kurtosis measures on the distributions seen in panel (a) indicate high-probability tilts being associated with higher kurtosis. Error bars indicate one standard error.

Time-Course Analyses

Because there are significant effect of probability on RT and the precision measures, 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 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 = 0.877). Post hoc t-tests demonstrated a significant difference, (t(19) = 3.93, p < .001), in RT between high (M = 1157ms, SD = 338ms) and low (M = 1293ms, SD = 387ms) probability tilts in the second bin (trials 51-100). This difference was also present 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 = 0.497). 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).

# Figure 8

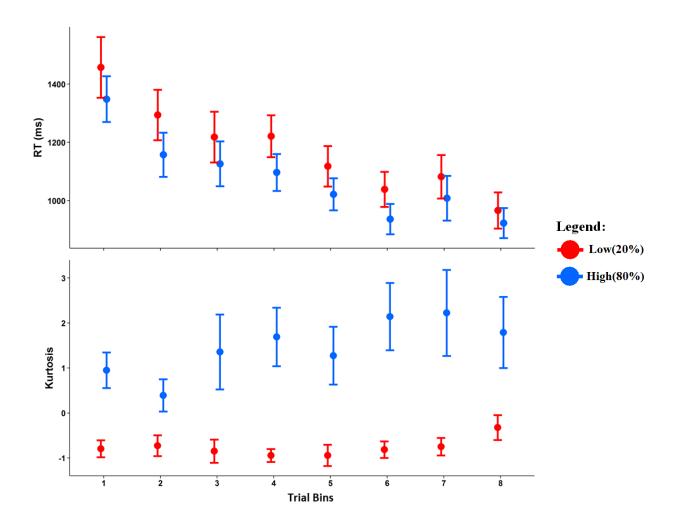


Figure 8. Development of RT and kurtosis difference across trials in *Experiment 1a*. Each bin indicates 50-trial segments. High-probability tilts are indicated by blue, low-probability by red. Error bars indicate one standard error.

#### Orientation Analysis

People demonstrate biases towards cardinal (horizontal and vertical) directions. Across tasks, these are better estimated or perceived than oblique directions (Appelle, 1972). Therefore, it was also of interest to examine if the differences in precision across the probability conditions also differ as a function of orientation.

Orientations across the 400 trials were grouped up into bins of 20 degrees, and the kurtosis measure was applied on each orientation bin of each condition of each participant. A repeated measures ANOVA across the 2 levels of probability and 9 levels of orientation revealed 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 of stimulus orientation, (ps < .05). As  $Figure\ 9$  demonstrates, the kurtosis for the high-probability vertical tilts was the highest.

#### Mixture Model Analysis

The findings on probability effects on kurtoses by Anderson were replicated, with the additional findings that these kurtosis differences developed rapidly, and were also modulated by the orientation of the Gabor. As highlighted by *Figure 1*, kurtosis differences can reflect differences in the mixing of gaussian components. This mixture hypothesis was examined by fitting the data on angular errors with a mixture model.

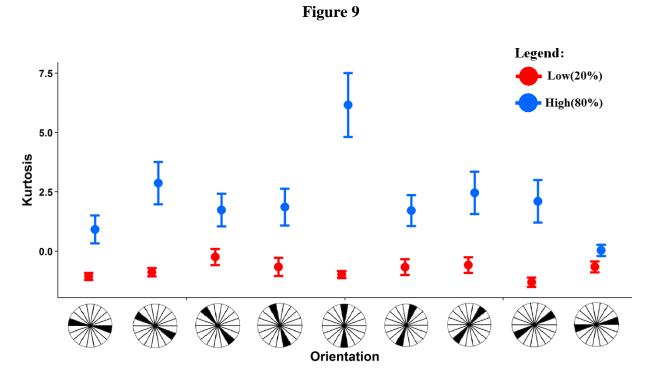


Figure 9. Interaction of probability and orientation in Experiment 1a. Each bin indicates 20-degree orientation segments (exemplified by the figures in the x-axis). High-probability tilts are indicated by blue, low-probability by red. High-probability vertical tilts are associated with the highest kurtosis. Error bars indicate one standard error.

A component selection analysis was carried out. The Akaike's information criterion (AIC), Schwartz's Bayesian information criterion (BIC), Bozdogan's consistent AIC (CAIC), and Integrated Completed Likelihood (ICL), are measures which assess the number of components that give the maximum log-like estimation, taking into account over-fitting from increasing the number of parameters. While there are minor differences in the calculations involved across these measures that could affect the optimal model, all measures reliably found a two-component model optimal, for both the high and low-probability error distributions.

The error distributions from each participant were fitted with the two-component model. The two components were free to have any mu (mean) and any sigma (standard deviation). A fifth free parameter, *lambda*, controlled the proportion of each component's contribution to the final mixture. Figure 10a illustrates the model fit (bottom panel) to participants' error distributions (top panel). Figure 10b compares the behavioural mean errors and kurtoses to that of the model output. All possible pairwise comparisons of the model to the behavioural data were non-significant (ps > .9), suggesting that the mixture model was accurately fitting the participant data. Figure 11 depicts the five parameters for each probability condition. The means of the two components of both probabilities were not significantly different from zero (all ps > .05). However, there was a clear difference between the standard deviations of the two gaussian components making up each fit: one gaussian is wider (mean sigma of 29.9 deg, SD = 15.8 deg) and the other narrower (mean sigma of 9.1 deg, SD = 4.5 deg). This difference in sigma between components is significant, (t(39) = 10.3, p < .001). As seen in Figure 11, the proportion of the narrow component was significantly higher (t(19) = 4.16, p < .001) for the high-probability tilts (M = 73.6%, SD = 34.2%), than low-probability tilts (M = 37.2%, SD = 33.8%).

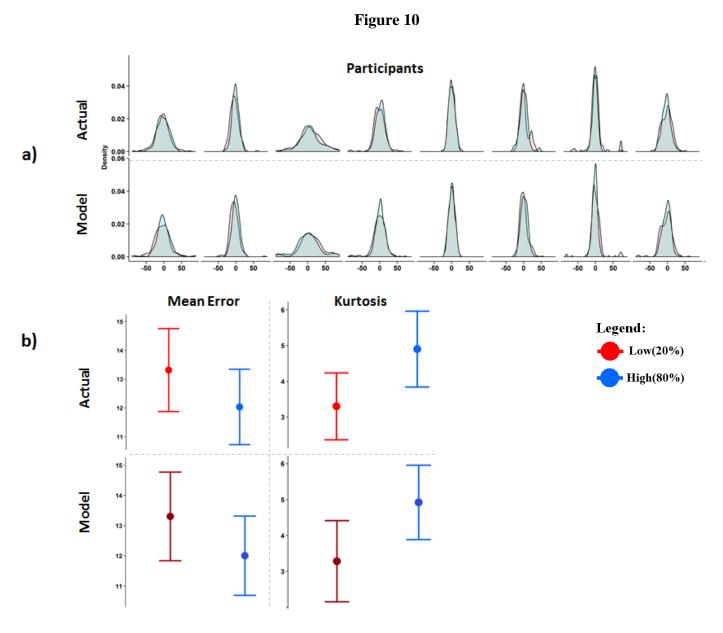


Figure 10. Mixture model fits for Experiment 1a. Panel (a) shows how the model distribution (bottom panel) fits the behavioural error distribution (top panel). X-axis: Angular Error, Y-axis: Density. Blue distributions indicate the distributions of angular errors for the high-probability trials, red for low.

Panel (b) compares the actual (top) versus the fit (bottom) measured means on mean error (left) and kurtosis (right). Red lines indicate the low-probability trials, blue for high. Error bars indicate one standard error.

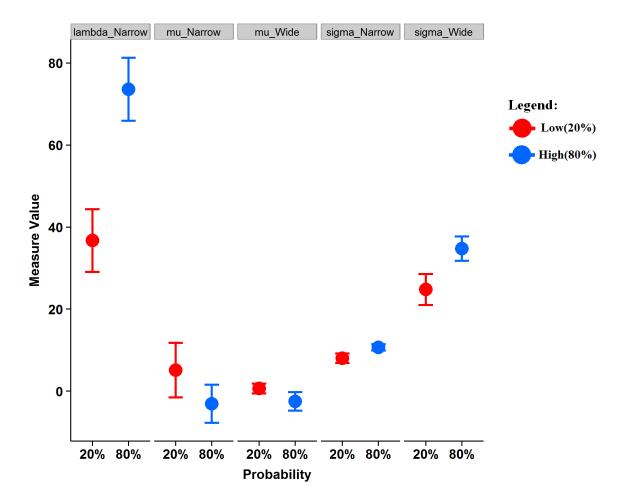


Figure 11. Optimal mixing components for Experiment 1a. Red markers indicate the low-probability trials, blue for high. The lambda measure gives the proportion of the narrow gaussian that lends to the optimal mix, and is expressed as a percentage of the final mix. The other measures (mu –mean, sigma – standard deviation) indicate the mean fits of the two components (narrow and wide) in terms of degrees. The mixture model indicates that the difference between the high and low-probability error distributions can be captured by using different mixing proportions of a narrow zero-centred gaussian and a wide zero-centred gaussian. Error bars indicate one standard error.

Post-study questionnaire

None of the 20 participants were able to accurately describe the location-orientation conjunction.

#### **Discussion**

Orientation probability affects participants' estimation performance. Participants were both faster and more precise in estimating probable tilts, as compared to the rarer tilts. This pattern of data is consistent with the Anderson study and with the vast literature on probability effects across a range of detection tasks. The findings on kurtosis differences were also replicated: The distribution of estimation errors from high-probability trials demonstrated increased kurtosis over the one for low-probability trials.

The mixture model suggested that a two-component model was optimal in representing the error distributions of high and low-probability trials, where the two components are zero-centred gaussians that significantly differed in their variances. As hypothesized, the error distributions for high-probability tilts were associated with more narrow gaussians than for low-probability trials. This simple shift in proportion between the narrow and wide gaussian components comprising the mixture was sufficient for the model to replicate the behavioural differences seen in both the mean error and kurtosis measurements. An implication of the mixture model is that there could be separate perceptual mechanisms, or 'modes', guiding perceptual estimation. One might allow for coarse estimations, leading to a wide distribution of errors. The other might allow for more precise estimations. If true, then probability information could be biasing participants to rely more on one 'mode'. The net effect of this shift in

'perceptual modes' is that for high-probability tilts, participants end up making precise judgements and smaller errors when prior experience informs them that the tilt is likely.

Differences in perception across probability conditions can parsimoniously account for probability effects both in precision and in RT. If participants rely less on the 'precise' mode for the rare tilts, the perceptual information cannot be as well-encoded as for high-probability tilts. Poorer encoding of the rarer tilts should be expected to cause imprecision: On average, low-probability tilts are associated with larger mean angular errors. Poorer encoding would also be expected to cause uncertainty in participants' estimations: Participants do show implicit signs of being more uncertain in estimating low-probability tilts, taking longer to start making their estimations. Participants also demonstrate uncertainty by making more vacillations for low-probability trials, causing them to be slower in confirming their responses.

The uncertainty associated with low-probability tilts is unlikely to stem from explicit awareness of the distribution of orientations: Participants cannot explicitly report the probability distribution. To further examine this claim, participants can be made to explicitly report how *confident* they are of their estimations on every trial. Lack of probability-related differences in confidence values for the different probability conditions would further support the notion that the mechanisms which allow for the switch in detection 'modes' acts implicitly. The interaction found between orientation and probability suggests that this mechanism involves V1 neuron tuning. *Experiment 1b* was also intended to replicate that finding.

## **Experiment 1b**

Experiment 1b was carried out to ascertain whether participants might be able to explicitly report how confident they are of their responses for high versus low-probability tilts. If the mechanism that allows for precise estimations operates explicitly, participants should show probability-related differences in confidence reports. It also served to replicate the interaction between orientation and probability seen in Experiment 1a.

#### Methods

Twenty additional students (9 male, 11 female) took part in *Experiment 1b*. 19 participants used their right hand and 1 used their left. All participants had normal or corrected-to-normal vision, were not colour-blind, and did not have any known auditory deficits.

The procedure was similar to that of *Experiment 1a*. The only difference was that *before* participants were given the auditory feedback, there was a separate screen on which participants controlled a slider to make their confidence judgements on how they think they did on that particular trial (see *Figure 12*). Using the same three keyboard buttons, they could move the continuous slider that always began with a default value of 50, either towards the left (Completely Unsure, value of 0), or towards the right (Completely Sure, value of 100). Time participants took to make the confidence judgement was recorded as well. The distribution of the Gabor orientations was identical to *Experiment 1a*.

Figure 12

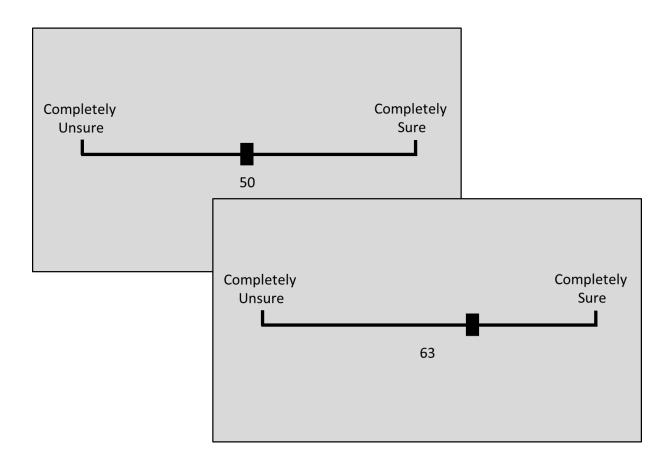


Figure 12. Confidence measure scale used in Experiment 1b. Participants control a continuous slider that by default starts at the midpoint. The central number assigns them a confidence value based on the position of the slider. Confidence analyses were carried out on these values.

## **Results**

## Estimation Task analysis

T-tests were again carried out between the high and low probability tilts on the various measures. There was a significant effect of RT, (t(19) = 2.66, p = .015), with high-probability tilts (M = 1370 ms, SD = 370 ms) faster estimated than low-probability tilts (M = 1430 ms, SD = 370 ms). There was also 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 = 230 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).

In 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 deg, SD = 4.1 deg) than low-probability tilts (M = 12.3 deg, SD = 4.7 deg). High probability tilts (M = -1.60, SD = 3.58) were marginally biased towards the vertical (t(19) = -1.98, p = 0.062). Low probability tilts (M = -1.35, SD = 3.61) were not (t(19) = -1.68, p = 0.109). There was no significant difference in bias between the probability conditions (t(19) = 0.514, t(19) = 0.613).

Examining the kurtosis measurement the same way 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 1<sup>st</sup> 50 trials, (t(19) = 2.36, p = .029).

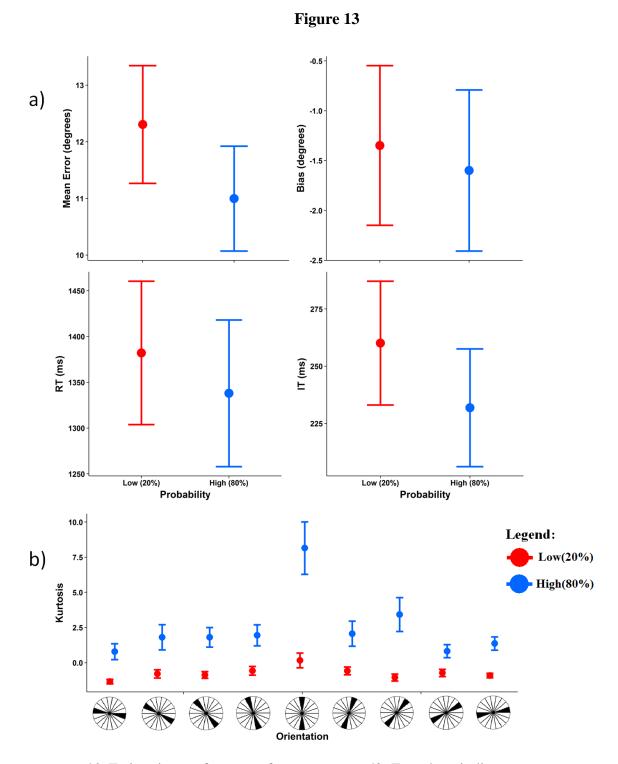


Figure 13. Estimation performance for Experiment 1b. Error bars indicate one standard error.

Confidence Analysis

There was a significant, moderately strong correlation between the estimation error and the confidence values (r = -.36, p < .001), with smaller confidence being associated with larger errors. Running a two-tailed paired t-test on the confidence reports by participants 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).

Post-study questionnaire

None of the twenty participants explicitly and accurately described the distribution of orientations.

## **Discussion**

The data from *Experiment 1b* largely replicates that of *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 the kurtosis measure were again seen across the probability conditions: High-probability vertical tilts were estimated most precisely. The main departure of this dataset from *Experiment 1a's* was that there was no difference in the time used to make the movements, with no difference in the amount of

vacillations, made between the conditions. The presence of the confidence scale might have caused them to make more deliberate movements. Regardless, the time taken to initiate movement was significantly different, indicating that these participants were also uncertain about their estimations of low-probability tilts. However, this uncertainty was not explicit. Especially considering that there was a moderately strong correlation between confidence and error made, participants' failure to demonstrate probability-based confidence differences was most likely due to them being unaware of the probability distribution.

Studies on statistical learning (e.g., Cosman & Vecera, 2014) have suggested that capacity-limited working memory representations might not be a requirement in picking up 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 simpler symbol detection studies, it seems as if ten target instances are sufficient for the probability effect to be fully-realised (Hon, Yap & Jabar, 2013; Hon & Jabar, submitted). Here, probability effects in the relatively more complex orientation estimation task also manifests very quickly, being observable both in RT and in precision measures within the first 50-100 trials. In addition to being unable to report the probability distributions at the end of the task, participants were also unable to report awareness of such probability effects taking place on a trial by-trial basis.

Probability effects are therefore likely due to implicit or passive mechanisms. What might this implicit mechanism be? Both *Experiments 1a* and *1b* highlighted an interaction between probability and orientation: Participants are especially precise in estimating high-probability vertical orientation. Given neurophysiological data suggesting different tuning widths

for different preferred-directions, it is possible that probability effects have a similar neural locus: Experience might render orientation-selective V1 neurons more or less sensitive to orientations similar to the one it prefers. Hypothetically, such a mechanism could operate implicitly if sensitivity shifts are just dependant on the rate of activation of the neurons.

However, it has been suggested that conditional probability effects have to be preceded by explicit, deliberative, learning before it can affect task performance in visual search (Cort & Anderson, 2013). As an additional test to help disambiguate between probability learning being explicit or implicit, the difficulty associated with the learning can be increased. In *Experiment 2*, the location-orientation junction from *Experiment 1* was made conditional on another feature. If the increased complexity prevents the learning and usage of probability information, it would suggest that the learning of spatial-featural regularities would have to be deliberate before probability effects manifest. On the other hand, retaining probability-sensitivity even in such instances would suggest that this learning is implicit and robust to task complexity.

## **Experiment 2**

Experiment 2 extended Experiment 1 by examining the orientation probability effect under a more complex distribution. The colour of the fixation symbol randomly alternated, and the location-orientation conjunction from Experiment 1 was made conditional on this colour cue. For example, left-titling was more likely only on the left side, but only when the fixation symbol was cyan. Given participant's inability to explicitly report the probability distribution and inability to explicitly report any probability-related confidence differences in the previous experiments, it was unlikely that participants could learn such complex relationships

deliberately. Instead, finding probability effects in *Experiment 2* would suggest that probability learning is implicit and robust.

## Methods

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 colour-blind, and did not have any known auditory deficits.

The paradigm used was similar to *Experiment 1*'s. The probability distribution was made more complex by having the tilt-location conjunction be dependent on the colour of the fixation symbol. Half the participants saw the distribution depicted in *Figure 14*. 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 colour-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 colour cues.

Forty practice trials were given prior to the main task. To prevent probability learning 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.

## Figure 14

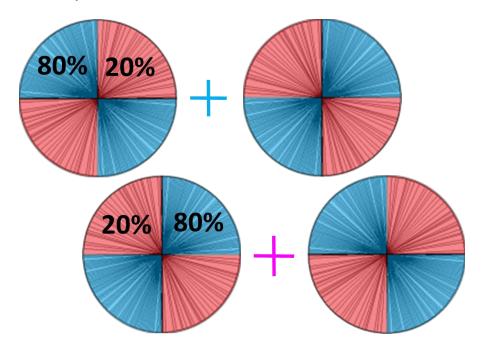


Figure 14. Experiment 2 trial distribution. The fixation symbol randomly changes in colour, and the location-orientation conjunction follows this colour cue. The lines within the shaded region show the actual orientations seen by the first participant. This colour-location-orientation mapping is reversed in half of the participants.

## **Results**

Post-study questionnaire

No participant explicitly and accurately described the probability distribution presented.

No participant attempted to guess the significance of the colour cue.

Cue Colour

Pairwise t-tests were run across the colour cue conditions (cyan or magenta) across both probability conditions. The RT, mean angular error and kurtosis measures all revealed no significant effect of colour cue (all ps > .05). Additionally, trials with colour cues repeated (e.g., cyan on trial 3 and cyan on trial 4), were contrasted with non-repeats of colour cues. There was no significant effect of colour repetition on any of the measures used, (all ps > .05). Therefore, the data were collapsed across the cue colour.

## Estimation Data

There was a significant effect of RT, (t(19) = 2.44, p = .025), with high-probability tilts (M = 1140 ms, SD = 230 ms) faster estimated than low-probability tilts (M = 1180 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 did not show a significant probability effect,  $(t(19) < 1 \ 1.88, p > 0.05)$ , 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 < 0.001), a significant main effect of orientation, (F(8,152) = 5.5, MSE = 6.2, p < 0.001), and a significant two-way interaction, (F(8,152) = 2.5, MSE = 6.8, p = 0.014).

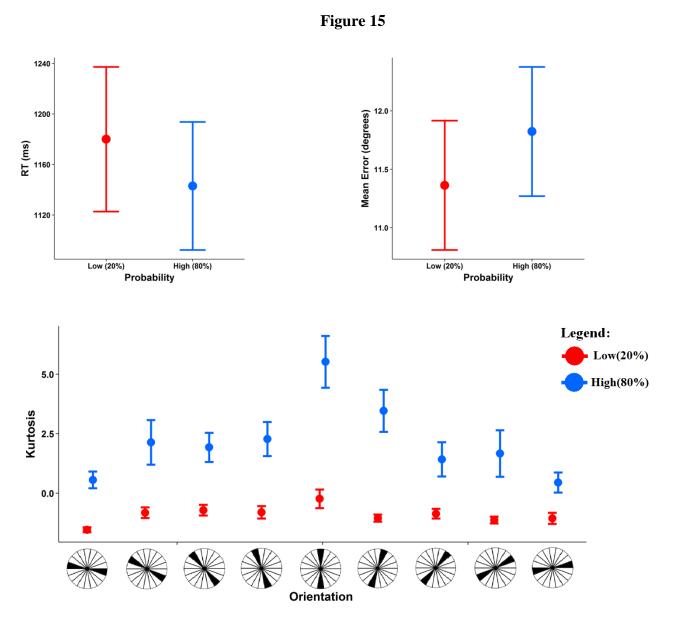


Figure 15. Estimation performance for Experiment 2. Error bars indicate one standard error.

## Time-course

To ascertain how fast these probability effects developed, the probability effect was examined across trials. Similar to *Experiment 1*, significant probability effects were observed within the 1<sup>st</sup> 50 trials for both the RT measurement, (t(19) = 2.58, p = .033), and the kurtosis measurement, (t(19) = 2.58, p = .018).

## Mixture model

The data on angular errors was fit with a mixture model. The AIC, BIC, CAIC and ICL adjusted log-likelihood analyses all suggested a two-component model was optimal for both the high and low-probability error distributions. The means of the two components for both probabilities were not significantly different from zero (all ps > .05). There was a significant difference between the variances of the two gaussian components (t(39) = 11.1, p < .001). One gaussian is wider (mean variance of 30.1 deg, SD = 15.8 deg), and the other narrower (mean variance of 9.2 deg, SD = 4.6 deg). The (lambda) proportion of the narrower gaussian was significantly higher (t(19) = 2.67, p = .015) for the high probability tilts (M = 74.8%, SD = 35.5%), than the low-probability tilts (M = 45.1%, SD = 36.4%).

Figure 16

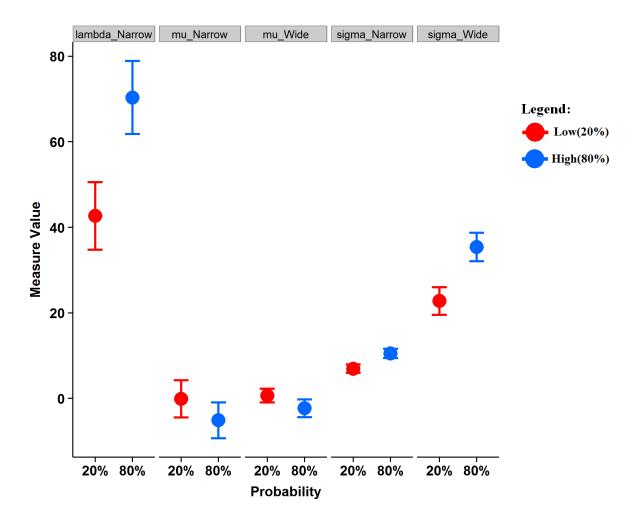


Figure 16. Optimal mixing components for Experiment 2. Red markers indicate the low-probability trials, blue for high. The lambda measure gives the proportion of the narrow gaussian that lends to the optimal mix, and is expressed as a percentage of the final mix. The other measures (mu –mean, sigma – standard deviation) indicate the mean fits of the two components (narrow and wide) in terms of degrees. The mixture model indicates that the difference between the high and low-probability error distributions can be captured by using different mixing proportions of a narrow zero-centred gaussian and a wide zero-centred gaussian. Error bars indicate one standard error.

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## **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 difference in precision, the kurtosis measure did show the same trend seen in the previous experiments. The interaction between orientation and probability was replicated, with participants being most precise for high-probability vertical tilts. The mixture model analyses again suggested a two-component model to be optimal, the difference in error distributions between the probability conditions largely resting on how these components are mixed. Had explicit or deliberate consideration of the probability information been required for one to demonstrate the probability effect, one would have expected the effect to be diminished for Experiment 2, due to the demands on the participants to keep track of the conditional probabilities. The fact that participants reliably showed the effect, coupled with the apparent inability for participants to verbalise what the probability distributions were suggests that the 'learning' of these probability distribution is largely implicit.

If probability learning mechanisms are implicit, how sensitive can they be? Probability studies using simple symbol detection find fine-grained sensitivity to probability information: Small differences in stimulus probability results in observable changes at the behavioural level (Hon & Jabar, submitted; Dykes & Pascal, 1981). Is that level of sensitivity to visual-spatial statistical information present even in a more complex task such as orientation estimations? This was investigated in *Experiment 3*, which used multiple probabilities. If the implicit mechanisms

behind probability effects are sensitive to fine-grained probability differences, this should be observable at the behavioural level.

## **Experiment 3**

Experiment 3 sought to extend the findings of Experiments 1 and 2. By using multiple probability levels, it was examined if the implicit mechanisms behind the probability effect are sensitive to fine-grained differences in probability. Furthermore, mixture model analyses were performed as a test of the hypothesis that probability affects performance by weighting the influence of one 'mode' of estimation over another. If true, the model should show that two-component fits are optimal, despite there being three distinct probability values. The only differences in error distributions across the three probability-values should be the mixing proportions of the two components.

#### **Methods**

Thirty-six participants (11 males, 25 females) took part in *Experiment 3*. They did not take part in the previous experiments. 31 participants used their right hand and 5 used their left. All participants had normal or corrected-to-normal vision, were not colour-blind, and did not have any known auditory deficits. The paradigm used was the similar, with two differences. The Gabors now only appeared centrally, in foveal vision. Instead of a strict high or low probability, probabilities were graded. This graded probability was imposed by splitting the possible orientations into *three* 'chunks' and associating the orientation falling within each region with a different probability of 10%, 30% or 60% (see *Figure 17*). The orientation-to-probability associations were counterbalanced across the participants.



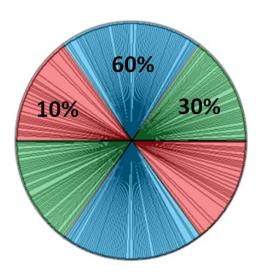


Figure 17. Experiment 3 trial distribution. Gabors appeared in the center of the display.

Orientations are divided up to fall into one of three-similarly sized regions. 60% of the orientations fell within the blue region, 30% in the green region and 10% in the red region. The order of these regions was counterbalanced across participants. The lines within the coloured regions show the actual orientations that the first participant saw.

## **Results**

# Post-study questionnaire

Four of the thirty-six participants managed to correctly report an approximate region of the highest probability tilts, e.g., "Vertical directions were most common" or "Things that look like '/' were most common". None realised 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 = 1290 ms, SD = 410 ms) and 10% (M = 1430 ms, SD = 530 ms), (t(35) = 2.19, p = .035), and between the 10% and the 60%, (M = 1270 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 suggested 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 = 8.36deg, SD = 2.62deg) and 10% (M = 10.1deg, SD = 4.54deg), (t(35) = 2.79, p = .008), and between the 10% and the 60%, (M = 8.51deg, SD = 3.12deg), (t(35) = 3.21, p = .003), with there being no significant difference between the 30% and 60%, (t(35) < 1, t(35) < 1,

The results above suggest that there is a probability effect, but only between the lowest (10%) and the higher (30% and 60%) probabilities. Given the results from *Experiment 1* and *Experiment 2* that suggested a possible interplay between orientation biases and probability

effects, this was evaluated for *Experiment 3*. As before, orientations were chunked into 20-degree bins and the kurtosis measurements calculated. *Figure 18* shows the same effects seen in *Experiments 1* and 2. 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). To see if separating out the orientations can reveal that there actually is a graded effect, t-tests were done on this set of data: 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), with there now also being a significant difference between the 30% and 60%, (t(157) = 2.37, p = .019).

To examine how fast such probability effects developed, trial bins were compared. Within the 1<sup>st</sup> 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.



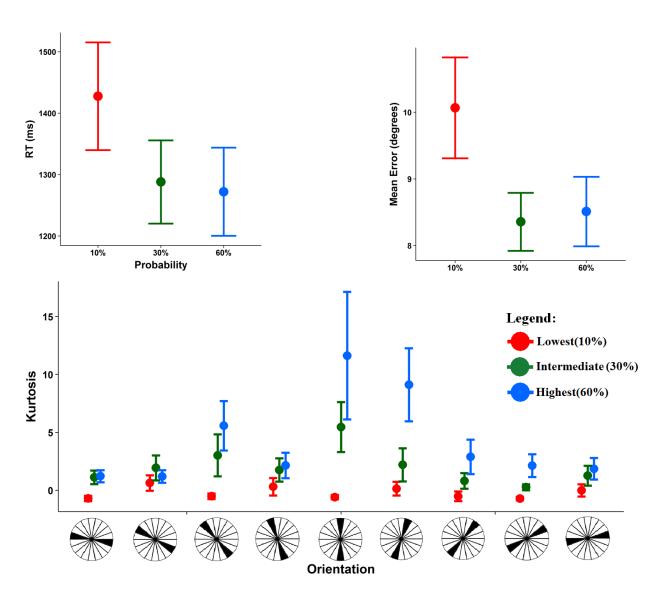


Figure 18. Estimation performance for Experiment 3. Red markers indicate the lowest probability trials (10%), green for 30% and blue for 60%. Error bars indicate one standard error.

## Mixture model

The data on angular errors from Experiment 3 was fit with a mixture model. The AIC, BIC, CAIC and ICL adjusted log-likelihood analyses all suggested that a two-component model was optimal, even though there were three probability conditions. Each distribution was fit with two components to look at mixture proportions (see Figure 19). The data from one subject was dropped from this analysis because the model algorithm could not reach a stable convergence point. There was a clear difference between the variances of the two gaussian components making up each fit: one gaussian wide (mean variance of 16.6 deg, SD = 14.0 deg) and the other narrow (mean variance of 4.7 deg, SD = 3.1 deg). This difference in the variance between components was significant, (t(104) = 10..0, p < .001). Looking at the differences in the proportion of these two components across the error distributions of the three error probabilities, a one-way repeated measure ANOVA revealed a significant effect of probability, (F(2,68) =4.21, MSE = 1129, p = .021). Paired t-tests revealed that the 10% tilts (M = 29.9%, SD = 27.3%) were associated with a significantly lower proportion of the narrower gaussian component than 30% tilts (M = 45.2%, SD = 38.9.1%) and 60% tilts (M = 55.4%, SD = 40.1%), (both ps < .05). The difference in proportion between the 60% and 30% was not significant, but did show the expected difference in direction.

Figure 19

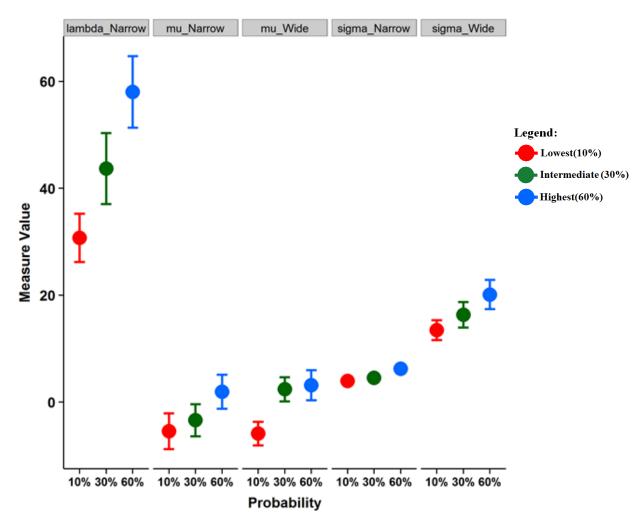


Figure 19. Optimal mixing components for Experiment 3. Red markers indicate the lowest probability trials (10%), green for 30% and blue for 60%. The lambda measure gives the proportion of the narrow gaussian that lends to the optimal mix, and is expressed as a percentage of the final mix. The other measures (mu –mean, sigma – standard deviation) indicate the mean fits of the two components (narrow and wide) in terms of degrees. Error bars indicate one standard error.

#### **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 could be because examining the shape of the error distributions that participants make might be more informative than just looking at performance summary statistics. Across all measures, participants do clearly differentiate between a 10% and a 30% tilt probability, suggesting that probability differences do not have to be drastic for behavioural differences to be observable.

The mixture model analysis suggested that the error distributions across the different probabilities still comprised a mix of *two* components: a wide and a narrow gaussian. The difference in distributions largely rests on the proportion of one component to the other. This finding supports the hypothesis that what probability information does it to shift the reliance on one 'mode' of perception over the other. In *Experiments 1* and 2, it might have been suggested that the two 'modes' might be due to participants not following instructions or moving their eyes, to result in some trials where some stimuli are processed in foveal vision, and others in peripheral vision. This cannot account for the two-component model still being the best fit for the data from *Experiment 3*, where all stimuli were shown in foveal vision. Additionally, *Experiment 3* again demonstrated an interaction between tilt-probability and orientation. As discussed earlier, this would be expected if they both affect neural tuning. Potentially, the hypothetical 'modes' of perception could be linked to neural tuning differences. This idea will be explored in the next section.

Table 1

# Summary of probability effects across experiments

Measure	Expt 1a (Basic)	Expt 1b (Confidence)	Expt 2 (Conditional)	Expt 3 <sup>^</sup> (Graded)
Reaction Time	t (19) = 5.20 ***	t (19) = 2.66 *	t (19) = 2.44 *	F(2,70) = 3.08 *
Mean Angular Error	t (19) = 3.08 **	t (19) = 3.53 **	t (19) < 1	F(2,70) = 6.95 **
Mixing Proportions	t (19) = 4.16 ***	t (19) = 1.56	t (19) = 2.67 *	F (2,68) = 4.21 *
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

<sup>^</sup> Comparing across graded probabilities

<sup>\*</sup> p < .05, \*\* p < .01, \*\*\* p < .001

#### **General Discussion**

Probability effects in RT are well-documented in symbol detection, as are probability effects in detection accuracy in visual search paradigms. The experiments reported here, as in the Anderson study, suggest that there are robust probability effects in perceptual estimations as well. In orientation estimations, higher-probability tilts are estimated faster *and* more precisely than are lower-probability tilts.

The experiments presented here further examined the characteristics of those probability effects. The effects occur without participants being able to explicitly describe the probability distributions, or being more confident of making judgements of one probability over another. The probability effects develop very quickly, being observable within only fifty to a hundred trials into the experiment, with participants showing some signs of sensitivity to fine differences in probability. Additionally, these behavioural effects develop even when the probability distributions are highly complex. 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.

How might probability change the quality of perceptual representations? People – and non-human animals – have been found to be more accurate in perceiving cardinal directions than oblique directions (Appelle, 1972). In cats, these orientation biases have been suggested to be in part due to tuning differences across neurons with different preferred orientations (Li, Peterson, & Freeman, 2003). Since the probability effect apparently interacts with orientation, it would suggest that probability affects neural tuning of orientation-selective V1 neurons as well. In

macaques, orientation tuning of neurons in the V1 region is not static, but instead changes over time (Ringach, Hawken & Shapley, 1997). In orientation training of rhesus monkeys, only the V1 neurons preferring the trained orientation showed tuning changes, suggesting specific increases in neuronal sensitivity (Schoups et al., 2001). Given these information, it might be possible that neurons' orientation tuning over time occurs differently according to the rate of occurrence of the orientations: Perhaps the rate at which the neuron is 'activated' affects its sensitivity to its preferred direction. However, if this is true, then *Experiment 2* would also suggest that this occurrence-dependant tuning would have to be context-sensitive to other non-orientation features, such as the colour of another stimulus in another location. Additionally, the data suggests that this tuning would have to occur very rapidly, approximately within 100 trials. Schoups et al. had monkeys practice the orientations 2000-5000 trials daily for several months.

Instead of neurons being tuned directly by contextually-constrained occurrence rates, 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). Neural tuning width is related to the sensitivity of the neurons. Relying completely on one set of neurons with a specific sensitivity should result in estimation precision in the behavioral task that is different as compared to when relying on a set of neurons that has a different tuning. However, perceptual decisions are also based on different neural activity depending on the complexity of the task. Making *precise* discriminations between very similar stimuli might rely on the activity of neurons tuned *away* from the target feature (Scolari & Serences, 2010). By comparison, *coarse* discrimination of distinct features might depend more on listening to the most responsive neurons, which are ones

tuned *on* the target features (Ditterich, Mazurek & Shadlen, 2003). Therefore, optimal V1 sensitivity would vary depending on what level of discrimination is needed, and separate populations with tuning differences might allow for flexibility in how these discrimination 'modes' operate.

The orientation estimation task likely depends on both these discrimination 'modes'. Because high-probability tilts occur frequently, that might cause participants to adopt more of a 'precise' mode to tell the difference between similar orientations. Where the tilts occur infrequently, it might be enough to rely more on the neurons which subserve the 'coarse' mode. Accordingly, the sensitivity of the neurons relied on would change how well-encoded the orientations of the observed Gabors can be, especially given the short presentation time (60ms). In the case of high probability tilts, relying more on the 'precise' mode would result in betterencoded perceptual representations, which would result in more confident estimations, reducing RT and vacillations, as well as resulting in more precise estimations. Consistent with the idea of there being two perceptual 'modes', the mixture models suggest that there are always two components present in participants' response distributions: One is precise and associated with smaller errors (narrow gaussian); the other is coarse and associated with larger errors (wide gaussian). The model also suggests that all that that is needed to account for the difference in the shape (kurtosis) of the response distributions is for probability to change the relative contribution of each component. Assuming that these components are linked to the two detection 'modes', which are in turn linked to the different V1 populations, what probability might be doing is to assign more weight to output of one neural population over the other.

As compared to V1 neurons being constantly tuned and re-tuned through experience, it would be more resource-efficient and quicker, given existing population differences in tuning, to weight the output of one population over another. This would account for how probability effects can rapidly develop. Regardless of whether sensitivity changes in feature-processing neurons happens directly or indirectly, it is particularly elegant as an explanation for probability effects in general since it could be extended to account for probability effects in other non-orientation scenarios. Still, while suggestions about a mechanistic link between estimation performance and neural tuning differences are intriguing, it ought to be explored further, either neurophysiologically or computationally, before any concrete claims can be made.

Other accounts for the data should be considered. There is a potential issue with 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 (see *Figures 4* and *14*). 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 (Figure 17)*, 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 & Druker (2013) study used a vertical start. Re-analysing that dataset shows the same trend in precision: near-vertical tilts showed an increased precision. Orientation effects were therefore not likely to have been caused by the experiments, but likely reflect pre-existing orientation sensitivity differences, perhaps due to differences in V1 neural tuning.

It can be argued that repetition effects are confounds in probability-related studies, since high-probability targets are more likely repeated, while rare targets are not. In detection tasks,

probability effects are still present when repetition is accounted for (Hale, 1969). Repetition effects are even less of a concern in orientation estimation because probability is not restricted to a single orientation. It may be the case that a left-tilting Gabor on the left might follow another left-tilting Gabor on the left, but there could be a 40-degree difference in their orientation, which is unlikely to lead to repetition priming. Additionally, the use of the conditional cue in *Experiment 2* further reduces the chances of this repetition effect being a factor: Even the high probability 'zone' is randomly switching from trial to trial.

Probability effects are robust and evident across various tasks. Unfortunately, they are also ill-understood. Although detection tasks might be more related to real-world tasks where the increased miss-rates of rare targets are an issue (e.g., in security and medical screenings), what has hopefully been demonstrated here is that studying probability effects in the context of how they affect perceptual estimations can result in a richer set of data than could be obtained from detection tasks alone. In the orientation estimation task, the use of the kurtosis measurement to look at the shape of the error distributions participants make not only mirrors the probability effect seen in traditional measures such mean accuracy and RT, but also serves to highlight possible processes that govern participants' perceptions of the target stimuli. More can be learnt about the nature of probability effects by examining perceptual estimations in other featuredimensions, such as location, colour, or pitch. Particularly, it might be of interest to examine how probability manipulations affect the types of errors that participants make for other such features. If the kurtosis measure proves robust across those tasks as well, it would support the hypothesis that probability information affects perceptual representations of the stimuli, perhaps by affecting the sensitivity of the neural populations that code for the relevant target features.

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Age:
Gender:
Are you: left-handed, right-handed, mixed-handed, or ambidextrous? (Circle one.)
Do you have normal, corrected, or impaired vision? (Circle one.)
If you have impaired vision, please describe the impairment:
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.