

Acquisition, representation, and transfer of models of visuo-motor error

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We examined how human subjects acquire and represent models of visuo-motor error and how they transfer information about visuo-motor error from one task to a closely related one. The experiment consisted of three phases. In the *training phase*, subjects threw beanbags underhand towards targets displayed on a wall-mounted touch screen. The distribution of their endpoints was a vertically elongated bivariate Gaussian. In the subsequent *choice phase*, subjects repeatedly chose which of two targets varying in shape and size they would prefer to attempt to hit. Their choices allowed us to investigate their internal models of visuo-motor error distribution, including the coordinate system in which they represented visuo-motor error. In the *transfer phase*, subjects repeated the choice phase from a different vantage point, the same distance from the screen but with the throwing direction shifted 45°. From the new vantage point, visuo-motor error was effectively expanded horizontally by $\sqrt{2}$. We found that subjects incorrectly assumed an isotropic distribution in the choice phase but that the anisotropy they assumed in the transfer phase agreed with an objectively correct transfer. We also found that the coordinate system used in coding two-

dimensional visuo-motor error in the choice phase was effectively one-dimensional.

Introduction

People compensate—in part—for unavoidable noise in their perceptual and motor systems. Studies typically find that human decisions in reaching tasks are close to those predicted by Bayesian decision theory, maximizing expected Bayes gain (Battaglia & Schrater, 2007; Faisal & Wolpert, 2009; Hudson, Maloney, & Landy, 2008; Jazayeri & Shadlen, 2010; Körding & Wolpert, 2004; Trommershäuser, Landy, & Maloney, 2006; Trommershäuser, Maloney, & Landy, 2003; Wei & Körding, 2010). This near-optimal performance could be taken as evidence that human subjects have an objectively correct internal model of their own random motor errors. However, Zhang, Daw, and Maloney

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(2013) demonstrated that many previous studies may simply be insensitive to systematic deviations from optimal: In a typical motor decision task (Trommershäuser et al., 2003), a virtual subject who had a Gaussian motor error distribution but who mistakenly assumed as her internal model a uniform cylindrical distribution would still be able to achieve near-optimality (Zhang et al., 2013).

Zhang et al. (2013) developed a choice task that in principle allowed them to estimate the anisotropy (direction of elongation) of the subjects' internal model from choice data. They used this task to measure the anisotropy of subjects' internal models of the distribution (probability density function) of visuo-motor error in a speeded reaching movement. The logic of their test (in a simplified, qualitative version) is illustrated in Figure 1A.

Subjects' true error distributions were vertically elongated. If a subject's internal model were correctly vertically elongated (first row), the subject would judge her chances of hitting the vertical rectangular target to be greater than her chances of hitting the horizontal rectangular target (the probabilities in this example are 0.78 and 0.52). If she incorrectly believed that her motor error was isotropic, she would be indifferent between the targets. Zhang et al. (2013) found that 17 out of 18 subjects were insensitive to the anisotropy in their true distribution and that they incorrectly assumed an isotropic model.

Isotropy bias

We call this phenomenon *isotropy bias*. Similar failure to compensate for the anisotropy in speeded reaching movements was present in the results of Hudson, Tassinari, and Landy (2010), where the anisotropy was artificially introduced into the subjects' visuo-motor error by jittering the display screen. But why should subjects' internal models have such systematic deviations from true? And is the isotropy bias specific to reaching movements, or is it present in other visuo-motor tasks?

Possibility one

The isotropy bias is adaptive, reflecting the influence of a prior belief shaped by previous experience. That is, an isotropic internal model may be consistent with subjects' typical experience in similar reaching tasks outside laboratory settings. Indeed, the motor error distribution in several previously studied speeded reaching movements was indistinguishable from isotropic (e.g., Trommershäuser et al., 2003). Still, we cannot expect that all error distributions in reaching tasks are isotropic: According to Schmidt's law for speeded movements (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979), the motor variance parallel to the

movement direction should be larger than that perpendicular to the movement direction (e.g., the vertically elongated distribution found by Zhang et al., 2013).

Possibility two

The isotropy bias arises from constraints in human cognition. The literature of categorical learning suggests that people have difficulty in spontaneously learning two-dimensional probability distributions (Ashby, Queller, & Berretty, 1999; Goudbeek, Cutler, & Smits, 2008; Jüttner & Rentschler, 1996). This constraint could be the cognitive limitation behind the isotropy bias. In effect, subjects choose to represent a two-dimensional objective visuo-motor error distribution as a one-dimensional distribution.

Goals

1. Testing isotropy bias

The first goal of the present study is to understand whether the isotropy bias observed in speeded reaching movements is due to adaptive behaviors or cognitive constraints—a problem on Marr's (1982) computational-theory level. To tell apart these two possibilities, we investigated a second motor task that is somewhat less common in everyday life: underhand throwing (Figure 1B). The sources of error in movement in the horizontal and vertical directions are very different, and it was plausible we would find large anisotropies.

Horizontal error in this task is primarily a consequence of misorientation of the plane in which the arm swings, while vertical error—in contrast—is determined by the timing of release and velocity of the hand at the release point. Given that the two components of error are generated by very different neural mechanisms, there is little reason to expect that error distributions would be isotropic. If there were no cognitive limits on their learning ability, subjects should be able to choose anisotropic internal models if, in fact, their actual error distributions were markedly anisotropic.

2. Testing transfer

Our second goal was to test whether subjects could correctly transfer their internal model of error distribution—correct or incorrect—to a task situation they had never experienced—a task that effectively required a scaling of the isotropy of the motor distribution. We did this as a way to uncover the possible cognitive constraints on the representation of motor distributions (Maloney & Mamassian, 2009; Zhang, Paily, & Maloney, 2015). Although transfer of motor skills is well documented (Schmidt & Lee, 2005), the transfer of humans' knowledge of their own motor uncertainty had rarely been studied before. Such transfer is an

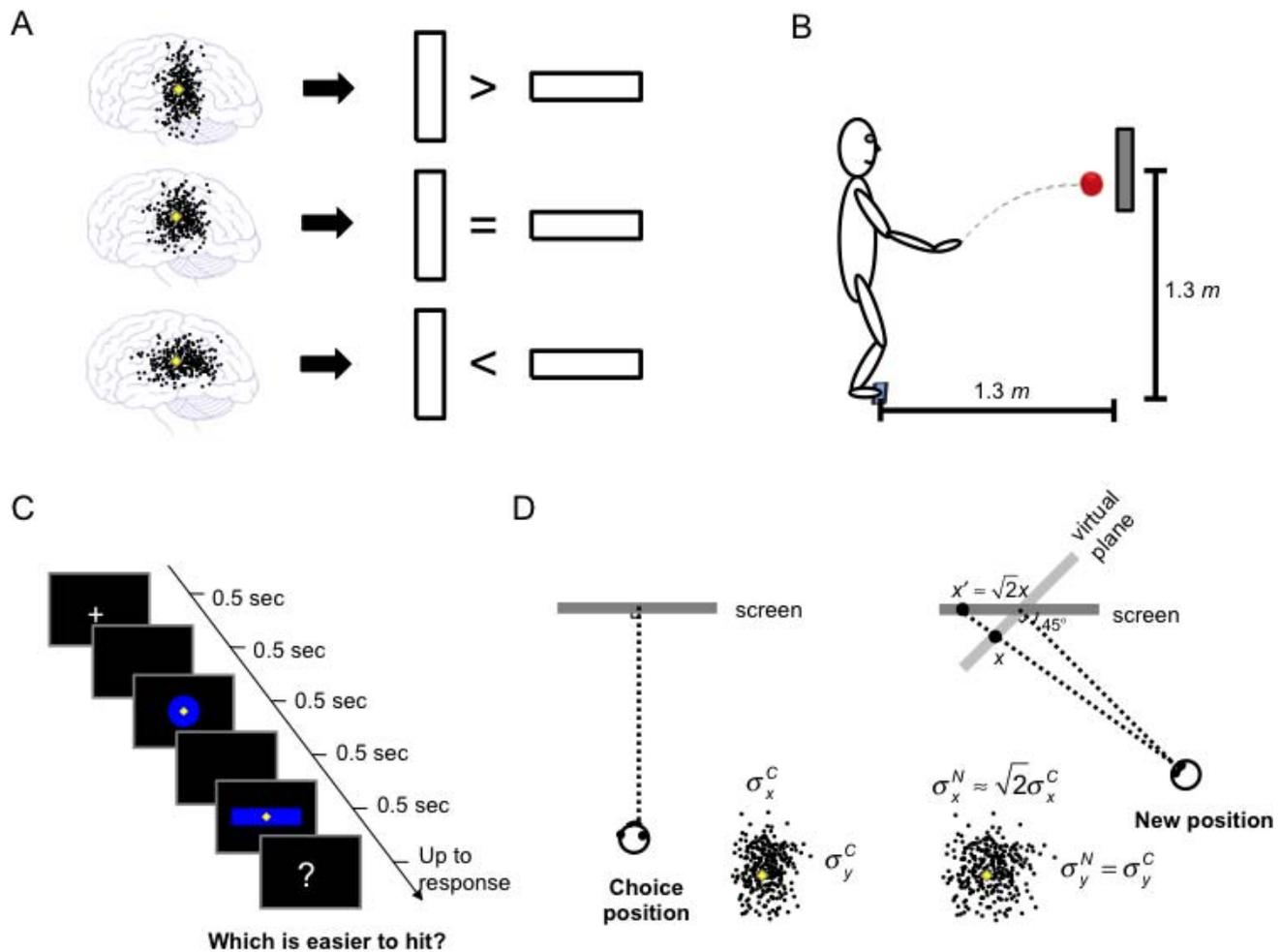


Figure 1. Experimental task and motivation. (A) The rationale for the choice task. Whether the subject's internal model of visuo-motor error distribution was vertically elongated, isotropic, or horizontally elongated should determine her choice between vertical and horizontal targets. Conversely, the subject's choices among different targets would allow us to make inferences about her internal model. (B) Training. On each trial, the subject threw a beanbag underhand to hit a target at the center of a wall-mounted touch screen. (C) Choice. The subject held a beanbag in her hand and stood either at the position where she was trained to throw (choice position) or at a new position that was the same distance from the screen but at a 45° viewing angle. On each trial, the subject saw a pair of sequentially displayed targets and was asked to verbally report whether the first or the second target was easier to hit, assuming she attempted the targets from where they stood. The subject did not throw the beanbag or receive feedback. (D) The objectively correct transfer from the choice to the new position. Suppose the standard deviations of the subject's visuo-motor error distribution on the screen are σ_x and σ_y . The geometric relationship between the choice and the new positions would determine the on-screen error distribution at the new position with standard deviations satisfying $\sigma_x^N \approx \sqrt{2}\sigma_x^C$ and $\sigma_y^N = \sigma_y^C$.

example of second-order judgment or metacognition (Barthelmé & Mamassian, 2009; Fleming, Maloney, & Daw, 2013) and an example of decision from models (Zhang et al., 2015).

To test transfer, we required each subject to complete the choice task (Figure 1C, described later) at two different positions (Figure 1D): first standing at the choice position, which had a 90° viewing angle to the screen, and then moving to a new position that had the same distance to the screen but was 45° to the right of the screen.

Changing to the second position resulted in a geometric transformation of the effective motor error

on the screen (Figure 1D). In particular, if we denote the horizontal and vertical standard deviations of the endpoints at the choice position (90°) as σ_x^C and σ_y^C , and those at the new position (45°) as σ_x^N and σ_y^N , we have

$$\begin{aligned} \sigma_x^N &= \sqrt{2}\sigma_x^C \\ \sigma_y^N &= \sigma_y^C \end{aligned} \quad (1)$$

We estimated subjects' internal models at the choice and new positions separately and tested whether the transfer from the former to the latter agreed with the objectively correct transfer.

Of course, there are at least two ways the visual system can effectively transfer in our tasks. The subject may scale the internal model of visuo-motor error or alternatively apply a reciprocal scaling to the target. For our purposes these are equivalent, and we refer to both as transfer.

3. Coordinate systems

Our third goal was to investigate the coordinate system used to represent visuo-motor error. We will present results in terms of Cartesian coordinates $\phi(x, y)$. However, there is little reason to believe that the visuo-motor system uses a Cartesian representation, and—as we will see—our results indicate that a one-dimensional coordinate system similar to polar coordinates (r, θ) but with only the single parameter r better accounts for our data.

Estimating internal models

We employed the choice task developed by Zhang et al. (2013): After training on beanbag throwing, subjects were asked to choose between pairs of virtual targets differing in size and configuration (Figure 1C). Hitting either target would earn the same reward, and subjects' task was in effect to decide which of the two targets offered the greater probability of earning the reward. Since these choices trade off the chances of hitting different locations, subjects' choices between a specific pair of targets would depend on their internal model of their own visuo-motor error distribution. Conversely, based on these choices we could gain information about a subject's internal model (Maloney & Mamassian, 2009; Zhang et al., 2013) and compare it with the subject's true visuo-motor error distribution in training.

Subjects' visuo-motor error in beanbag throwing was distributed as a bivariate Gaussian, vertically elongated. In Figure 2A we summarize the expected results for an ideal movement planner: The internal distribution matches the external and is transferred correctly. In Figure 2B we summarize what actually occurred in the experiment: Estimates of subjects' internal distributions were close to isotropic. Finally, they correctly transformed their *incorrect*, isotropic estimates to the new position. They were wrong, but they were consistent.

Methods

Ethics statement

The experiment adhered to the tenets of the Declaration of Helsinki and was approved by the University Committee on Activities Involving Human

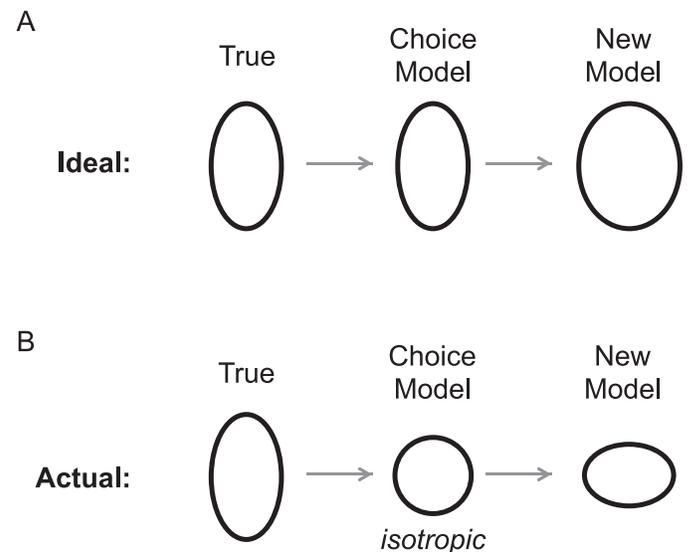


Figure 2. Summary of ideal and actual results. (A) Ideal movement planner. (B) Real subjects. Each ellipse represents a one-standard-deviation contour of a bivariate Gaussian distribution (arbitrary unit). “True” denotes the observer’s true visuo-motor error distribution in the throwing task. “Choice Model” and “New Model” respectively denote the observer’s internal model of visuo-motor error distribution at the choice and new positions. Subjects tended to underestimate their visuo-motor variance in the choice task. They also incorrectly assumed that their distributions were isotropic. However, the anisotropy they assumed at the new position agreed with an objectively correct transfer of an isotropic distribution.

Subjects of New York University. All subjects gave informed consent prior to the experiment.

Subjects

Fifteen subjects—eight male and seven female, aged 18 to 36 (median 22)—participated. All had normal or corrected-to-normal vision and were right-handed. None reported considerable experience with underhand throwing. Subjects were unaware of the purpose of the experiment. Subjects received US\$12 per hour plus a performance-related bonus.

Apparatus and stimuli

Stimuli were presented on a 22-in. (47.6×30.2 cm) monitor mounted on the wall, the center of which was 1.3 m above the ground. The monitor was covered with a CycloTouch Multi-touch Screen Overlay Kit to make it equivalent to a touch screen. We stabilized the monitor to ensure that it would not appreciably move or vibrate in response to the impact of flying beanbags. Beanbags were uniform balls with a diameter of 6.4 cm

and a mass of 130 g. Targets for the throwing or choice tasks were blue filled shapes, whose center was marked with a small yellow diamond (0.5×0.5 cm). Targets were presented at the center of the screen on a black background. The Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) was used to control the experiment. The endpoints of the thrown beanbags were recorded using the Multi-touch Screen Overlay Kit.

Procedure and design

Each subject completed three phases: training, choice, and transfer. The whole experiment took approximately 2.5 hr.

Training phase

In the training phase, subjects stood 1.3 m away from and at 90° to the screen (Figure 1B). On each trial, their task was to throw a beanbag underhand to hit the target on the screen. When the beanbag impacted the screen, the target disappeared and was followed by a visual feedback of 2 s: A white (in the case of hit) or red (in the case of miss) dot indicated the endpoint of the beanbag. If the beanbag missed the screen entirely, the experimenter pressed a key and the subject saw the text “OUT.”

The target was a circle (radius 4.4 cm), a horizontal rectangle (13.9×3.5 cm), or a vertical rectangle (3.5×13.9 cm). Each subject completed 300 throwing trials, with each target repeated 100 times in random order. The training phase allowed both subjects and us to assess subjects’ visuo-motor error distributions.

We required subjects to use their right hand to throw, with their feet parallel, together, and stationary, their right shoulder aligned with the center of the screen, and their right arm kept close to their side. Feedback marking the mean endpoint was shown on the screen for every 15 throws. To reduce fatigue, we asked subjects to take a 15-s break after every 15 trials and whenever they felt tired. Subjects were monetarily motivated to make accurate throws: They knew that at the end of the training, two trials would be randomly drawn from their 300 trials as bonus trials, for each of which—if they had hit the target on that trial—they would win an additional \$2.

Choice phase

The choice phase took place immediately after the training phase. On each trial, the subject stood at the position where she was trained in throwing (*choice position*), facing the screen, beanbag in her right hand. The task was to choose, given a pair of targets (rectangle and circle), the target that was easier to hit. The time course of the task is shown in Figure 1C. The

order of the circle and the rectangle was randomized across trials. Subjects were prompted to answer the question “Which is easier to hit? First or second?” The experimenter recorded subjects’ verbal responses by key press.

The rectangle had four possible sizes: its shorter side was 2.9, 3.9, 5.3, or 7.1 cm, and its long side was 4 times the length of its shorter side. The rectangle had two possible orientations: horizontal or vertical. For each of these eight rectangles, we varied the radius of the paired circle using a one-up/one-down adaptive staircase procedure that terminated after 60 trials. All staircases were randomly mixed and resulted in $8 \times 60 = 480$ trials in total.

At the end of the choice phase, subjects attempted to hit the chosen targets from eight of their choice trials picked at random. Subjects won \$2 for each successful hit.

Transfer phase

Subjects then moved to a *new position*, to their right, that had the same distance from the center of the screen but a 45° viewpoint to the screen (Figure 1D, right). As in the choice phase, they were asked to choose which of two targets would be easier to hit if they threw from the new position. The choice trials in the transfer phase (the new position) were the same as in the choice phase (the choice position).

Preanalyses for individual subjects

True visuo-motor error distribution

The subjects’ horizontal and vertical errors decreased across training. We modeled this visuo-motor learning as follows. Denote the horizontal and vertical errors of subjects’ endpoint (i.e., deviations from the center of the target) as (x, y) . We modeled (x, y) in the throwing task as a bivariate Gaussian random variable centered at $(0, 0)$ with standard deviations that decreased as exponential functions of the trial number t , separately for the horizontal and vertical directions.

To estimate the exponential learning functions, we first divided the 300 throwing trials into 20 bins of 15 trials. We assumed that the (x, y) values of the i th bin B_i was generated by the bivariate Gaussian distribution:

$$\phi_{B_i}(x, y) = \frac{1}{2\pi\sigma_x^{B_i}\sigma_y^{B_i}} \exp\left(-\frac{x^2}{2(\sigma_x^{B_i})^2} - \frac{y^2}{2(\sigma_y^{B_i})^2}\right). \quad (2)$$

In the throwing task, one subject had 14% and all the other subjects had less than 5% of their throws miss the screen. When the beanbag missed the screen entirely, we had no records of (x, y) and only knew that the endpoint was outside the screen region S . The

likelihood that the endpoint E was observed on a specific trial was therefore

$$f(E|\sigma_x^{B_i}, \sigma_y^{B_i}) = \begin{cases} \phi_{B_i}(x, y), & \text{if } E \text{ is on the screen} \\ 1 - \int_S \phi_{B_i}(x, y), & \text{if } E \text{ is outside the screen} \end{cases} \quad (3)$$

We estimated $\sigma_x^{B_i}$ and $\sigma_y^{B_i}$ for each bin using maximum-likelihood estimates.

We then fitted $\sigma_x^{B_i}$ and $\sigma_y^{B_i}$ to three-parameter exponential functions of trial number t :

$$\begin{aligned} \sigma_x(t) &= \theta_x + \kappa_x e^{-v_x t} \\ \sigma_y(t) &= \theta_y + \kappa_y e^{-v_y t}, \end{aligned} \quad (4)$$

where θ_x , κ_x , v_x , θ_y , κ_y , and v_y are free parameters, and the trial number of the i th bin is defined as the central number of the bin $t = 8 + 15(i - 1)$. With the fitted Equation 4, we could estimate the standard deviations for any trial.

Subjects' internal model of visuo-motor error distribution

We assume that subjects choose targets that maximize their probability of winning. The visual errors in perceiving the configuration of the targets are omitted. We define subjects' internal model of their visuo-motor error distribution (subjective error distribution) as the distribution that predicts subjects' choices between targets (Maloney & Mamassian, 2009), and use the pattern of choices to estimate the subjective distribution.

We estimated subjects' internal models of their visuo-motor error for the choice position and the new position separately, each as a bivariate Gaussian distribution:

$$\psi(x, y|\sigma_x, \sigma_y) = \frac{1}{2\pi\sigma_x\sigma_y} \exp\left(-\frac{x^2}{2(\sigma_x)^2} - \frac{y^2}{2(\sigma_y)^2}\right), \quad (5)$$

where σ_x and σ_y are free parameters, denoted σ_x^C and σ_y^C for the choice position and σ_x^N and σ_y^N for the new position.

We assume subjects would aim at the center of the target. For a specific trial with targets T_1 and T_2 , the perceived probabilities p_1 and p_2 of hitting them were the integrals of the probability density of the subjective visuo-motor error distribution contained in the targets:

$$\begin{aligned} p_1 &= \int_{T_1} \psi(x, y|\sigma_x, \sigma_y) dx dy, \\ p_2 &= \int_{T_2} \psi(x, y|\sigma_x, \sigma_y) dx dy \end{aligned} \quad (6)$$

We modeled subjects' choice on the trial as a Bernoulli random variable, with the probability of choosing T_2 as a logistic function of $p_1 - p_2$ following the normalized expected utility model (Erev, Roth, Slonim, & Barron, 2002):

$$\Pr(T_2) = \frac{1}{1 + e^{(p_1 - p_2)/(\tau D)}}, \quad (7)$$

where $D = p_1(1 - p_2) + (1 - p_1)p_2$ is a normalization term and $\tau > 0$ is a temperature parameter determining the randomness of the choice—the lower the temperature, the closer the subject to an ideal observer who always chooses the target that is more likely to be hit. We estimated τ , σ_x^C , and σ_y^C (or σ_x^N and σ_y^N) using maximum-likelihood estimates.

Exclusion of subjects

Two types of subjects were excluded from the group analyses of the choice task because their subjective error distributions were not estimable from their choices. First, we excluded subjects who violated dominance, i.e., those who preferred the circle even when the circle was small enough to be contained in, and thus dominated by, the rectangle, or vice versa. A subject would be excluded if she still preferred the circle when the diameter of the circle was 20% less than the shorter side of the rectangle or still preferred the rectangle when the diameter of the circle was 20% greater than the longer side of the rectangle. The subjective error distribution was undefined for subjects who violated dominance. One subject was excluded for violating dominance.

Second, we excluded subjects whose choices were indistinguishable from those predicted by an area-matching strategy. Subjects with an area-matching strategy would choose the target with the larger area. Subjects' choice on a specific trial was modeled as a Bernoulli random variable, with the probability of choosing T_2 determined by

$$\Pr(T_2) = \frac{1}{1 + e^{(A_1 - A_2)/(\tau(A_1 + A_2))}}, \quad (8)$$

where A_1 and A_2 are the areas of the targets T_1 and T_2 and $\tau > 0$ is a temperature parameter determining the randomness of the choice. We estimated τ using maximum-likelihood estimates. We compared the Gaussian model (Equation 5) with the area-matching model in goodness of fit using nested hypothesis tests (Mood, Graybill, & Boes, 1974, p. 440). If a subject's Gaussian model did not fit better than her area-matching model at the 0.05 significance level, we excluded the subject. Two subjects were excluded at the choice position and one additional subject was excluded at the new position. These subjects might really have

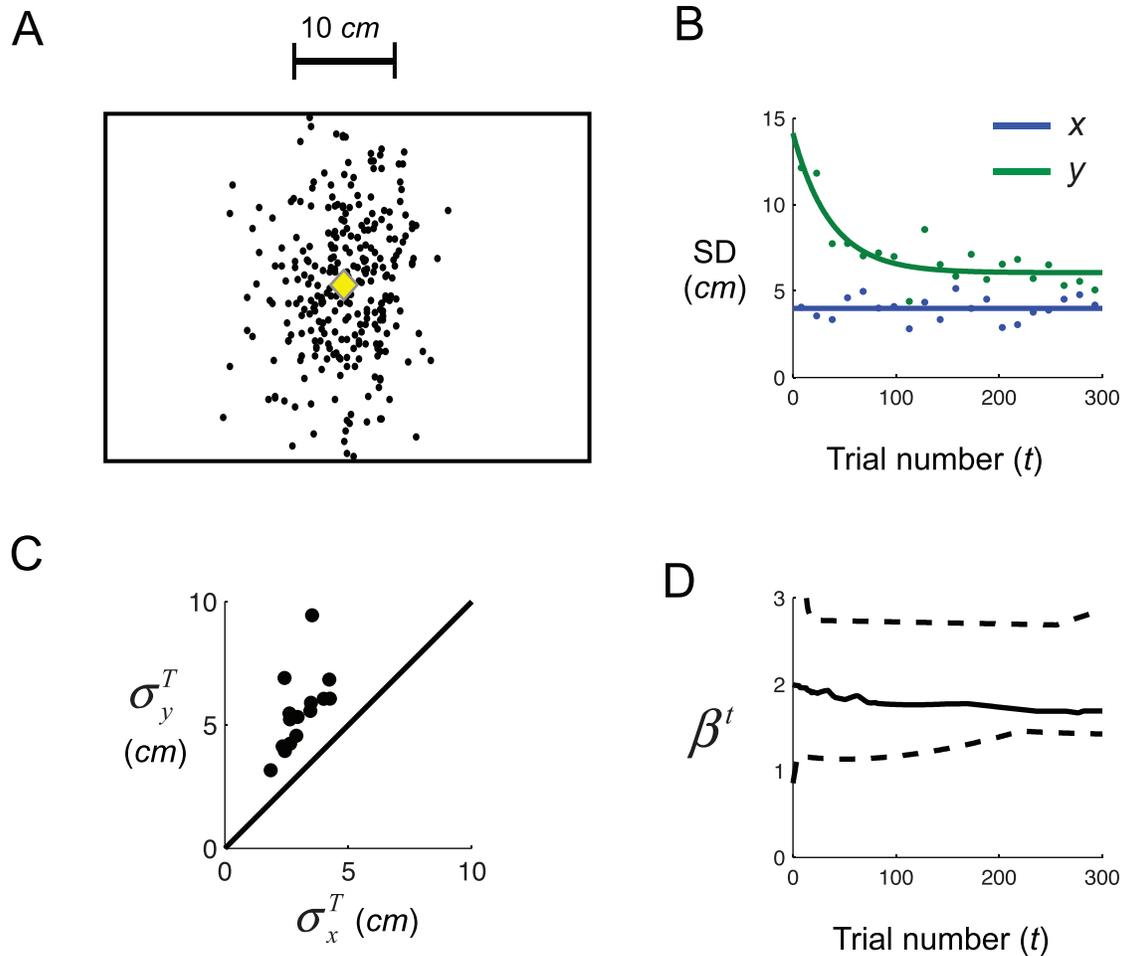


Figure 3. True visuo-motor error distribution. (A) Endpoints for one subject. Each dot denotes an endpoint on the screen. The yellow diamond marks the center of the screen and the target. (B) Standard deviations of visuo-motor error as functions of trial number for one subject. Blue and green are respectively for the horizontal and vertical directions. Dots denote standard deviations estimated in bins of 15 trials. Curves denote exponential fits (see Methods). (C) Vertical versus horizontal standard deviations at the end of training (i.e., $t = 300$). Each dot denotes one subject. Note that all subjects had a vertically elongated distribution. (D) Vertical-to-horizontal ratio as a function of trial number. The solid line denotes median ratios across subjects. Dashed lines denote the minimum and maximum ratio across subjects.

used an area-matching strategy so that their choices did not rely on their internal models of visuo-motor error distribution, or they might simply have assumed σ_x^C and σ_y^C (or σ_x^N and σ_y^N) that were much larger than the sizes of the targets. In either case, their internal models were unidentifiable from their choices.

Results

True visuo-motor error distribution

Subjects were trained to throw beanbags underhand for 300 trials. Figure 3A shows the distribution of one typical subject's endpoints. It is a bivariate Gaussian distribution, elongated in the vertical direction.

We modeled how the standard deviations of subjects' visuo-motor error decreased across training (see Methods). Figure 3B shows the horizontal and vertical standard deviations of the typical subject as exponential functions of the trial number. For this subject, the vertical direction exhibited more rapid improvement than the horizontal direction, and performance stabilized after approximately 50 trials. These results confirm that—in the throwing task—horizontal and vertical errors behave differently and there is little reason to expect isotropy. Some other subjects had a greater improvement in the horizontal direction instead (see Figure 4 for all subjects' curves).

Denote the horizontal and vertical standard deviations estimated at the end of the training phase as σ_x^T and σ_y^T (“T” stands for “true”). We define the overall standard deviation as $\sigma^T = \sqrt{\sigma_x^T \sigma_y^T}$ and the vertical-to-

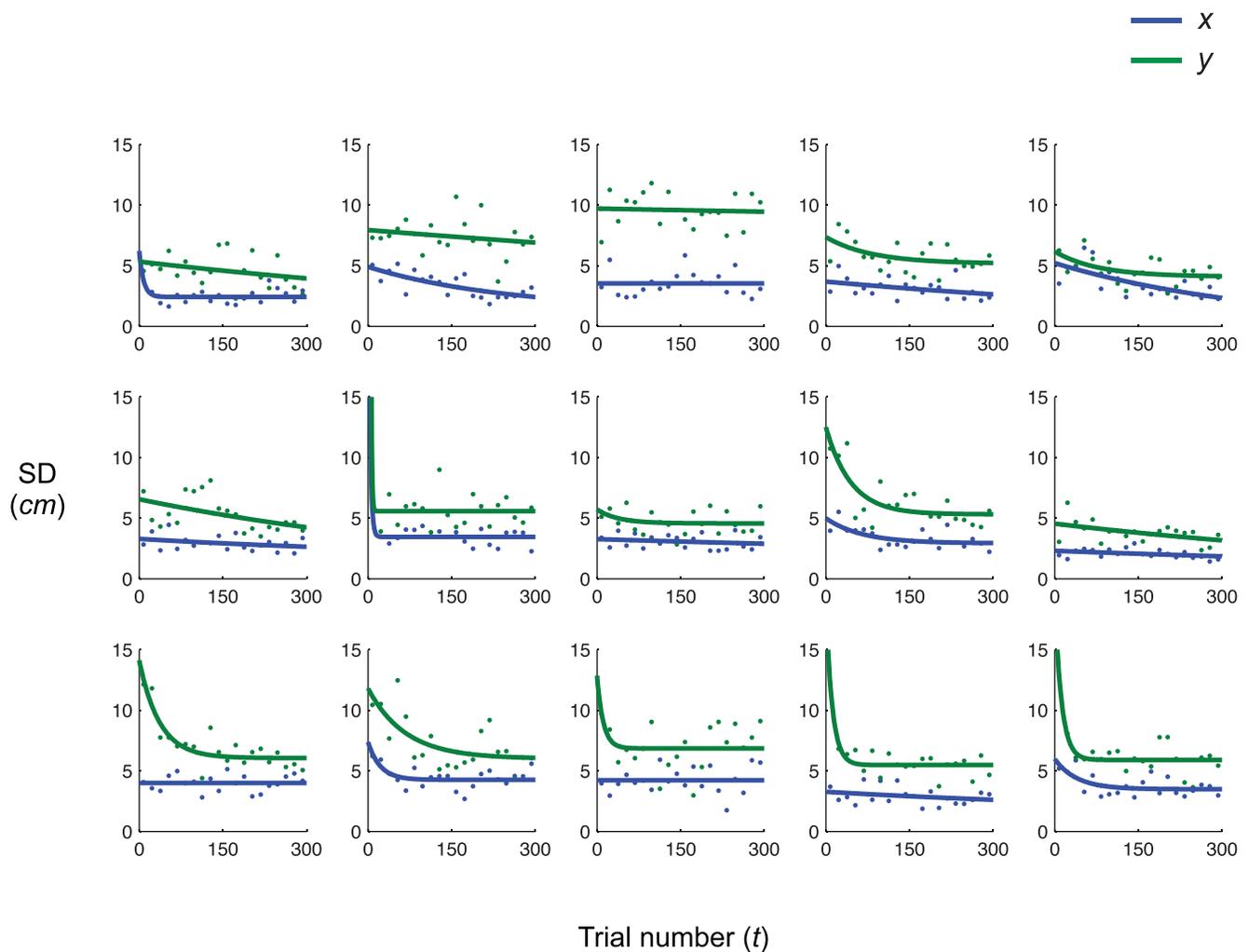


Figure 4. Standard deviations of visuo-motor error as functions of trial number for each subject. Each panel denotes one subject (the rightmost three subjects on the bottom row were excluded from the group analyses of the choice task). Blue and green are respectively for the horizontal and vertical directions. Dots denote standard deviations estimated in bins of 15 trials. Curves denote exponential fits (see Methods).

horizontal ratio of standard deviations as $\beta^T = \sigma_y^T / \sigma_x^T$. The counterpart measures at a specific trial t are denoted σ_x^t , σ_y^t , σ^t , and β^t .

What all subjects had in common was an elongation in the vertical direction ($\beta^T > 1$). At the end of the training (Figure 3C), the ratio β^T of the vertical to the horizontal standard deviation had a mean of 1.84 across the 15 subjects. The ratio varied with subject and changed across training, but except for the first few trials, the ratio for any subject across trials was well above 1 (Figure 3D).

Internal models at the choice and new positions

Based on each subject's choices, we estimated the horizontal and vertical standard deviations assumed in the subject's internal model of her visuo-motor error

distribution (see Methods) separately for the choice position (denoted σ_x^C and σ_y^C) and the new (transfer) position (denoted σ_x^N and σ_y^N). In the group analyses hereafter, we excluded subjects who violated dominance or used an area-matching strategy (see Methods for the logic and criteria). There were 12 valid subjects (three subjects excluded) for the choice position and 11 for the new position (one additional subject excluded).

Learning of the anisotropy estimate

In their internal models at the choice position, subjects underestimated the vertical-to-horizontal ratio of their visuo-motor error distribution, mean $\beta^C = 1.17$ versus $\beta^T = 1.85$, paired-sample two-tailed t test, $t(11) = -4.08$, $p = 0.002$. This underestimation could not be explained as a delayed estimation of the true distribu-

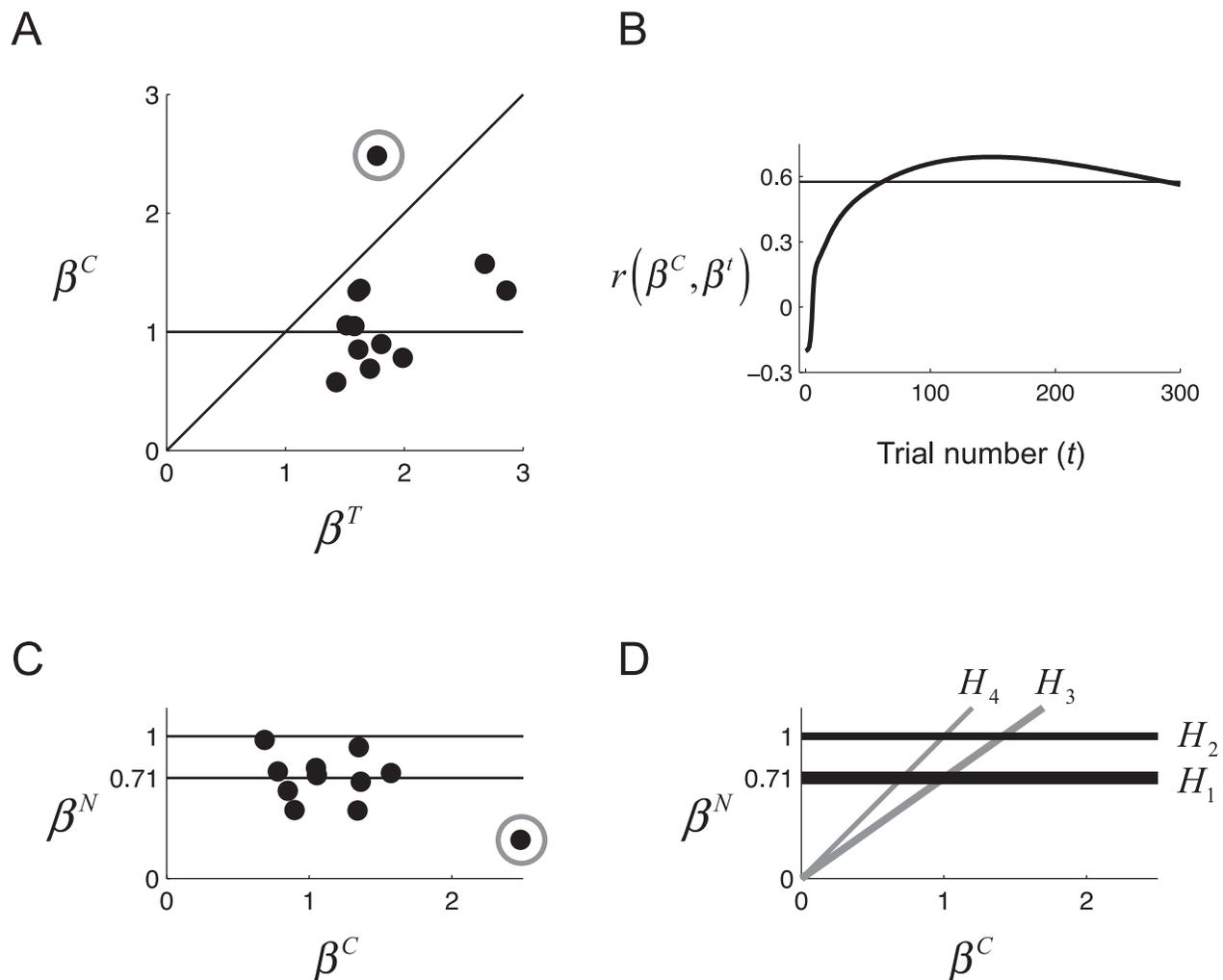


Figure 5. Vertical-to-horizontal ratio assumed in the internal model. (A) Choice-versus-true ratio. Each dot is for one subject. The outlier (circled) that was outside the regression line of β^C over β^T of all subjects at the 0.05 significance level was excluded from group analysis. (B) Correlation between the choice and true ratios as a function of trial number. The value at each trial number denotes the Pearson's correlation coefficient between the true ratio estimated at the trial and the choice ratio. The horizontal line marks the significance level of 0.05. (C) Ratio assumed at the new position versus the choice ratio. Each dot is for one subject. The same outlier circled as in (A). (D) Four hypotheses on transfer. Each line corresponds to one possible hypothesis concerning the relationship between the choice and new ratios. Hypothesis H_1 , that subjects assumed a vertical-to-horizontal ratio of $1/\sqrt{2}$ independent of the ratio they assumed at the choice position, best accounted for subjects' choices (see text for likelihood tests among hypotheses).

tion: As shown in Figure 3D, the median vertical-to-horizontal ratio was even larger at earlier stages of training. Subjects were effectively assuming an isotropic distribution, i.e., the value of β^C was indistinguishable from 1 (one-sample two-tailed t test), $t(11) = 1.12$, $p = 0.29$.

How did the vertical-to-horizontal ratio assumed in subjects' internal model arise from their training experience? Figure 5A shows β^C against β^T for each subject. The data point of one subject (circled) was outside the regression line of β^C over β^T of all data points at the 0.05 significance level. When this outlier was excluded, there was a marginally significant correlation between β^C and β^T , Pearson's $r = 0.56$, $p =$

0.072. The positive correlation between β^C and β^t was higher for the last three quarters of trials in training than in the first one quarter of trials (Figure 5B). That is, the vertical-to-horizontal ratio assumed in subjects' model reflected the true ratio in recent experience, though the magnitude of the true ratio was considerably underestimated.

If subjects incorrectly assumed an isotropic distribution during choice, then we might expect that their transfer distribution would also be in error but might correspond to a correct transfer of their erroneous estimate of their distribution in choice. We consider this possibility next.

Transfer of the anisotropy estimate

According to an objectively correct transfer from the training to the new position, we should have $\beta^N = \beta^C / \sqrt{2}$. But as Figure 5C shows, the value of β^N was constantly around $1/\sqrt{2}$ (0.71), irrespective of the value of β^C . This observation was confirmed by the following model comparison procedure.

We considered four possible hypotheses concerning transfer:

$$\begin{aligned} H_1 : \beta^N &= 1/\sqrt{2} + \varepsilon, \\ H_2 : \beta^N &= 1 + \varepsilon, \\ H_3 : \beta^N &= 1/\sqrt{2}\beta^C + \varepsilon, \\ H_4 : \beta^N &= \beta^C + \varepsilon \end{aligned} \quad (9)$$

where ε is a zero-mean Gaussian error term whose variance is a free parameter. We fitted the four models using maximum-likelihood estimates to predict the values of β^N . H_1 was the best among the four models according to the estimated likelihood: When the outlier subject (circled in Figure 5C, same as in Figure 5A) was excluded, H_1 was 289 times more likely than the second best model to produce the observed values of β^N ; when the outlier subject was not excluded, the likelihood ratio of H_1 to the second best model was 1,321. We conclude that subjects assumed a different vertical-to-horizontal ratio in their internal model at the new position from that of the choice position, but instead of transforming the ratio they had learned to the new position, they transformed an isotropic model in the objectively correct way to the new position.

Coordinate systems for visuo-motor error

The values of σ_x^C and σ_y^C were highly correlated (Pearson's $r = 0.89$, $p < 0.001$), as were σ_x^N and σ_y^N (Pearson's $r = 0.92$, $p < 0.001$), while the Pearson's correlation between σ_x^T and σ_y^T was only $r = 0.58$, $p = 0.048$ (computed for the valid subjects at the choice position; the correlation for the valid subjects at the new position was $r = 0.62$, $p = 0.041$).

The medium-size correlation between σ_x^T and σ_y^T was expected: There was little reason to expect that different subjects had the same vertical-to-horizontal ratio for their motor variances. If subjects had estimated their horizontal and vertical variances independently, we would expect that the correlations between parameters of the subjects' model distributions would be no higher than those of their true distributions, since the former—based on the latter—would be further corrupted by visuo-motor or neural noise: Correlation should not increase.

However, according to bootstrapping tests (Efron & Tibshirani, 1993), the correlations between horizontal and vertical standard deviations in subjects' internal

models were marginally significantly higher than that of the true distribution (one-tailed test, $p = 0.084$ and $p = 0.065$, respectively, for the choice and new positions). The two results taken together would be expected no more than $p = 0.0055$ of the time if the null hypothesis of independence of horizontal and vertical directions were true.

These results suggest that a single parameter r controls both vertical and horizontal standard deviations. Indeed, if the visuo-motor system uses an isotropic representation, then there would be no reason to have two separate parameters σ_x and σ_y for horizontal and vertical variances—they must be equal. Moreover, if the isotropy assumption were correct, then the visuo-motor system could combine estimates of vertical and horizontal deviations across trials to get a more accurate estimate of r .

In the following analyses, we used the overall standard deviation (σ^T , σ^C , and σ^N) as the variance estimate for the true distribution and subjects' models. Results based on the horizontal and vertical standard deviations were similar.

Learning and transfer of the variance estimate

How were subjects' internal models built upon their experience in training? How were subjects' internal models at the new position related to their internal models at the choice position? The most obvious attempts led to negative results: No significant correlations were found between σ_x^C and σ_x^T , σ_y^C and σ_y^T , σ_x^C and σ_y^T , or σ_y^C and σ_x^T for any trial number t (Pearson's correlation $p > 0.52$). The standard deviations assumed in subjects' internal models at the new position could not be predicted by those at the old position either: There were no significant correlations between σ_x^N and $\sqrt{2}\sigma_x^C$, nor between σ_y^N and σ_y^C (Pearson's correlation $ps > 0.23$).

Subjects' visuo-motor variance decreased across training (Figures 3B and 4). Here we introduced second-order measures concerning the change rate of visuo-motor variance at trial number t : horizontal rate $\delta_x^t = \sigma_x^t / \sigma_x^{t-1}$, vertical rate $\delta_y^t = \sigma_y^t / \sigma_y^{t-1}$, and overall rate $\delta_{xy}^t = \sqrt{\delta_x^t \delta_y^t}$. The lower the change rate, the faster the decrease in visuo-motor variance. A change rate of 1 means no improvement in visuo-motor variance.

We found that how much the variance assumed in subjects' internal model over- or underestimated the true variance could be predicted by the vertical change rate but not by the horizontal or overall change rate. As we considered how subjects misrepresented their variance at the new position, relative to that predicted from the objectively correct transfer, we found that, again, the vertical change rate but not the horizontal or overall change rate of true variance proved to be a

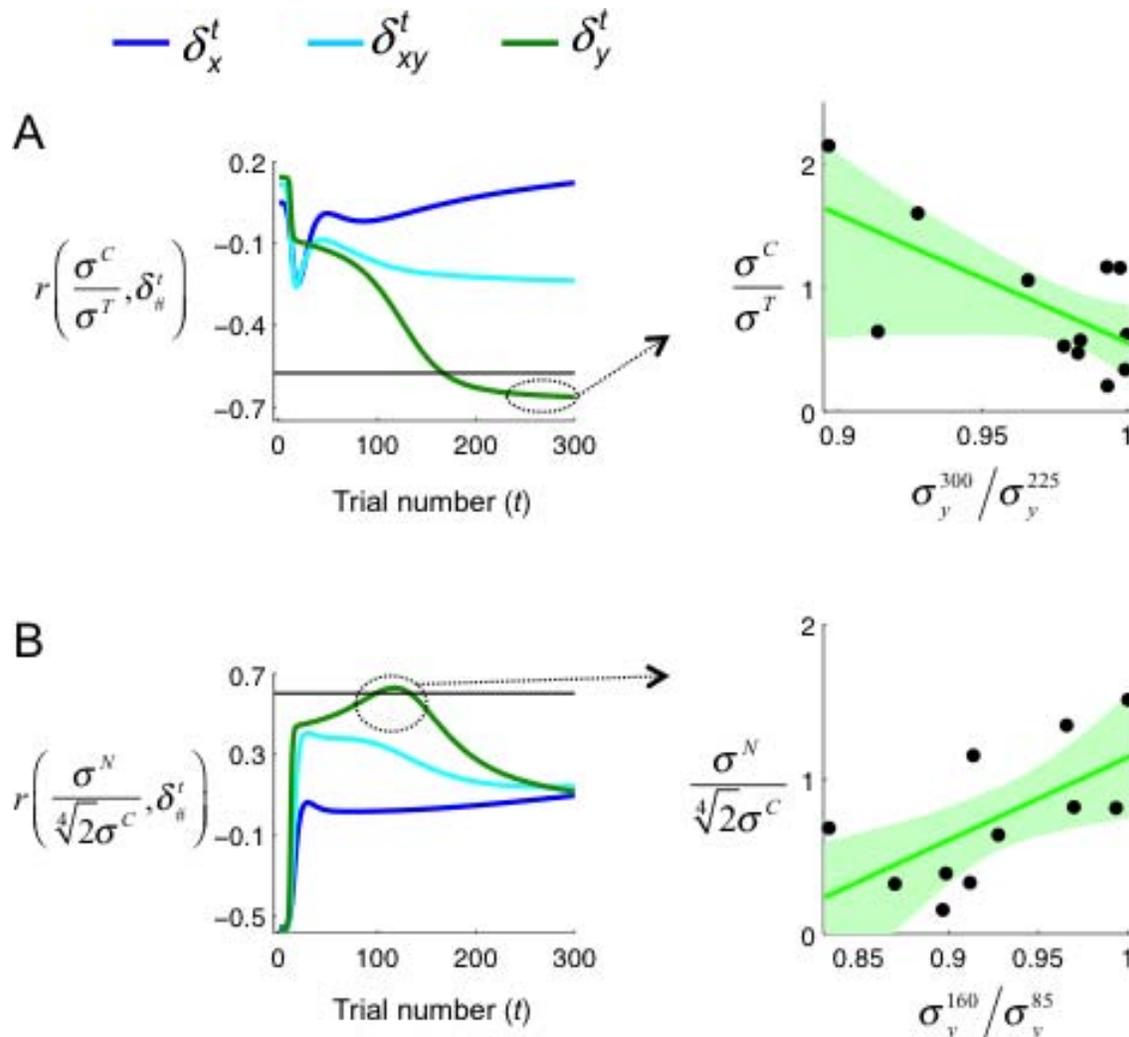


Figure 6. Standard deviations assumed in the internal model. The symbols δ_x^t , δ_y^t , and δ_{xy}^t denote the change rate of true standard deviations at trial number t , respectively, for the horizontal direction, the vertical direction, and overall (i.e., $\delta_{xy}^t = \sqrt{\delta_x^t \delta_y^t}$). (A) Learning. Left: Pearson's correlation between the misestimation of true standard deviation at the choice position (σ^C/σ^T) and the change rates. The horizontal line marks the significance level of 0.05. The correlation was significant only for the vertical change rate (green curve) in the second half of the training phase. A 75-trial range of the most prominent correlations was from trial 225 to trial 300. Right: The correlation σ^C/σ^T predicted by $\sigma_y^{300}/\sigma_y^{225}$. Each dot denotes one subject. Solid line denotes the linear prediction. Shadow denotes its 95% confidence interval. (B) Transfer. Left: Pearson's correlation between the mistransfer of standard deviation from the choice position to the new position (σ^N/σ^C) and the change rates. The horizontal line marks the significance level of .05. The correlation was significant only for the vertical change rate (green curve) in the second quarter of the training phase. A 75-trial range of the most prominent correlations was from trial 85 to trial 160. Right: The correlation σ^N/σ^C predicted by $\sigma_y^{160}/\sigma_y^{85}$. Each dot denotes one subject. Solid line denotes the linear prediction. Shadow denotes its 95% confidence interval.

significant predictor. See the Appendix and Figure 6 for details.

Discussion

We investigated how people learn and represent internal models of their own visuo-motor error distribution and how they transfer these models to

novel situations. Subjects were first trained in an underhand beanbag-throwing task, and we tracked their visuo-motor error distribution from trial to trial. We then asked subjects to choose between pairs of targets while standing at the trained (choice) position or at an untrained new position. Based on their choices, we could estimate the anisotropy of their internal models of visuo-motor error distribution at the choice and new positions (Maloney & Mamassian, 2009; Zhang et al., 2013).

All subjects' visuo-motor error distributions were vertically elongated (anisotropic) bivariate Gaussian. At the end of training, the vertical standard deviation was, on average, 1.84 times the horizontal standard deviation. However, we found that the internal models subjects assumed at the choice position were significantly less vertically elongated and were indistinguishable from isotropic. That is, we replicated the isotropy bias originally found in the speeded reaching-movement literature (Hudson et al., 2010; Zhang et al., 2013) in a visuo-motor task that recruits different muscular components in the vertical and horizontal directions.

One open question is whether observers would internalize their error distribution better if they received a different kind of feedback. We do note that the feedback we gave them is already more than they might receive in an everyday throwing task (during training, after each toss, we marked the point they hit with a dot). But still, it would be of interest to find out if there is some way to convey to the subjects their actual error distributions.

The tendency to assume an isotropic distribution in the overpracticed reaching task might be the result of adaptive tuning to experience preceding the experiment. That we found the isotropy bias in the underhand throwing task allows us to exclude this possibility. It is more likely that subjects had difficulty learning anisotropic probability distributions. Indeed, the isotropy bias proved to be highly resistant to conflicting experience: Subjects were trained on different targets, and they hit the vertical targets much more often than the horizontal targets (on average, 38% vs. 26%).

Intriguingly, subjects' internal model at the new position was effectively anisotropic: The vertical-to-horizontal ratio was indistinguishable from $1/\sqrt{2}$. It is as if they incorrectly assumed an isotropic distribution at the choice position but correctly predicted how this anisotropy ratio (i.e., 1) would change with their throwing angles to the screen. Of course, an alternative strategy they might have pursued would be to scale the apparent target to match its cross section projected into the fronto-parallel plane. This strategy would be indistinguishable from scaling the distribution. A possible way for subjects to implement this strategy is to rely on their retinal image for their judgments. Direct access to the retinal image is uncommon in human perception but may characterize the motor system (Goodale & Milner, 1992).

Subjects did not have difficulty in representing or computing on two-dimensional anisotropic distributions, which implies, similar to probabilistic inference (Acerbi, Vijayakumar, & Wolpert, 2014), that the difficulty is mainly in learning distributions. Of course, one possibility is that they in effect transform the target, using its projection as seen from the new

position, and still assume an isotropic distribution. In the following, we discuss the implications of our results in terms of cognitive constraints and neural coding.

The isotropy bias: Cognitive constraints

It is well documented that people have difficulty compensating for bimodal visuo-motor error distributions: They often treat bimodal distributions as unimodal (Scheidt, Dingwell, & Mussa-Ivaldi, 2001). Even if they can finally learn a bimodal distribution, it may take thousands of trials (Körding & Wolpert, 2004). Similar unimodal bias is also observed in learning other types of probability distributions (Flannagan, Fried, & Holyoak, 1986; Nisbett & Kunda, 1985). It is as if people have expectations for unimodal distributions before they have any experience about the distribution to be estimated. It is possible that the isotropy bias is another type of expectation embedded in human cognition.

If the isotropy bias reflects subjects' expectations when they enter the task, subjects should converge to an anisotropic distribution to a greater and greater extent after more and more exposure to the distribution. Whether this is true is an empirical question to be further tested. At least according to the present study and Zhang et al. (2013), 300 trials of training are not sufficient to eliminate the isotropy bias.

Alternatively, subjects may simply not be able to estimate the probability distributions of two or more dimensions simultaneously. Evidence comes from unsupervised categorization tasks: When there are two feature dimensions and both are useful for perfect categorization, subjects' categorization behavior shows that they have access to only the distribution of one dimension and not the joint distribution of the two dimensions (Ashby et al., 1999; Goudbeek et al., 2008; Jüttner & Rentschler, 1996). In the case of two-dimensional visuo-motor error distributions, estimating the distribution on the radial dimension but omitting it on the angular dimension would correspond to the isotropy bias.

Coordinate systems

For subjects' internal models at both the choice and new positions, the extremely high positive correlation between the horizontal and vertical standard deviations demonstrates that the two directions are not independently coded. In effect, one parameter r controls both the horizontal and vertical standard deviations of the distributional representation. One possibility is that polar coordinates (r, θ) rather than Cartesian coordinates (x, y) are used in coding two-dimensional

visuo-motor error distributions. If so, the isotropy bias is due to the visuo-motor system's bias to base judgments on r alone, ignoring direction θ . This possibility echoes the fact that humans typically use polar coordinates to code spatial locations (Huttenlocher & Lourenco, 2007).

The existence of the isotropy bias hints that the angle dimension receives little attention in the coding of visuo-motor error distributions. We noticed that the angle dimension also has low priority in spatial coding: Young children (Sandberg, Huttenlocher, & Newcombe, 1996) and monkeys (Merchant, Fortes, & Georgopoulos, 2004) use two types of spatial codes for radius but only one type of code for angle, though they use both types to code angle when angle is presented alone.

However, we emphasize that we have no evidence concerning the second parameter of the “polar-like” coordinate system. Whether it is direction θ remains to be determined.

Keywords: perception and action, movement planning, visuo-motor uncertainty, representation, transfer, choice

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Appendix

Detailed results on the variance estimate

Learning of the variance estimate

We found that how much the variance assumed in subjects' internal model over- or underestimated the true variance could be predicted by the vertical change rate but not by the horizontal or overall change rate. The left panel of Figure 6A shows Pearson's correlations between σ^C/σ^T and δ_x^t (δ_y^t , δ_{xy}^t) as a function of the trial number t . There was a significant negative correlation between σ^C/σ^T and δ_y^t for the second half of the training phase ($ps < 0.05$). In contrast, for any trial t , the correlation between σ^C/σ^T and δ_x^t and between σ^C/σ^T and δ_{xy}^t was not significant ($ps > 0.41$).

The right panel of Figure 6A shows σ^C/σ^T as a linear function of $\sigma_y^{300}/\sigma_y^{225}$. The measure $\sigma_y^{300}/\sigma_y^{225}$ reflects the accumulated δ_y^t over trial 225 to trial 300, the 75-trial range with the largest negative correlation between σ^C/σ^T and δ_y^t . That σ^C/σ^T decreased with $\sigma_y^{300}/\sigma_y^{225}$ (σ^C/σ^T negatively correlated with δ_y^t) was counterintuitive, which means subjects who had a greater decrease in motor variance would more likely overestimate their motor variance at the end of training.

The first explanation that came to our mind for the negative correlation was a delayed estimation, an idea that subjects' internal models failed to catch the quick change of their motor variance and reflected their motor variance at an earlier time point. If this were true, subjects who had a greater decrease in motor variance would not show a greater overestimation of variance when the variance at an earlier time point was used as reference. To test this hypothesis, we replaced σ^C/σ^T with σ^C/σ^t and computed the correlation between

σ^C/σ^t and δ_y^t for a different trial number t (1–300). Inconsistent with the prediction of delayed estimation, the correlation was negative for trials as early as trial 5.

We conjecture that the negative correlation between σ^C/σ^T and δ_y^t suggests a reverse effect of the internal model on motor performance: Subjects who were less likely to underestimate their motor variance would have a greater improvement in motor variance. This hypothesis—that the internal model not only passively represents motor performance but also guides the improvement of motor performance—remains to be tested in the future.

Transfer of the variance estimate

If subjects made the correct transfer ($\sigma_x^N = \sqrt{2}\sigma_x^C$, $\sigma_y^N = \sigma_y^C$), they would have $\sigma^N = \sqrt[4]{2}\sigma^C$. The left panel of Figure 6B shows Pearson's correlations between $\sigma^N/(\sqrt[4]{2}\sigma^C)$ and δ_x^t (δ_y^t , δ_{xy}^t) as a function of the trial number t . There was a significant positive correlation

between $\sigma^N/(\sqrt[4]{2}\sigma^C)$ and δ_y^t during the second quarter of the training phase ($ps < 0.05$). In contrast, for any trial t , the positive correlation between $\sigma^N/(\sqrt[4]{2}\sigma^C)$ and δ_x^t and between $\sigma^N/(\sqrt[4]{2}\sigma^C)$ and δ_{xy}^t was insignificant ($ps > 0.21$).

This positive correlation indicates that subjects who had a greater decrease in their motor variance would underestimate their motor variance at the new position to a greater extent. It is as if subjects were more optimistic about the new position when they had experienced a greater improvement during training. The right panel of Figure 6B shows $\sigma^N/(\sqrt[4]{2}\sigma^C)$ as a linear function of $\sigma_y^{160}/\sigma_y^{85}$ (the accumulation of δ_y^t over a 75-trial range of the largest positive correlation between $\sigma^N/(\sqrt[4]{2}\sigma^C)$ and δ_y^t). Note that for subjects who had no improvement in the range ($\sigma_y^{160}/\sigma_y^{85} = 1$), the variance assumed in the internal model at the new position was close to that predicted by the objectively correct transfer ($\sigma^N/(\sqrt[4]{2}\sigma^C) = 1$).