

Bayesian integration in sensorimotor learning

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When we learn a new motor skill, such as playing an approaching tennis ball, both our sensors and the task possess variability. Our sensors provide imperfect information about the ball's velocity, so we can only estimate it. Combining information from multiple modalities can reduce the error in this estimate^{1–4}. On a longer time scale, not all velocities are a priori equally probable, and over the course of a match there will be a probability distribution of velocities. According to bayesian theory^{5,6}, an optimal estimate results from combining information about the distribution of velocities—the prior—with evidence from sensory feedback. As uncertainty increases, when playing in fog or at dusk, the system should increasingly rely on prior knowledge. To use a bayesian strategy, the brain would need to represent the prior distribution and the level of uncertainty in the sensory feedback. Here we control the statistical variations of a new sensorimotor task and manipulate the uncertainty of the sensory feedback. We show that subjects internally represent both the statistical distribution of the task and their sensory uncertainty, combining them in a manner consistent with a performance-optimizing bayesian process^{4,5}. The central nervous system therefore employs probabilistic models during sensorimotor learning.

Subjects reached to a visual target with their right index finger in a virtual-reality set-up that allowed us to displace the visual feedback of their finger laterally relative to its actual location (Fig. 1a; see Methods for details). On each movement, the lateral shift was randomly drawn from a prior distribution that was gaussian with a mean shift of 1 cm to the right and a standard deviation of 0.5 cm (Fig. 1b). We refer to this distribution as the true prior. During the movement, visual feedback of the finger position was only provided briefly, midway through the movement. We manipulated the reliability of this visual feedback on each trial. This feedback was either provided clearly (σ_0 condition, in which the uncertainty comes from intrinsic processes only), blurred to increase the uncertainty by a medium (σ_M) or large (σ_L) amount, or was withheld altogether leading to infinite uncertainty (σ_∞). Visual information about the position of the finger at the end of the movement was provided only on clear feedback trials (σ_0) and subjects were instructed to get as close to the target as possible on all trials.

Subjects were trained for 1,000 trials on the task, to ensure that they experienced many samples of the lateral shift drawn from the underlying gaussian distribution. After this period, when feedback was withheld (σ_∞), subjects pointed 0.97 \pm 0.06 cm (mean \pm s.e.m. across subjects) to the left of the target showing that they had learned the average shift of 1 cm experienced over the ensemble of trials (Fig. 1a, example finger and cursor paths shown in green). Subsequently, we examined the relationship between imposed lateral shift and the final location that subjects pointed to. On trials in which feedback was provided, there was compensation during the second half of the movement (Fig. 1a, example finger and cursor paths for a trial with lateral shift of 2 cm shown in blue). The visual feedback midway through the movement provides information about the current lateral shift. However, we expect some uncertainty in the visual estimate of this lateral shift. For example, if the lateral shift is 2 cm, the distribution of sensed shifts over a large number of trials would be expected to have a gaussian distribution centred on 2 cm with a standard deviation that increases with the blur (Fig. 1c).

There are several possible computational models that subjects could use to determine the compensation needed to reach the target on the basis of the sensed location of the finger midway through the movement. First (model 1), subjects could compensate fully for the

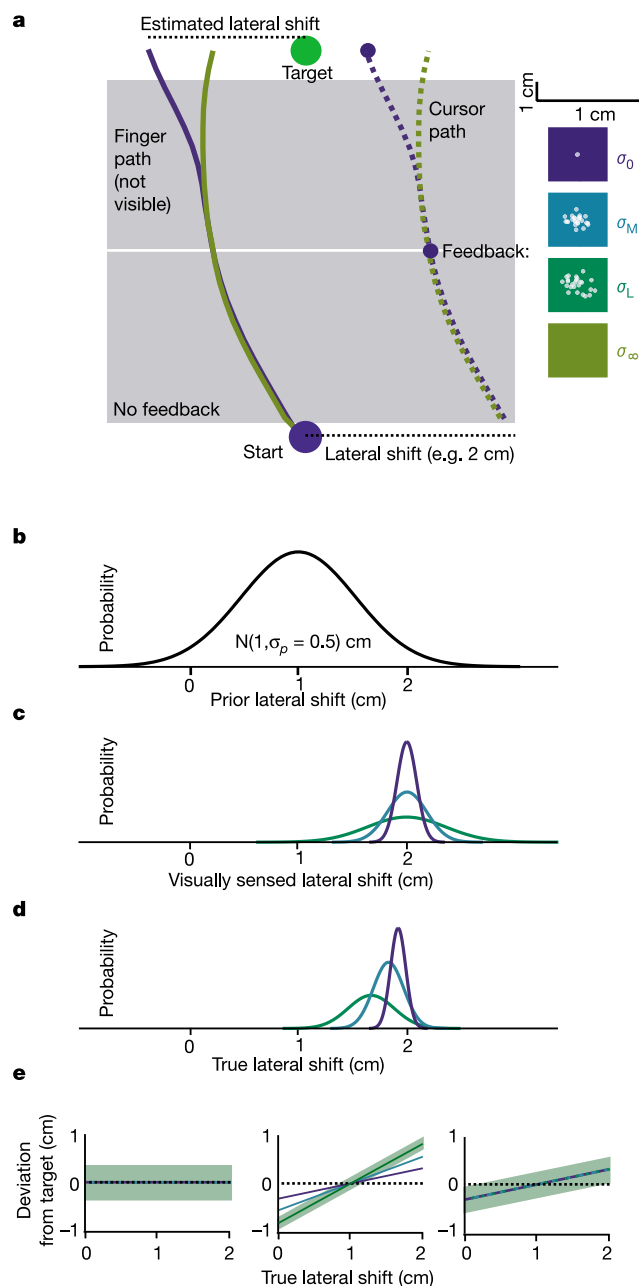


Figure 1 The experiment and models. **a**, As the finger moves from the starting circle, the cursor is extinguished and shifted laterally from the true finger location. The hand is never visible. Halfway to the target, feedback is briefly provided clearly (σ_0) or with different degrees of blur (σ_M and σ_L), or withheld (σ_∞). Subjects are required to place the cursor on the target, thereby compensating for the lateral shift. The finger paths illustrate typical trajectories at the end of the experiment when the lateral shift was 2 cm (the colours correspond to two of the feedback conditions). **b**, The experimentally imposed prior distribution of lateral shifts is gaussian with a mean of 1 cm. **c**, A diagram of the probability distribution of possible visually experienced shifts under the clear and the two blurred feedback conditions (colours as in **a**) for a trial in which the true lateral shift is 2 cm. **d**, The estimate of the lateral shift for an optimal observer that combines the prior with the evidence. **e**, The average lateral deviation from the target as a function of the true lateral shift for the models (for σ_L the green shading shows the variability of the lateral deviation). Left, the full compensation model; middle, the bayesian probabilistic model; right, the mapping model (see the text for details).

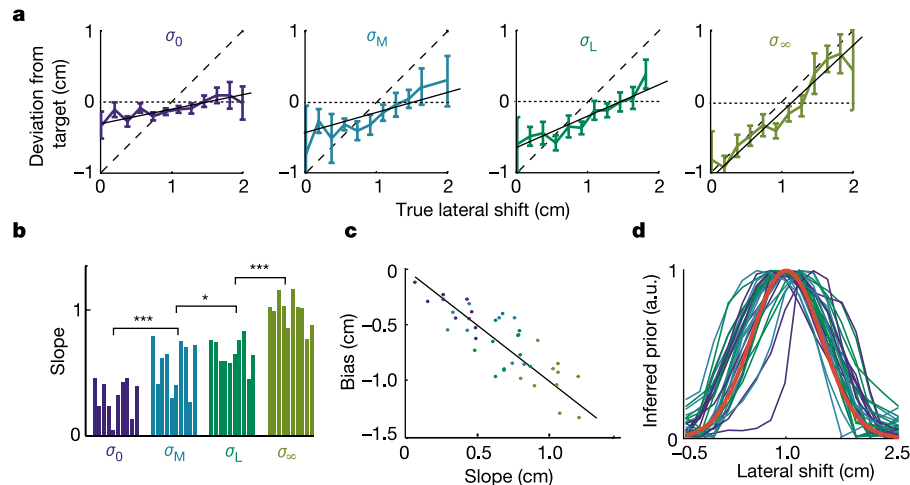


Figure 2 Results for a gaussian distribution. Colour codes as in Fig. 1. **a**, The lateral deviation of the cursor at the end of the trial as a function of the imposed lateral shift for a typical subject. Error bars denote s.e.m. The horizontal dotted lines indicate the prediction from the full compensation model and the dashed line is the fit for a model that ignores sensory feedback on the current trial and corrects only for the mean over all trials. The solid line is the bayesian model with the level of uncertainty fitted to the data. **b**, The slopes for the linear fits are shown for the full population of subjects. On the basis of the

hypothesis that the slope should increase with increasing visual uncertainty, we performed a repeated-measures analysis of variance on the slope, with visual uncertainty as a factor (main effect of visual uncertainty $F_{3,27} = 82.7$; $p < 0.001$). Planned comparisons of the slopes between adjacent uncertainty levels were all significant (asterisk, $p < 0.05$; three asterisks, $p < 0.001$). **c**, The bias against gain for the linear fits for each subjects and condition. The solid line shows the bayesian solutions. **d**, The inferred priors and the true prior (red) for each subject and condition.

visual estimate of the lateral shift. In this model, increasing the uncertainty of the feedback for a particular lateral shift (by increasing the blur) would affect the variability of the pointing but not the average location. Crucially, this model does not require subjects to estimate their visual uncertainty or the prior distribution of shifts. Second (model 2), subjects could optimally use information about the prior distribution and the uncertainty of the visual feedback to estimate the lateral shift. We can see intuitively why model 1 is sub-optimal. If, on a given trial, the subject sensed a lateral shift of 2 cm, there are many true lateral shifts that can give rise to such a perception. For example, the true lateral shift could be 1.8 cm with a visual error of +0.2 cm, or it could be a lateral shift of 2.2 cm with a visual error of -0.2 cm. Which of the two possibilities is more probable? Given gaussian noise on the visual feedback, visual errors of +0.2 cm and -0.2 cm are equally probable. However, a true lateral shift of 1.8 cm is more probable than a shift of 2.2 cm given that the prior distribution has a mean of 1 cm (Fig. 1b). If we consider all possible shifts and visual errors that can give rise to a sensed shift of 2 cm, we find that the most probable true shift is less than 2 cm. The amount by which it is less depends on two factors, the prior distribution and the degree of uncertainty in the visual feedback. As we increase the blur, and thus the degree of uncertainty, the estimate moves away from the visually sensed shift towards the mean of the prior distribution (Fig. 1d). Without any feedback (σ_∞) the estimate should be the mean of the prior. Such a strategy can be derived from bayesian statistics and minimizes the subject's mean squared error.

A third computational strategy (model 3) is to learn a mapping from the visual feedback to an estimate of the lateral shift. By minimizing the error over repeated trials, subjects could achieve a combination similar to model 2 but without any explicit representation of the prior distribution or visual uncertainty. However, to learn such a mapping requires knowledge of the error at the end of the movement. In our experiment we only revealed the shifted position of the finger at the end of the movement on the clear feedback trials (σ_0). Therefore, if subjects learn a mapping, they can only do so for these trials and apply the same mapping to the blurred conditions (σ_M , σ_L). This model therefore predicts that the average shift of the response towards the mean of the prior should be the same for all amounts of blur.

By examining the influence of the visual feedback on the final deviation from the target we can distinguish between these three models (Fig. 1e). If subjects compensate fully for the visual feedback (model 1), the average lateral deviation of the cursor from the target should be zero for all conditions. If subjects combine the prior and the evidence provided by sensory feedback (model 2), the estimated lateral shift should move towards the mean of the prior by an amount that depends on the sensory uncertainty. For a gaussian distribution of sensory uncertainty, this predicts a linear relationship between lateral deviation and the true lateral shift, which should intercept the abscissa at the mean of the prior (1 cm) and with a slope that increases with uncertainty. Finally, the mapping model (model 3) predicts that subjects should compensate for the seen position independently of the degree of uncertainty. Thus, all conditions should exhibit the same slope as the clear feedback condition (σ_0) of model 2. An examination of the theoretically determined mean squared error for the three models shows that it is minimal for model 2. Even though model 1 is on average on target, the variability in the response is higher than in model 2 (green shading in Fig. 1e shows the variability for the σ_L condition), leading to a larger mean squared error.

The lateral deviation from the target as a function of the lateral shift is shown for a representative subject in Fig. 2a. This shows a slope that increases with increasing uncertainty and is, therefore, incompatible with models 1 and 3. As predicted by model 2, the influence of the feedback on the final pointing location decreases with increasing uncertainty. The slope increases significantly with uncertainty in the visual feedback over the subjects tested (Fig. 2b). The bias and the slope should have a fixed relationship if we assume that subjects do bayesian estimation. We expect no deviation from the target if the true lateral shift is at the mean of the prior (1 cm). This predicts that the sum of the slope and offset should be zero, as observed in Fig. 2c. Subjects thus combine prior knowledge of the distribution with sensory evidence to generate appropriate compensatory movements.

Assuming that subjects use a bayesian strategy, we can furthermore use the errors that the subjects made during the trials to infer their degree of uncertainty in the feedback. For the three levels of imposed uncertainty, σ_0 , σ_M and σ_L , we find that subjects' estimates of their visual uncertainty are 0.36 ± 0.04 , 0.67 ± 0.1 and

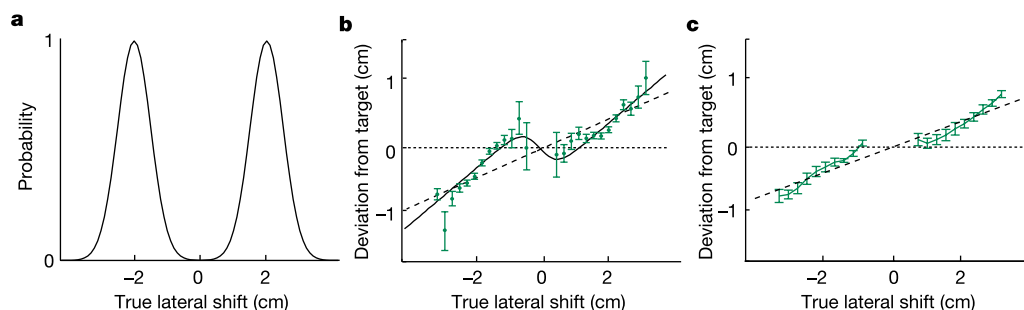


Figure 3 Results for a mixture of gaussian distributions. **a**, The experimentally imposed prior distribution of lateral shifts is a mixture of two gaussians. **b**, The lateral deviation of the cursor at the end of the trial as a function of the true lateral shift for a typical subject. Error bars denote s.e.m. The horizontal dotted lines indicate the prediction from

the full compensation model, the dashed line is the fit for a bayesian model with a single gaussian prior, and the solid line is the fit for a bayesian model with a prior that is a mixture of two gaussians. **c**, The lateral deviation across subjects (mean \pm s.e.m. across subjects) is shown with a linear regression fit, demonstrating the nonlinearity of the data.

0.8 ± 0.1 cm (means \pm s.e.m. across subjects), respectively. We have also developed a novel technique that uses these estimates to infer the priors used by the subjects. Figure 2d shows the priors inferred for each subject and condition. This shows that the true prior (red line) was reliably learned by each subject.

To examine whether subjects can learn complex distributions, a new group of subjects were exposed to a bimodal distribution (Fig. 3a) consisting of a mixture of two gaussians separated by 4 cm. Here, the bayesian model predicts a nonlinear relationship between true shift and lateral deviation, with the precise shape depending on the uncertainty of the visual feedback. Figure 3b shows a single subject's lateral deviation together with the fit of a bayesian model (solid line) in which we fit two parameters: the separation of the two gaussians and the variance of the visual uncertainty. The nonlinear properties are reflected in the empirical data and are consistent over the subjects (Fig. 3c) with a fitted separation of 4.8 ± 0.8 cm (mean \pm s.e.m. across subjects), close to the true value of 4 cm, suggesting that subjects represent the bimodal prior. Taken together, our results demonstrate that subjects implicitly use bayesian statistics.

Many technically challenging problems have been addressed successfully within the bayesian framework^{7,8}. It has been proposed that the architecture of the nervous system is well suited for bayesian inference^{9–13} and that some visual illusions can be understood within the bayesian framework¹⁴. However, most models of the sensorimotor system consider a cascade of mappings from sensory inputs to the motor output^{15–17}. These models consider input–output relationships and do not explicitly take into account the probabilistic nature of either the sensors or the task. Recent models of motor control have begun to emphasize probabilistic properties^{18–24}. Unlike the visual system, which loses much of its plasticity once it has passed its critical period, the motor system retains much of its plasticity throughout adult life. We could therefore impose a novel prior on the subjects and measure its influence on sensorimotor processing. To show quantitatively that the system performs optimally would require a direct measure of sensory uncertainty before it is integrated with the prior. However, such a measure cannot easily be obtained as even a naive subject would integrate feedback with their natural, but unknown, prior. However, by imposing experimentally controlled priors we have shown that our results qualitatively match a bayesian integration process. A bayesian view of sensorimotor learning is consistent with neurophysiological studies showing that the brain represents the degree of uncertainty when estimating rewards^{25–27} and with psychophysical studies addressing the timing of movements^{28,29}. Although we have shown only the use of a prior in learning hand trajectories during a visuomotor displacement, we expect that such a bayesian process might be fundamental to all aspects of sensorimotor control and learning. For example, representing the distribution of dynamics of

objects, such as their mass, would facilitate our interactions with them. Similarly, although the possible configurations of the human body are immense, they are not all equally likely and knowledge of their distribution could be used to refine estimates of our current state. Taking into account a priori knowledge might be key to winning a tennis match. Tennis professionals spend a great deal of time studying their opponent before playing an important match, ensuring that they start the match with correct a priori knowledge. □

Methods

Experimental details

Six male and four female subjects participated in this study after giving informed consent. Subjects made reaching movements on a table during which an Optotrak 3020 tracking system (Northern Digital) measured the position of their right index finger. A projection–mirror system prevented direct view of their arm and allowed us to generate a cursor representing their finger position that could be displayed in the plane of the movement (for details of the set-up see ref. 30). Subjects saw a blue sphere representing the starting location, a green sphere representing the target and a white sphere representing the position of their finger (Fig. 1a). Subjects were requested to point accurately to the target. When the finger left the start position, the cursor representing the finger was extinguished and displaced to the right by an amount that was drawn each trial from a gaussian distribution with mean of 1 cm and standard deviation of 0.5 cm. Midway through the movement (10 cm), feedback of the cursor centred at the displaced finger position was flashed for 100 ms. On each trial one of four types of feedback (σ_0 , σ_M , σ_L , σ_∞) was displayed; the selection of the feedback was random, with the relative frequencies of the four types being (3, 1, 1, 1) respectively. The σ_0 feedback was a small white sphere. The σ_M feedback was 25 small translucent spheres, distributed as a two-dimensional gaussian with a standard deviation of 1 cm, giving a cloud-type impression. The σ_L feedback was analogous but had a standard deviation of 2 cm. No feedback was provided in the σ_∞ case. After another 10 cm of movement the trial was finished; feedback of the final cursor location was provided only in the σ_0 condition. The experiment consisted of 2,000 trials for each subject. On post-experimental questioning, all subjects reported being unaware of the displacement of the visual feedback. Only the last 1,000 trials were used for analysis. Subjects were instructed to take into account what they saw at the midpoint and to get as close to the target as possible; we took the lateral deviation of the finger from the target as a measure of subjects' estimate of the lateral shift. By averaging over trials we could obtain this estimate uncorrupted by any motor output noise, which we assumed to have mean of zero.

Bayesian estimation

We wish to estimate the lateral shift x_{true} of the current trial given a sensed shift x_{sensed} (also known as the evidence) and the prior distribution of lateral shifts $p(x_{\text{true}})$. From Bayes rule we can obtain the posterior distribution, that is the probability of each possible lateral shift taking into account both the prior and the evidence,

$$p(x_{\text{true}}|x_{\text{sensed}}) = p(x_{\text{sensed}}|x_{\text{true}}) \frac{p(x_{\text{true}})}{p(x_{\text{sensed}})}$$

where $p(x_{\text{sensed}}|x_{\text{true}})$ is the likelihood of perceiving x_{sensed} when the lateral shift really is x_{true} . We assume that visual estimation is unbiased and corrupted by gaussian noise so that

$$p(x_{\text{true}}|x_{\text{sensed}}) = \underbrace{\frac{1}{\sigma_{\text{sensed}} \sqrt{2\pi}} e^{-(x_{\text{true}} - x_{\text{sensed}})^2 / 2\sigma_{\text{sensed}}^2}}_{p(x_{\text{sensed}}|x_{\text{true}})} \underbrace{\frac{1}{\sigma_{\text{prior}} \sqrt{2\pi}} e^{-(x_{\text{true}} - 1\text{cm})^2 / 2\sigma_{\text{prior}}^2}}_{p(x_{\text{true}})} \underbrace{p(x_{\text{sensed}})}_{p(x_{\text{sensed}})}$$

For the optimal estimate we can find the maximum by differentiation, which represents the most probable lateral shift. For gaussian distributions such an estimate also has the

smallest mean squared error. This estimate is a weighted sum of the mean of the prior and the sensed feedback position:

$$x_{\text{estimated}} = \frac{\sigma_{\text{sensed}}^2}{\sigma_{\text{sensed}}^2 + \sigma_{\text{prior}}^2} [1 \text{ cm}] + \frac{\sigma_{\text{prior}}^2}{\sigma_{\text{sensed}}^2 + \sigma_{\text{prior}}^2} x_{\text{sensed}}$$

Given that we know σ_{prior}^2 , we can estimate the uncertainty in the feedback σ_{sensed} by linear regression from Fig. 2a.

Resulting mean squared error

The mean squared error (MSE) is determined by integrating the squared error over all possible sensed feedbacks and actual lateral shifts

$$\text{MSE} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} (x_{\text{estimated}} - x_{\text{true}})^2 p(x_{\text{sensed}} | x_{\text{true}}) p(x_{\text{true}}) dx_{\text{sensed}} dx_{\text{true}}$$

For model 1, $x_{\text{estimated}} = x_{\text{sensed}}$, and this gives $\text{MSE} = \sigma_{\text{sensed}}^2$.

Using the result for $x_{\text{estimated}}$ from above for model 2 gives $\text{MSE} = \sigma_{\text{sensed}}^2 \sigma_{\text{prior}}^2 / (\sigma_{\text{sensed}}^2 + \sigma_{\text{prior}}^2)$, which is always lower than the MSE for model 1. If the variance of the prior is equal to the variance of the feedback, the MSE for model 2 is half that of model 1.

Inferring the used prior

An obvious choice of $x_{\text{estimated}}$ is the maximum of the posterior

$$p(x_{\text{true}} | x_{\text{sensed}}) = \frac{1}{\sigma_{\text{sensed}} \sqrt{2\pi}} e^{-(x_{\text{true}} - x_{\text{sensed}})^2 / 2\sigma_{\text{sensed}}^2} p(x_{\text{true}}) / p(x_{\text{sensed}})$$

The derivative of this posterior with respect to x_{true} must vanish at $x_{\text{estimated}}$. This allows us to estimate the prior used by each subject. Differentiating and setting to zero we get

$$\left. \frac{dp(x_{\text{true}})}{dx_{\text{true}}} \right|_{x_{\text{estimated}}} = \frac{(x_{\text{estimated}} - x_{\text{sensed}})}{\sigma_{\text{sensed}}^2}$$

We assume that x_{sensed} has a narrow peak around x_{true} and thus approximate it by x_{true} . We insert the σ_{sensed} obtained above, affecting the scaling of the integral but not its form. The average of x_{sensed} across many trials is the imposed shift x_{true} . The right-hand side is therefore measured in the experiment and the left-hand side approximates the derivative of $\log(p(x_{\text{true}}))$. Since $p(x_{\text{true}})$ must approach zero for both very small and very large x_{true} , we subtract the mean of the right-hand side before integrating numerically to obtain $\log(p(x_{\text{true}}))$, which we can then transform to estimate the prior $p(x_{\text{true}})$.

Bimodal distribution

Six new subjects participated in a similar experiment in which the lateral shift was bimodally distributed as a mixture of two gaussians:

$$p(x_{\text{true}}) = \frac{1}{2\sqrt{2\pi}\sigma_{\text{prior}}} \left(e^{-(x - x_{\text{sep}}/2)^2 / \sigma_{\text{prior}}^2} + e^{-(x + x_{\text{sep}}/2)^2 / \sigma_{\text{prior}}^2} \right)$$

where $x_{\text{sep}} = 4$ cm and $\sigma_{\text{prior}} = 0.5$ cm. Because we expected this prior to be more difficult to learn, each subject performed 4,000 trials split between two consecutive days. In addition, to speed up learning, feedback midway through the movement was always blurred (25 spheres distributed as a two-dimensional gaussian with a standard deviation of 4 cm), and feedback at the end of the movement was provided on every trial. Fitting the bayesian model (using the correct form of the prior and true σ_{prior}) to minimize the MSE between actual and predicted lateral deviations of the last 1,000 trials was used to infer the subject's internal estimates of both x_{sep} and σ_{sensed} . Some aspects of the nonlinear relationship between lateral shift and lateral deviation (Fig. 3a) can be understood intuitively. When the sensed shift is zero, the actual shift is equally likely to be to the right or the left and, on average, there should be no deviation from the target. If the sensed shift is slightly to the right, such as at 0.25 cm, then the actual shift is more likely to come from the right-hand gaussian than the left, and subjects should point to the right of the target. However, if the sensed shift is far to the right, such as at 3 cm, then because the bulk of the prior lies to the left, subjects should point to the left of the target.

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Functional genomic hypothesis generation and experimentation by a robot scientist

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The question of whether it is possible to automate the scientific process is of both great theoretical interest^{1,2} and increasing practical importance because, in many scientific areas, data are being generated much faster than they can be effectively analysed. We describe a physically implemented robotic system that applies techniques from artificial intelligence^{3–8} to carry out cycles of scientific experimentation. The system automatically