Rapidly learned stimulus expectations alter perception of motion

Supplementary Materials

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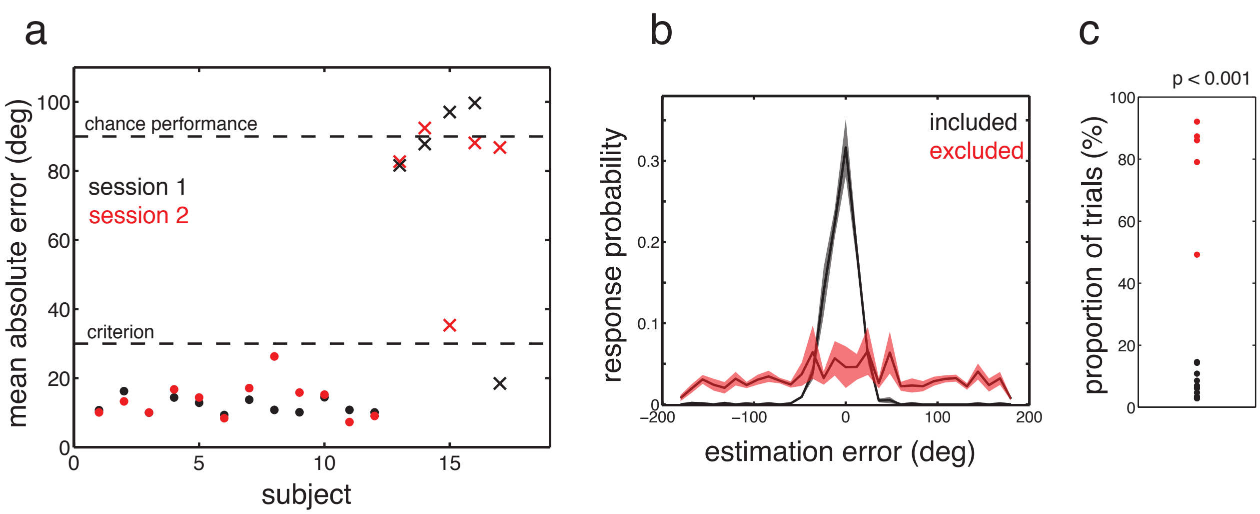
Performance of subjects in detection and estimation task

In order to ensure that participants performed adequately in the psychophysical task we used a predetermined performance criteria for inclusion into the study. Firstly, participants were required to detect the motion stimuli on more than 80% of trials with the high contrast motion stimuli and also make active estimates of the motion directions by clicking the mouse. Secondly, their average estimation performance on the high contrast stimuli had to be within 30° of the correct angle.

We discounted 3/20 participants who did not meet our first criterion in either experimental session. The included participants managed to both detect stimuli and click on the mouse during stimulus presentation to make an estimation of motion direction, on almost every trial with the high contrast stimuli (97±0.3% of trials).

The 17/20 participants who passed the criterion for the detection task could be separated according to their estimation performance into two distinct groups (supplementary figure 1a):

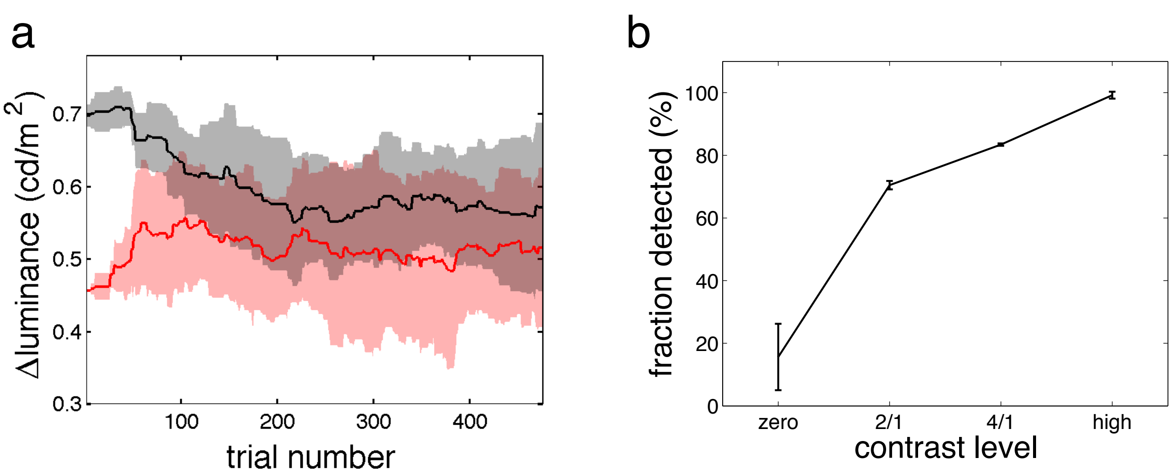


Supplementary figure 1: Performance of different participants in estimation task, with the high contrast stimuli. (a) The mean absolute estimation error is plotted separately for each experimental session (session 1 and 2 are plotted in blue and red respectively), and for each participant. Participants whose rms estimation error was less than 30° in both sessions were included in our analysis, and are denoted by filled dots while participants who did not meet this criterion were discounted from our analysis are denoted by crosses. The mean absolute error that corresponds to chance performance in the task (90°) and our criterion rms error (30°) are denoted by horizontal dashed lines. (b) Response probability histogram of estimation error with the high contrast stimuli, for included (red) and excluded participants (red). (c) Fraction of trials where participants moved the bar less than 1° from its initial position during the estimation task. Included and excluded participants are shown in red and black respectively.

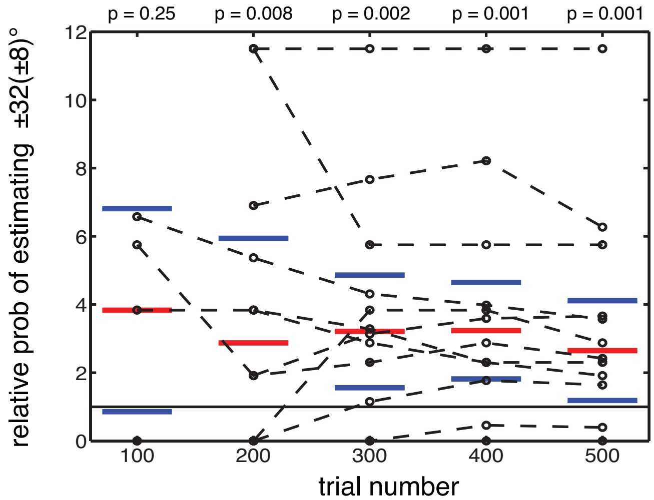
12/20 participants who passed our criterion and performed well in the estimation task (population averaged absolute error of 12.8±0.9°) and 5/20 participants who failed our criterion for the estimation task, performing at near chance levels (with an average rms error of 77.0±4.9°, compared to an average absolute error of 90° that would be expected if they made completely random estimations). Supplementary figure 1b illustrates the estimation error response probability histograms for included participants (blue) and excluded participants (red) in response to the high contrast stimuli. It is clear from this plot that the excluded participants performed extremely badly at the estimation task, with a distribution of estimation errors that was almost uniform ($p = 0.19$, 2-way within-subjects ANOVA), even with the highly visible high contrast stimuli.

If excluded participants really were not attempting the estimation task at all, then we thought it likely that they would click on the bar immediately during the estimation task, without moving it from its initial (random) orientation. This is indeed what we found: on average the excluded participants did not move the bar more than 1° from its initial position on 79±5% of trials with the high contrast stimuli; significantly more than 7±1% of trials for included participants ($p<0.001$ rank-sum test; supplementary figure 1, right panel). Excluded participants also performed the estimation task more quickly than included participants, further supporting the argument that they were not really trying to do well in this task (average reaction time of 1.44±0.07s as opposed to 0.89±0.12s for the included versus the excluded participants; $p = 0.027$, rank-sum test).

In summary, this evidence suggests that rather than just performing worse in the estimation task due to finding it difficult, excluded participants did not try to perform the estimation task at all: as they left the estimation bar in its initial position and performed at near chance levels, even with the highly visible high contrast motion stimuli.



Supplementary figure 2: (a) Population averaged stimulus contrast, relative to background contrast, for the 4/1 (blue) and 2/1 (red) staircased contrast levels, plotted against trial number (from the 1st experimental session only). (b) Fraction of stimuli detected at each of the 4 different contrast levels. In both plots, results are averaged over all participants, and the standard deviation is denoted by shaded curves and error bars respectively.



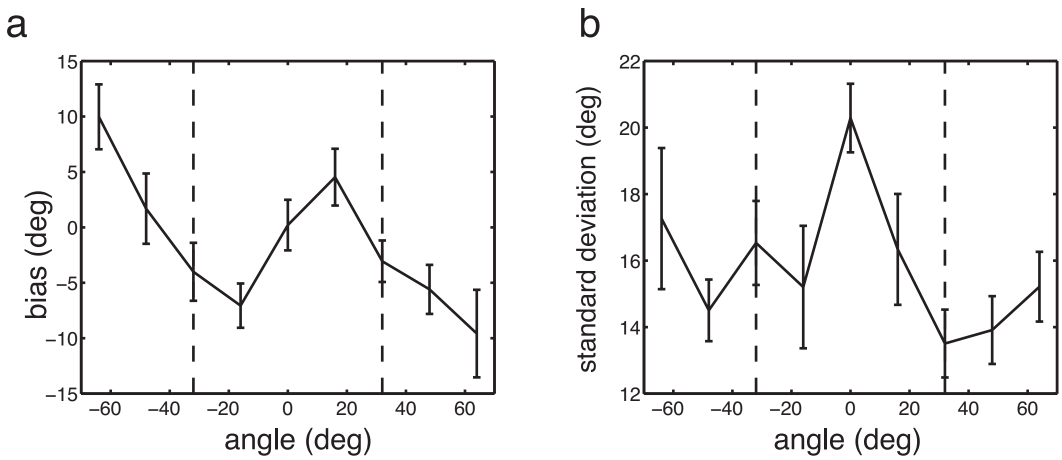
Supplementary figure 3: Probability ratio that individual participants estimated within 8° from the most frequently presented motion directions (±32°) relative to other 16° windows, for trials where no stimulus was presented, but where they reported detecting a stimulus. This probability ratio is calculated for each participant after every 100 trials (this calculation takes into account data from all trials up to that point; here we show the first 500 trials from the first session only). Median values are indicated by horizontal red lines, 25th and 75th percentiles by horizontal blue lines. Dashed lines correspond to the 'trajectories' of individual participants' 'p_{rel}' values. p-values indicate whether the probability ratio ('p_{rel}') was significantly different from 1 at each point in time.

Contrast levels

For each session, the staircases converged to stable luminance levels after roughly 100 trials (~25 trials per contrast staircase; supplementary figure 2a). The 2/1 and 4/1 staircases tracked contrasts where detection performance was near-threshold (stimulus detected on 70±0.4% and 83±0.2% of trials respectively; supplementary figure 2b). After discounting the first 100 trials from each session, the population averaged mean luminance (averaged over all trials) for the 2/1 and the 4/1 staircased contrast levels were 0.50±0.004cd/m^2 and 0.55±0.005cd/m^2 above background luminance respectively (errors are standard error on the mean). The population averaged standard deviation in the luminance of the 2/1 and the 4/1 staircased levels over the course of one experimental session was 0.051±0.001cd/m^2 and 0.054±0.001cd/m^2 respectively (errors are standard error on the mean). Notably, this was similar to the average luminance difference between the two levels (0.052±0.001cd/m^2). Finally, there was no significant difference between the luminance levels achieved for both staircases (p = 0.23, 3-way within-subjects ANOVA).

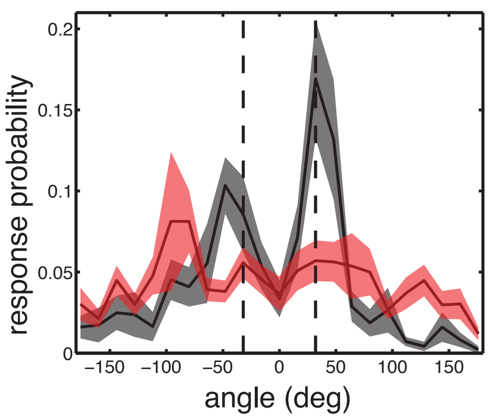
Development of 'no-stimulus' estimation bias

On trials where no stimulus was presented, but where participants reported detecting a stimulus, they were most likely to report motion directions close to the most frequently presented directions (see main paper). We quantified how likely individual participants were to make estimates that were close to the most frequently presented motion directions relative to other directions, by multiplying the probability that they estimated within 8° of these motion directions by the number of 16° bins ($p_{rel} = p(\theta_{est} = \pm 32(\pm 8)^\circ|\text{detected}) \cdot N_{bins}$). This probability ratio would be equal to 1 if participants were equally likely to estimate within 8° of ±32° as they were



Supplementary figure 4: The average estimation bias (a) and standard deviation of estimation responses (b), is plotted against stimulus motion direction. In both plots, results are averaged over all participants and error bars represent within-subject standard error.

to estimate within other 16° bins. To investigate how quickly these biases developed, we calculated this probability ratio for individual participants every 100 trials (including all responses up to that point; supplementary figure 3). For participants who had not reported detecting stimuli on any trials where none was presented, this probability ratio was undefined, so these data points were omitted from the plot (e.g. after 100 trials, only 4 participants were included, 11 participants were included after 200 trials, and 12 participants after 300 trials). After only 200 trials of the first session, the median probability ratio (‘ p_{rel}‘) was significantly greater than 1, indicating that on trials where no stimulus was presented, but where participants reported detecting a stimulus, they were biased to estimate motion in the most frequently presented directions after only 200 trials. Thus, expectations about which motion directions were most likely to occur were learned extremely rapidly, after a few minutes of task performance.



Supplementary figure 5: Probability distributions of participants’ estimates of motion direction when no stimulus was present. The two most frequently presented motion directions (±32°) are indicated by vertical dashed lines. Responses were divided into trials where participants reported detecting a stimulus (blue) and trials where they didn’t (red). Results are averaged over all participants and error bars represent within-subject standard error.

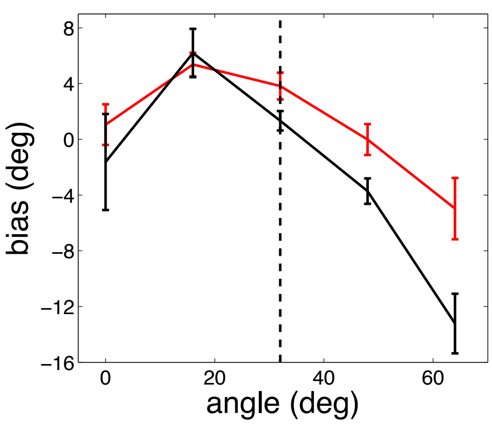
Full ‘unfolded’ plots of estimation performance

In the main text we averaged data from both sides of the central motion direction. Here we present versions of the plots where this has not been done. Supplementary figure 4 plots participants average estimation bias (left) and estimation standard deviation (right), plotted as a function of the presented stimulus motion direction. Supplementary figure 5 shows the estimation response probability when no stimulus was present, plotted for trials where participants detected a stimulus and click the mouse to make and estimation (black), alongside trials where participants didn’t detect a stimulus (but still clicked the mouse to make an estimation; red).

Estimation biases at different contrast levels

We were interested to see how changes in stimulus contrast affected participants' estimation behaviour. To do this, we first fitted psychometric curves to each participants detection responses, of the form: $p_{detect}(c) = \gamma + F(c)(1-\gamma)$. Here $p_{detect}(c)$ represents the probability that a participant detected a stimulus presented at a contrast c, γ is a constant representing the probability that a participant reported detecting a stimulus when none was displayed (the 'guess rate'), and $F(c)$ is a cumulative normal distribution (specified by two parameters; the mean and standard deviation of the corresponding normal distribution). To fit this function to each participants detection response data we set γ to be equal to the fraction of trials where the participant reported detecting a stimulus when none was presented, before fitting the two parameters of the cumulative normal distribution ($F(c)$) to the data, using a simplex algorithm (the Matlab function, 'fminsearch') that maximized the likelihood of generating the observed detection responses.

From the psychometric curves obtained for each participant, we selected a 'threshold contrast' c_{thresh} for each participant, where $F(c) = 0.75$. We then divided participants' estimation responses into two subsets: trials where the stimulus contrast was greater than c_{thresh}, (referred to as 'high contrast trials') and trials where the stimulus contrast was less than c_{thresh} (referred to as 'low contrast trials'). The population averaged mean luminance for the 'low' and 'high' contrast trials were 0.49±0.02cd/m^2 and 0.61±0.02cd/m^2 above background luminance respectively.



Supplementary figure 6: Estimation bias at different contrasts levels. Participants' estimation bias for the higher contrast trials (red) and lower contrast trials (black) are plotted against presented motion direction. Data points from either side of the central motion direction have been averaged together, so that the furthest left point corresponds to the central motion direction, and the vertical dashed line corresponds to data taken from the two most frequently presented motion directions (±32°). Results are averaged over all participants, and error bars represent the within-subjects standard error.

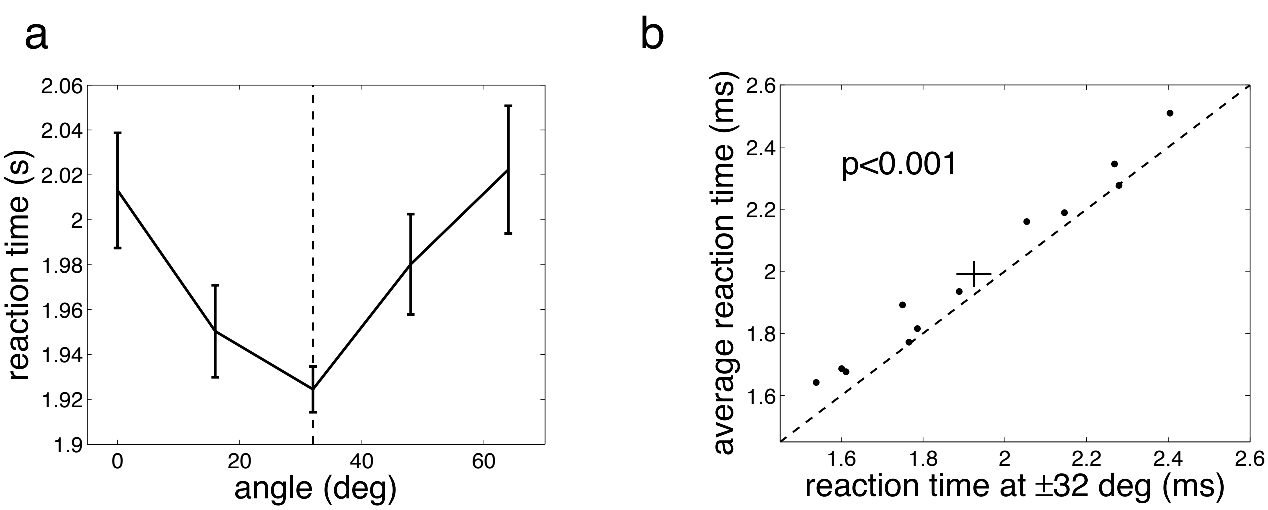
Supplementary figure 6 plots participants' estimation biases separately for 'low contrast trials' (black) and 'high contrast trials' (red) against the presented motion direction. Both curves exhibit a qualitatively similar shape: at both contrast levels, estimations of motion stimuli far away from the central motion direction (±64°) were biased towards the central motion direction. This bias reversed close to the central motion direction, so that for both contrast levels, estimations of motion stimuli presented at ±16° were biased away from the central motion direction, and towards the most frequently presented motion directions (±32°).

Importantly however, the magnitude of the estimation biases for stimuli moving far away from the central motion direction (±48° and ±64°) was much larger with the lower contrast stimuli than with the higher contrast stimuli. Overall there was a significant interaction between the effects of the two contrast levels and motion direction on the estimation bias ($p < 0.001$, 3-way within-subjects ANOVA).

In general the estimation standard deviation was significantly larger at the lower contrast level than at the higher contrast level (an average value of 17.8±1.7° at the higher contrast level versus 14.4±1.3° at the lower contrast level; p = 0.017, 3-way within-subjects ANOVA). However, there was no significant interaction between the effects of contrast level and presented motion direction on the estimation standard deviation (p = 0.10, 3-way within-subjects ANOVA).

Overall, these results are consistent with what we would expect if participants behaved as ideal Bayesian observers. When the contrast was decreased the width of participants' sensory likelihood should increase, with a corresponding increase in their estimation standard deviations. As a result, participants' estimates of motion direction would be more strongly influenced by their expectations, leading to stronger biases towards the most frequently presented motion directions, as we observed in our experimental data.

We attempted to model the observed contrast-dependent variations in participants' estimation behaviour using the Bayesian framework described in the main paper. However, for many participants' there were a relatively few number of data points per experimental condition when we divided the trials into different contrast levels. As a result we were unable to adequately constrain the model to fit the (relatively small) changes in participants' estimation behaviour with varying contrast levels. Future experiments, possibly with more data points per experimental condition, or a modified experimental design (e.g. using fixed, rather than staircased contrast levels), will be required to more accurately probe how participants' estimation behaviour varies with contrast.



Supplementary figure 7: Reaction time changes with stimulus motion direction. (a) Time taken for participants to click on the mouse and during stimulus presentation, measured from the initial presentation time. Data points from either side of the central motion direction have been averaged together, so that the furthest left point corresponds to the central motion direction, and the vertical dashed line corresponds to the most frequently presented motion directions (±32°). Results are averaged over all participants and error bars represent within-subject standard error. (b) Individual average reaction time for stimuli moving at ±32°, plotted against the reaction time over all other motion directions. The black cross marks the population mean, with the length of the lines on the cross equal to the standard error.

Reaction times

We measured participants reaction time in clicking the mouse during stimulus presentation, from trials where they also detected a stimulus. Supplementary figure 7a plots the reaction times in the estimation task as a function of stimulus motion direction. Supplementary figure 7b plots individual participants' reaction time for stimuli presented at ±32° versus their average reaction time for stimuli presented at all other motion directions. There was a significant effect of stimulus motion direction on participants' reaction time (p = 0.003, 3-way within-subjects ANOVA). For trials where participants detected a stimulus, there was a small, but highly significant reduction in their reaction time for the most frequently presented motion directions, relative to other motion directions (1924±86ms at ±32° versus 1991±85ms over all other motion directions; $p < 0.001$, signed rank test).

'Full' Bayesian model: including the detection task

In the main text we presented a simple Bayesian model (*BAYES_L-const*), which ignored the detection component of the task, looking exclusively at trials where participants correctly detected a stimulus. Here we present a model (*BAYES_dual*), which incorporates the detection task also.

The reasons for doing this were twofold. First, we were concerned that participants' behaviour in the detection task could have altered their behaviour in the estimation task. Therefore, it was important to check whether our model of participants' behaviour in the estimation task only (*BAYES_L-const*) gave consistent results to a model incorporating both the estimation and the detection task (*BAYES_dual*). Second, we were interested to see whether participants' behaviour in the detection task could also be explained within a Bayesian framework.

On a single trial, stimuli moved in a direction θ, and could either be present ($s = 1$) or not present ($s = 0$). On each trial participants made sensory measurements, $\{\theta_{obs}, s_{obs}\}$ with likelihood given by, $p_l(\theta_{obs}, s_{obs}|\theta, s)$. From Bayes' rule, the posterior probability, $p(\theta, s|\theta_{obs}, s_{obs})$, is obtained by multiplying the likelihood function ($p_l(\theta_{obs}, s_{obs}|\theta, s)$), with the prior probability ($p_{prior}(\theta, s)$):

$$p(\theta, s|\theta_{obs}, s_{obs}) \propto p_l(\theta_{obs}, s_{obs}|\theta, s) \cdot p_{prior}(\theta, s) \quad (1)$$

As explained in the main text, while participants cannot access the 'true' prior, directly, we hypothesized that they learned an approximation of this distribution, $p_{exp}(\theta, s)$.

For simplicity, we made the assumption that sensory observations of whether the stimulus was present (s_{obs}) were independent of sensory observations of motion direction (θ_{obs}), given θ and s, such that:

$$p_l(\theta_{obs}, s_{obs}|\theta, s) = p_l(\theta_{obs}|\theta, s)p_l(s_{obs}|\theta, s) \quad (2)$$

The sensory likelihood function for observations of the stimulus motion direction was parameterized as:

$$p_l(\theta_{obs}|\theta, s) = \begin{cases} \frac{1}{2\pi} & \text{if} \quad s = 0 \\ V(\theta, \kappa_l) & \text{if} \quad s = 1 \end{cases} \quad (3)$$

where $V(\theta, \kappa_l)$ denotes a von Mises (circular normal) distribution centered on θ, and with width determined by $1/\kappa_l$. Thus, for trials where no stimulus was presented, we assumed that participants were equally likely to make sensory observations that the stimulus was moving in any direction.

The sensory likelihood function for observations of whether the stimulus was present or not, was parameterized as:

$$p_l(s_{obs} = \{0,1\}|\theta, s) = \begin{cases} \{1-c, c\} & \text{if} \quad s=0 \\ \{1-d, d\} & \text{if} \quad s=1 \end{cases} \tag{4}$$

Previously, we found that the Bayesian model described in the main text, did not fit the data better when κ_l was allowed to vary with motion direction (*BAYES_L-var*), compared to when it was held constant (*BAYES_L-const*; figure 8). Consistent with this, for the *BAYES_dual* model presented here, the shape of the likelihood function was held constant with stimulus motion direction (i.e. 'κ_l' and '*d*' were held constant with presented motion direction).

We parameterized participants' learned approximation of the true prior ($p_{exp}(\theta, s)$) as:

$$p_{exp}(\theta, s) = \begin{cases} \frac{1}{2\pi}(1-b) & \text{if} \quad s=0 \\ b\left[V(-\theta_{exp}, \kappa_{exp}) + V(\theta_{exp}, \kappa_{exp})\right]/2 & \text{if} \quad s=1 \end{cases} \tag{5}$$

where the parameter 'b' describes participants' average expectation that a stimulus would be presented on each trial. Thus, we assumed that participants' expectation distributions did not vary with motion direction for trials where no stimulus was presented. On the other hand, their expectation distributions for trials where stimuli were presented varied with motion direction in the same way as the *BAYES_L-const* model described in the main text (compare equation 5 in the supplementary materials with equation 2 in the main text).

We hypothesized that participants performed the detection task by taking the maximum of the posterior distribution on each trial (as 's_{perc}' was required to be a discrete binary variable they could not take the mean of the posterior), such that:

$$s_{perc} = \text{argmax}_s[p(s|\theta_{obs}, s_{obs})] = \text{argmax}_s\left[p_l(s_{obs}|s)\int_\theta p_l(\theta_{obs}|\theta, s)p_{exp}(\theta, s)d\theta\right] \tag{6}$$

To be consistent with the *BAYES_L-const* model, the estimation task was performed on each trial by taking the mean of the posterior:

$$\theta_{perc} = \int \theta \cdot p(\theta|\theta_{obs}, s_{obs})d\theta = \frac{1}{Z}\int \theta \sum_s \left[p_l(s_{obs}|s)p_l(\theta_{obs}|\theta, s)p_{exp}(\theta, s)\right] d\theta \tag{7}$$

where Z is a normalization constant, chosen so that the sum of probability distribution (summed over both θ and s) was equal to one. As with the *BAYES_L-const* model, qualitatively similar results were obtained when we used the maximum of the posterior in our simulations, instead of the mean.

We allowed for 'motor noise' associated with participants indicating the estimated motion direction, as well as allowing for a fraction of trials ('α') where they made estimations that were completely random, so that estimation responses (θ_{est}) were related to perceptual estimates (θ_{perc}) according to:

$$p(\theta_{est}|\theta_{perc}) = (1-\alpha)V(\theta_{perc}, \kappa_m) + \alpha \tag{8}$$

In total, the *BAYES_dual* model had 7 free parameters that were fitted to the data for each participant: $\alpha, \kappa_l, c, d, \theta_{exp}, \kappa_{exp}$, and b. As described in the main text, we fitted these parameters to the data for each participant by choosing the parameter set that maximized the log-likelihood of generating the experimental data from the model.

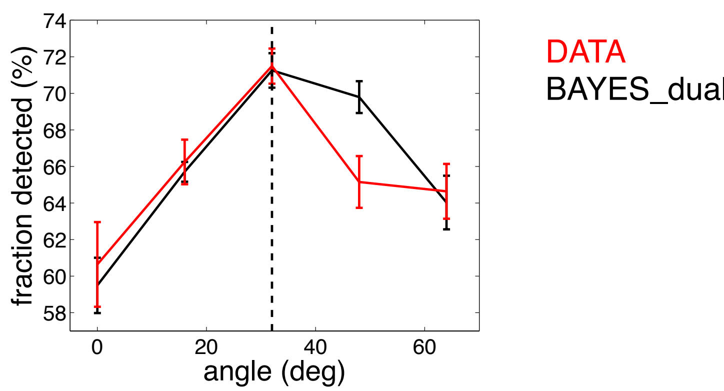
Now, as both $p_l(\theta_{obs}|\theta, s)$ and $p_{exp}(\theta, s)$ were assumed to be uniform with θ when $s = 0$ (from supplementary equation 4 and 5), supplementary equation 6 could be simplified to:

$$\theta_{perc} = \frac{1}{Z} \int \theta \cdot p_{exp}(\theta, s = 1) \cdot p_l(\theta_{obs}|\theta, s = 1) \cdot d\theta \quad \textbf{(9)}$$

This is essentially identical to the expression that we derived for the *BAYES_L-const* model in the main text, (compare this equation with equation 9 in the main text). Therefore, we might expect the predictions for the estimation task to be the same for both models. However, differences emerge between the structure of the two models if participants behave differently depending on whether they detected a stimulus. For example, we assume for the *BAYES_dual* model that on trials where participants did not detect a stimulus, they treated the estimation task as meaningless, making estimations that were completely random. This strategy would be consistent with our data: participants estimation distributions from trials where they both did not detect a stimulus or click on the mouse to indicate its motion direction was essentially uniform (p = 0.18, 3-way within-subjects ANOVA). Given this assumption, it is possible that the estimation distributions obtained for trials where a stimuli were detected would differ from the estimation distribution obtained for all trials.

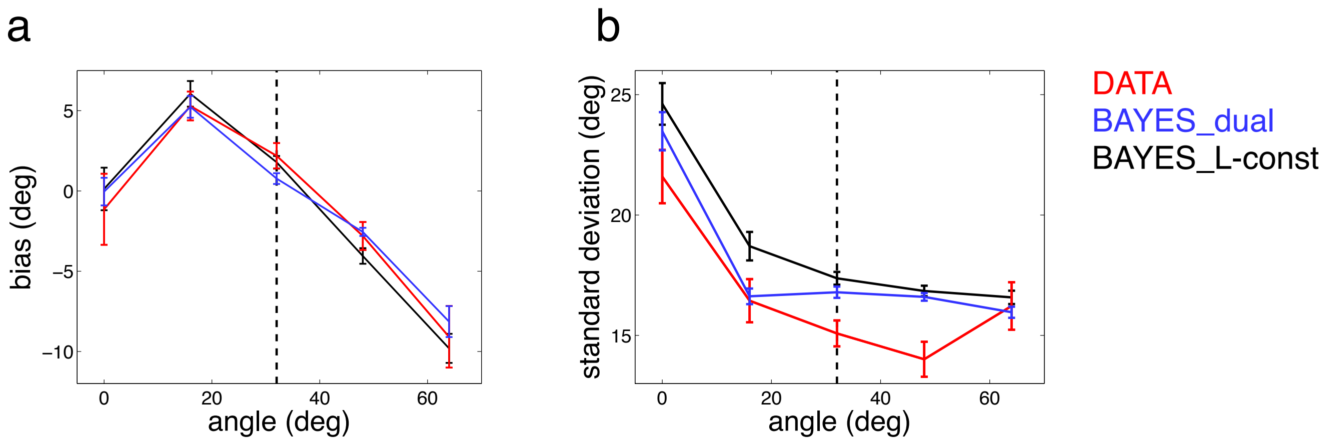
Results

The *BAYES_dual* model provided a reasonable qualitative fit for participants' responses in the detection task (with a mean absolute error of 1.50±0.58% detected; supplementary figure 8). The model exhibited increased detection performance for the most frequently presented motion directions, similar to what was observed experimentally (the model predicted 71.2±1.6% detected at ±32° versus 64.8±1.5% over all other motion directions compared to experimental observations of 71.5±2.5% detected at ±32°, versus 64.2±2.5% over all other motion directions). Overall our results were consistent with the hypothesis that participants behaved as optimal Bayesian observers in the detection task.



Supplementary figure 8: Fraction of motion stimuli that were detected, plotted against presented motion direction. Model predictions are plotted in black, experimental data is plotted in red. Data points from either side of the central motion direction have been averaged together, so that the furthest left point corresponds to the central motion direction, and the vertical dashed line corresponds to data taken from the two most frequently presented motion directions (±32°). Results are averaged over all participants and error bars represent within-subject standard error.

The estimation bias and standard deviation predicted by the *BAYES_dual* model are shown in supplementary figure 9 (blue), plotted alongside the predictions from the *BAYES_L-const* model (black) and the experimental



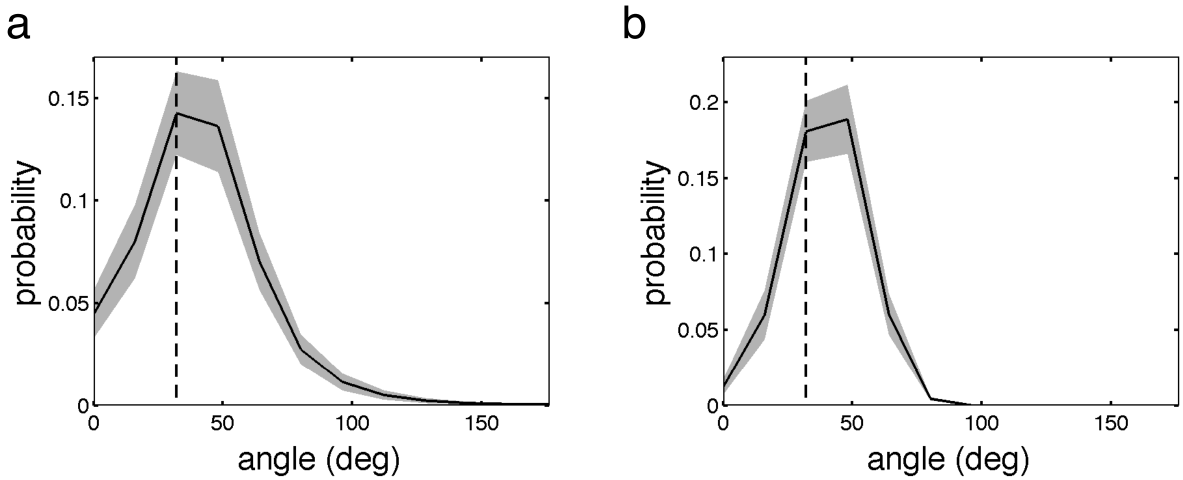
Supplementary figure 9: Predicted biases (a) and standard deviations (b) for the *BAYES_dual* model (which also models the detection task; blue) plotted alongside the *BAYES_L-const* model predictions (black), and the experimental data (red). Data points from either side of the central motion direction have been averaged together, so that the furthest left point corresponds to the central motion direction, and the vertical dashed line corresponds to the most frequently presented motion directions (±32°). Results are averaged over all participants and error bars represent the within-subject standard error.

data (red). Similar to the *BAYES_L-const* model, the *BAYES_dual* model provided a good fit for both participants' estimation biases and standard deviations (mean absolute error of 0.83° & 1.33°, for the fits of the estimation bias and standard deviation respectively; compared with 0.75° & 2.17° obtained with the *BAYES_L-const* model).

We considered the possibility that the detection task could have influenced participants' behaviour in the estimation task. For example, the *BAYES_dual* model predicted increased detection performance for the most frequently presented motion directions, so that stimuli that were perceived to be moving close to these directions would be more likely to be detected. This would then have increased the magnitude of the estimation biases that we measured, as we looked only at trials where stimuli were detected.

This interaction between the detection and the estimation task could also have been present in our analysis of the estimation responses of real participants. However, for the *BAYES_dual* model, the detection task had only a relatively minor influence on the magnitude of the measured estimation biases (verified by comparing the magnitude of the predicted estimation biases for trials where the stimulus was predicted to be detected, versus the the magnitude of the predicted estimation biases for all trials), suggesting that the detection task would also have had only a small influence on the measured estimation biases. Therefore, while it is possible that there could have been a small interaction between the two tasks, our modeling work suggests that participants' behaviour in the detection task had a small, and possibly negligible, impact on the experimentally measured estimation biases.

Finally, the *BAYES_dual* model was used to predict participants' estimation responses for trials where no stimulus was presented. These results are presented in the main text (figure 10).



Supplementary figure 10: Participants 'learned' prior distribution of presented motion directions, as predicted by the *BAYES_L-const* model (a) and the *BAYES_dual* model (b). Data points from either side of the central motion direction have been averaged together in both plots, so that the furthest left data point corresponds to the central motion direction, and the vertical dashed line corresponds to the most frequently presented motion directions (±32°). Results are averaged over all participants and error bars represent within-subject standard error.

Shape of the prior

Supplementary figure 10 plots the shape of participants' 'learned prior' required by the *BAYES_L-const* model and the *BAYES_L-dual* model to fit the experimental data (supplementary figure 10a and 10b respectively). The exact shape of the predicted distributions varied between the two models: the *BAYES_L-const* model produced a broader distribution than the *BAYES_dual* model. Indeed, even within each model, there were considerable variations in the location and width of the peaks between individual participants. However, the shape of the population averaged 'learned prior' distributions were qualitatively similar for both models: with a peak lying close to the most frequently presented motion directions (±32°), falling off close to the central motion direction (0°) and to either side of the most frequently presented motion directions (greater than +64° or less than -64°). Notably, the qualitative shape of both of these distributions was similar to the actual probability distribution of presented motion directions (figure 2), suggesting that participants learned a close approximation of this 'true' prior.