Human representation of visuo-motor uncertainty as mixtures of orthogonal basis distributions

Hang Zhang¹⁻⁶, Nathaniel D Daw⁴⁻⁶ & Laurence T Malonev⁴⁻⁶

In many laboratory visuo-motor decision tasks, subjects compensate for their own visuo-motor error, earning close to the maximum reward possible. To do so, they must combine information about the distribution of possible error with values associated with different movement outcomes. The optimal solution is a potentially difficult computation that presupposes knowledge of the probability density function (pdf) of visuo-motor error associated with each possible planned movement. It is unclear how the brain represents such pdfs or computes with them. In three experiments, we used a forced-choice method to reveal subjects' internal representations of their spatial visuo-motor error in a speeded reaching movement. Although subjects' objective distributions were unimodal, close to Gaussian, their estimated internal pdfs were typically multimodal and were better described as mixtures of a small number of distributions differing only in location and scale. Mixtures of a small number of uniform distributions outperformed other mixture distributions, including mixtures of Gaussians.

$$\mathbf{x}$$
..., \mathbf{x} ..., \mathbf{x} ..., \mathbf{x} ..., \mathbf{x} ..., \mathbf{x} ..., $\mathbf{b}_n(\mathbf{x})$..., \mathbf{x} ...

$$f(x) \approx \sum_{i=1}^{n} w_i b_i(x) \tag{1}$$

Received 18 March; accepted 5 June; published online 29 June 2015; doi:10.1038/nn.4055

¹Department of Psychology and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, China. ²PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing, China. ³Peking-Tsinghua Center for Life Sciences, Peking University, Beijing, China. ⁴Department of Psychology, New York University, New York, New York, New York, USA. 5Center for Neural Science, New York University, New York, New York, USA. 6Institute for the Interdisciplinary Study of Decision Making, New York University, New York, New York, USA. Correspondence should be addressed to H.Z. (hang.zhang@pku.edu.cn).

on and property

.... ,

and the second of the second o

RESULTS

Experiment 1: objective pdf

- د د د مان د د رد مان مان د د د - - الرائد ا

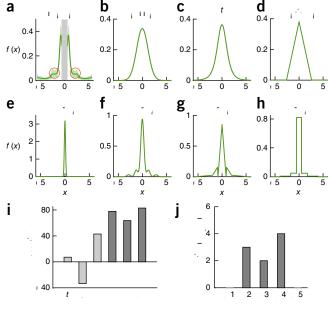
Experiment 1: internal pdf

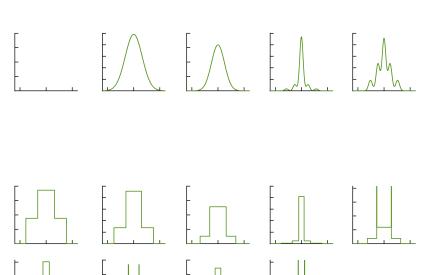
and the second of the second o

ARTICLES

Figure 3 Internal pdfs in the choice task of experiment 1. (a) Non-parametric visualization of the internal pdf for one subject. Green-shaded regions denote $\pm s.e.m.$ x is in the unit of the subject's horizontal s.d. estimated from the reaching task. The gray-shaded central range of [-0.6, 0.6] could not be reliably estimated in experiment 1 (Online Methods) and the visualization therefore gives information about the pdf only away from the origin. Two regions of interest are marked by red circles. The visualizations for all subjects are shown in **Supplementary Figure 1**. (b-h) Internal pdfs estimated from different models for the same subject. (i) AlCc difference between the Gaussian model and the other six models summed over the nine subjects. The unimodal models (including vG-mix) and mixture models are coded in light gray and dark gray, respectively. Positive difference indicates better fit. LD denotes linear decay. (j) Number of subjects best fit by each U-mix model.

from the color of : د **مارسور** داده رد در در مارسد، مارد در در د Unimodal distributions. $\mathbf{k} \qquad \qquad \mathbf{k} \qquad \mathbf{k} \qquad \qquad \mathbf{$ with the same of t - ، بیر د نہال بیاد ایک نہیں اور د Mixture distributions. . P.-Acres 180 c .**p.** (...,, - x)№ , . . , . . . **n** . . , . . **.** . . . $\mathcal{L}_{\mathbf{a}}$ $\mathcal{L}_{\mathbf{a}}$





a proper and the second of the

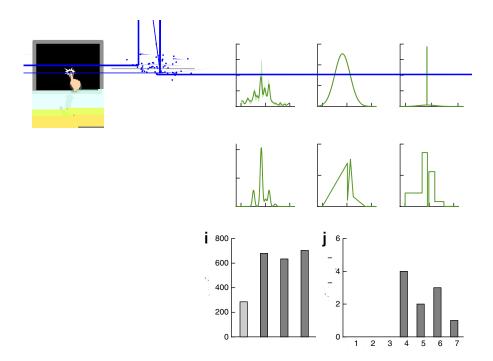


Figure 6 Experiment 3. (a) The reaching task. Left, the task. The task for experiment 3 was the same as that for experiment 1, except that a circular target was used. Right, the endpoints for one subject. (b) The choice task. The task for experiment 3 was the same as that for experiment 1, except that each pair of targets was a rectangle and a circle. (c) Design of the choice task. Ten different rectangles were used; for each, the radius of its paired circle was adjusted by adaptive procedures for 100 trials. (d) AICc difference between the Gaussian model and the other four models summed over the 18 subjects. The unimodal models (including vG-mix) and mixture models are coded in light gray and dark gray, respectively. Positive difference indicates better fit. (e) Number of subjects best fit by each U-mix model.

DISCUSSION

and the second of the second j. . . , . - j. . , ' ے در میل ایک میں میل میں امال میں امال میل میل میل میل

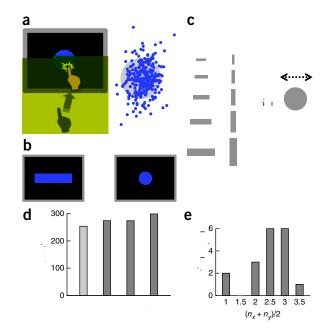
...... ,. j. ., \ldots , - \mathbf{x} , - \mathbf{x})... and the state of t **X**... ., .., .. , . . .

 $B = \{ 1, \dots, n \}, \dots \in \mathbb{R}^n \times \mathbb{R}^n : \mathbb{R}^n : \mathbb{R}^n \times \mathbb{R}^n : \mathbb{R}^n \times \mathbb{R}^n : \mathbb{R}^n \times \mathbb{R}^n : \mathbb{R}^n : \mathbb{R}^n \times \mathbb{R}^n : \mathbb{R}^n : \mathbb{R}^n \times \mathbb{R}^n : \mathbb{R}^n$..., (...**x** ..., - **x**) .;.,,,.,, ., <u>p</u> **½**. **.**

A company of the second A. . , and a second of the second o ر رایان مار رایانیان مار رماریی (مار با<mark>مار باریان ماریان ماریان ماریان</mark> ماریان أنجار بالمالية بالمرابع المرابع المنظر بمران المنظر المرابع والأراب والمراز والمراز والمراز مال

Relationship to previous measures

A .. 🎉 Simplifying probabilistic calculation and the state of t 26 29, 12 ..., p. 16 ..., p. 18 .



Discrete representation and near-optimal motor decisions

and the second of the second o ..., ,.., ,.., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., ,..., and the first of the contract 21 . , . **.** . . . 8. A مارد درد ماردومارد در x درد مار مارد دیا

the second of th و در در <mark>مان مان مان در در در مان مان در در مان مان در مان در داخ</mark> در د<mark>مان در داخ</mark> در در مان در در در در در در در В. . . . $(A_1, \dots, A_{n-1}, \dots, A_{n-1}$., ...,,..,... . . . , ... **X**... \mathbf{a}_{0} , \mathbf{c}_{0} , \mathbf{c}_{0} سال دی را دینال در از درد. این درد از درد از درد از دردی از میال دی در از دردی از این در از این کلا

Discrete representation as explanation for decision biases

 $15 \times 8(x) - 3((x) - 1 - (x) + (x) - 12(x) + (x) - ($

- Akaike, H. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19, 716–723 (1974).
- 19. Hurvich, C.M. & Tsai, C.-L. Regression and time series model selection in small samples. *Biometrika* **76**, 297–307 (1989).
- Stephan, K.E., Penny, W.D., Daunizeau, J., Moran, R.J. & Friston, K.J. Bayesian model selection for group studies. *Neuroimage* 46, 1004–1017 (2009).
- Zhang, H., Daw, N.D. & Maloney, L.T. Testing whether humans have an accurate model of their own motor uncertainty in a speeded reaching task. *PLOS Comput. Biol.* 9, e1003080 (2013).
- Oruç, I., Maloney, L.T. & Landy, M.S. Weighted linear cue combination with possibly correlated error. Vision Res. 43, 2451–2468 (2003).
- Acerbi, L., Wolpert, D.M. & Vijayakumar, S. Internal representations of temporal statistics and feedback calibrate motor-sensory interval timing. *PLOS Comput. Biol.* 8, e1002771 (2012).
- 24. Daw, N.D., Courville, A.C. & Dayan, P. Semi-rational models of conditioning: the case of trial order. in *The Probabilistic Mind: Prospects for Bayesian Cognitive Science* (eds. N. Chater & M. Oaksford) 431–452 (Oxford University Press, Oxford, 2008).
- Gershman, S. & Wilson, R. The neural costs of optimal control. Adv. Neural Inf. Process. Syst. 23, 712–720 (2010).
- Vul, E., Goodman, N.D., Griffiths, T.L. & Tenenbaum, J.B. One and done? Optimal decisions from very few samples. Cogn. Sci. 38, 599–637 (2014).
- Sanborn, A.N., Griffiths, T.L. & Navarro, D.J. Rational approximations to rational models: alternative algorithms for category learning. *Psychol. Rev.* 117, 1144 (2010).

- Vul, E., Hanus, D. & Kanwisher, N. Attention as inference: selection is probabilistic; responses are all-or-none samples. J. Exp. Psychol. Gen. 138, 546–560 (2009).
- Daw, N.D. & Courville, A. The pigeon as particle filter. in Advances in Neural Information Processing Systems (ed. J.C. Platt, D. Koller, Y. Singer & S. Roweis) 369–376 (MIT Press, 2007).
- 30. Maloney, L.T. Evaluation of linear models of surface spectral reflectance with small numbers of parameters. *J. Opt. Soc. Am. A* **3**, 1673–1683 (1986).
- 31. Körding, K.P. & Wolpert, D.M. The loss function of sensorimotor learning. *Proc. Natl. Acad. Sci. USA* 101, 9839–9842 (2004).
- Todorov, E. & Jordan, M.I. Optimal feedback control as a theory of motor coordination. Nat. Neurosci. 5, 1226–1235 (2002).
- Harris, C.M. & Wolpert, D.M. Signal-dependent noise determines motor planning. Nature 394, 780–784 (1998).
- Wolpert, D.M., Ghahramani, Z. & Jordan, M.I. An internal model for sensorimotor integration. *Science* 269, 1880–1882 (1995).
- 35. Hamilton, B.H. Does entrepreneurship pay? An empirical analysis of the returns to self-employment. *J. Polit. Econ.* **108**, 604–631 (2000).
- 36. Harvey, C.R. & Siddique, A. Conditional skewness in asset pricing tests. *J. Finance* 55, 1263–1295 (2000).
- 37. Kraus, A. & Litzenberger, R.H. Skewness preference and the valuation of risk assets. *J. Finance* **31**, 1085–1100 (1976).
- 38. Moskowitz, T.J. & Vissing-Jørgensen, A. The returns to entrepreneurial investment: a private equity premium puzzle? *Am. Econ. Rev.* **92**, 745–778 (2002).





 $\nabla b_i > 0, h_i$

doi:10.1038/nn.4055

P
y and the state of
Summary of statistical tests.
,, .,,,,,,
. 21 Δ C 18,19

\mathbf{x} ... \mathbf{x} \mathbf{x}

A Supplementary Methods Checklist

- Pelli, D.G. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* 10, 437–442 (1997).
 Brainard, D.H. The psychophysics toolbox. *Spat. Vis.* 10, 433–436 (1997).
- 41. Erev, I. et al. A choice prediction competition: choices from experience and from description. J. Behav. Decis. Mak. 23, 15-47 (2010).
- Rasmussen, C.E. & Williams, C.K.I. Gaussian Processes for Machine Learning (MIT Press, 2006).

NATURE NEUROSCIENCE doi:10.1038/nn.4055