

TECHNICAL COMMENT

NEURONAL MODELING

Comment on “Single-trial spike trains in parietal cortex reveal discrete steps during decision-making”

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Latimer *et al.* (Reports, 10 July 2015, p. 184) claim that during perceptual decision formation, parietal neurons undergo one-time, discrete steps in firing rate instead of gradual changes that represent the accumulation of evidence. However, that conclusion rests on unsubstantiated assumptions about the time window of evidence accumulation, and their stepping model cannot explain existing data as effectively as evidence-accumulation models.

Latimer *et al.* (1) analyzed the spiking activity of neurons in the lateral intraparietal (LIP) area of parietal cortex and challenged the hypothesis that these neurons represent the accumulation of noisy evidence bearing on a perceptual choice (e.g., drift diffusion). They conclude that these neurons represent jumps (or steps) from a neutral to a high or low state that represents the upcoming choice. Accordingly, the ramplike activity of LIP neurons is an artifact caused by averaging step functions occurring at different times. Conceptually, their step model implies that LIP activity represents either (i) the outcome of the decision, corresponding to steps synchronized to the end of the process, or (ii) the decision process itself, corresponding to the population average of all-or-none steps contributed by individual neurons at different times. Neither interpretation is consistent with existing data.

The first interpretation is refuted by choice-reaction time (RT) experiments (2). Aligned to the beginning of deliberation, the across-trial averages of such steps would resemble a ramp. However, aligned to the end of the decision, synchronous steps should be obvious [e.g., figures 2A and 3A in (2)]. The LIP data are inconsistent

with this idea (Fig. 1A): trials with long RT do not hover in a neutral state until the end of the decision [see also (3)].

The second interpretation could explain the ramps aligned to saccadic responses in the RT experiments. However, this interpretation is inconsistent with other experiments in which a sequence of shapes replaces random-dot motion to furnish discrete packets of evidence. Under these conditions, LIP neurons do not step to stereotyped high or low states. Instead, they produce graded responses throughout the decision according to the sign and strength of the evidence provided by the current shape (Fig. 1B). Further, the graded population responses are not simply a mixture of high and low steps (4, 5). If they were, the change

in firing rate induced by a shape should diminish for later shapes, because the neuron is more likely to have already stepped. This is clearly incorrect [see figures 3B and 4B in (4)]. Thus, LIP neurons encode multiple small, noisy changes in evidence (not one-time, all-or-nothing steps) in a manner consistent with diffusion or random-walk dynamics.

These points question the conclusions in (1). Then why do their analyses suggest stepping? Parietal activity can step in the context of quickly planned eye movements to visual targets (6, 7). In contrast, diffusion (ramping) dynamics arise when the decision to make such an eye movement results from the temporal integration of evidence over a more prolonged interval. Therefore, before using models to identify (or refute) neural correlates of an integration-based decision process, it is essential to (i) know that the neural activity in question is occurring in a behavioral context that is actually based on prolonged integration and (ii) focus any model comparison on the epoch in which this integration occurs.

Unfortunately, it is difficult to estimate the integration times from the behavioral data in (1). They did not use an RT experiment, and their monkey's accuracy is flat over the viewing durations they tested (Fig. 2, filled stars). It is possible to deduce integration times from a follow-up experiment in the same monkey, using a broader range of durations (Fig. 2, open symbols). Fitting these data with bounded diffusion (curves) yields a median integration time of ~250 ms (across all motion strengths). However, the monkey's accuracy is substantially worse in the earlier data, analyzed in (1). One possibility is that the poorer accuracy is explained by a combination of guessing and overall lower sensitivity—partially compensated by an elevated decision bound—whose net effect is longer integration times (~310 ms). Alternatively, the poor accuracy is explained by brief integration times (~70 ms) or possibly a different

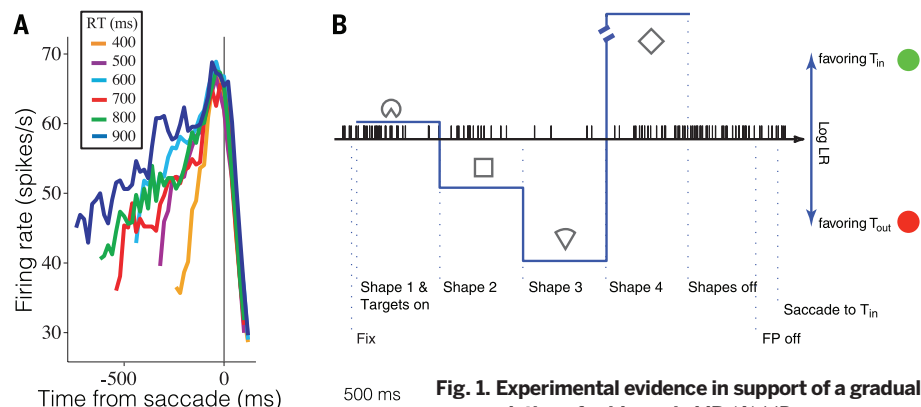


Fig. 1. Experimental evidence in support of a gradual accumulation of evidence in LIP. (A) LIP neurons ramp, on average, during an RT task. Averages are sorted by RT quantile (color), using trials in which the monkey chose the direction associated with the choice target in the neuron's response field. [Modified from (2), showing responses from ~200 ms after stimulus onset; see also figure 2, B and D, in (11)]. (B) LIP neurons undergo multiple incremental changes in firing rate on single trials. On this example trial, the monkey decided in favor of the green target in the neuron's response field, consistent with the accumulated evidence from the sequence of shapes [from movie 3 of (4)]. [For more single-trial examples, see the movies in (4) and movies 1 and 2 in (5). For population analyses, see (4, 5).]

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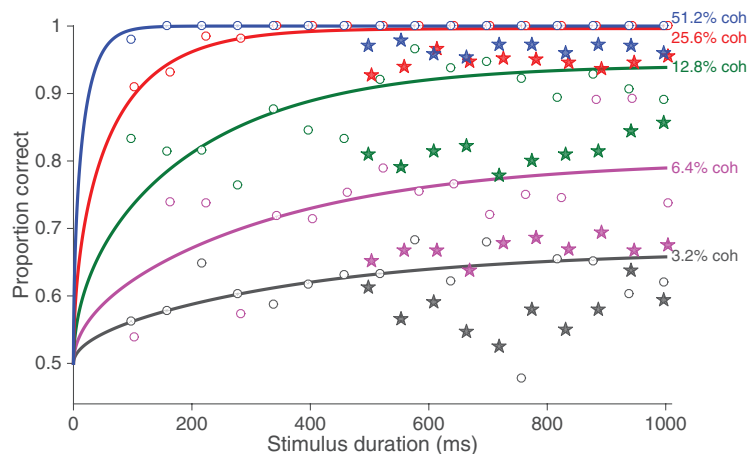


Fig. 2. Behavioral integration times are difficult to determine from the analyzed data set but are certainly shorter than the full 500- to 1000-ms viewing durations. Open circles correspond to behavioral data obtained after the collection of the neural recordings [figure 7D in (12)]. Smooth curves show fits of a bounded diffusion model, from which we estimate the median decision time to be ~250 ms across all motion strengths [methods explained in (13, 14)]. The neural data analyzed by Latimer *et al.* (1) accompanied the behavioral data shown by the filled stars [from figure 7A of (12)]. Accuracy was unaffected by viewing duration over the range tested, and overall performance was markedly poorer in this data set. [Data are from figure 7, A and D, in (12), with missing coherences kindly supplied by Latimer *et al.*]

strategy altogether, in which the monkey waits for salient features (extrema) in the random dots. These latter alternatives are consistent with our experience training monkeys on these kinds of tasks.

Most important, regardless of whether the integration times are 70 ms or 300 ms, they are substantially shorter than the 500- to 1000-ms duration of the trials. Accordingly, integration does not need to start at a consistent time within a trial. This potential variability exposes a critical bias in the model comparison: The stepping model is allowed the flexibility to account for random times of transitions, but the diffusion model is tethered to a fixed start time and therefore is unfairly penalized in comparison. A relatively short integration window occurring at random times during motion viewing can also explain other features of (1): the broad distribution of the time of the putative steps, the absence of a dependency of step times on motion strength, the pattern of response variance [figure 4A in (1)], the superior choice predictions of the step mod-

el, and its superior deviance information criterion (DIC).

Latimer *et al.* attempt to mitigate some of these concerns in their supplementary analysis of data from an RT experiment (2). However, that analysis also does not convincingly support a stepping model. Of the 16 neurons (of 54) chosen for analysis, only 10 exhibited the kind of coherence- and choice-dependent ramping that is the focus of the model comparison. Of these, four support diffusion. Moreover, the average Δ DIC in favor of steps is small (~19; 10 excluding the outlier), even though the comparison is biased toward that result: (i) the data include many high-motion strength trials with brief integration times (e.g., 12% of included trials have integration times <150 ms) that are likely to be seen as steps; (ii) their integration model assumes that the starting time of integration is fixed, despite the fact that it varies considerably across neurons [see figure S22 in (1)]; and (iii) their own simulations [figure S6 in (1)] show that their analysis can produce evidence for stepping even under simulations of diffusion.

Identifying the sources of these biases, including possibly their model's handling of negative-going rates (which are neither bounded nor stopped like the positive-going rates) [supplementary materials section 2.1, figure 1B, and figure S9 in (1)] and the inability to identify latent firing rates from the parameters of diffusion, should be addressed before applying these methods to richer data sets.

In summary, Latimer *et al.* present a statistical method for inferring discrete steps in firing rate from single neurons [similar to (8–10)] and use it to claim that averages of random steps are responsible for the evolving firing of LIP neurons during deliberative decision-making. However, they have not supported this claim, and they have not provided a plausible explanation for many experimental observations supporting the representation of accumulated noisy evidence by single neurons in LIP. At present, bounded diffusion provides the best account of the ensemble of neural data.

REFERENCES

1. K. W. Latimer, J. L. Yates, M. L. Meister, A. C. Huk, J. W. Pillow, *Science* **349**, 184–187 (2015).
2. J. D. Roitman, M. N. Shadlen, *J. Neurosci.* **22**, 9475–9489 (2002).
3. A. Bollimunta, D. Totten, J. Ditterich, *J. Neurosci.* **32**, 12684–12701 (2012).
4. T. Yang, M. N. Shadlen, *Nature* **447**, 1075–1080 (2007).
5. S. Kira, T. Yang, M. N. Shadlen, *Neuron* **85**, 861–873 (2015).
6. S. Barash, R. M. Bracewell, L. Fogassi, J. W. Gnadt, R. A. Andersen, *J. Neurophysiol.* **66**, 1095–1108 (1991).
7. J. W. Gnadt, R. A. Andersen, *Exp. Brain Res.* **70**, 216–220 (1988).
8. D. Commenges, J. Seal, *Stat. Med.* **4**, 91–104 (1985).
9. D. Commenges, J. Seal, F. Pinat, *Math. Biosci.* **80**, 81–108 (1986).
10. R. C. Wilson, M. R. Nassar, J. I. Gold, *Neural Comput.* **22**, 2452–2476 (2010).
11. A. K. Churchland, R. Kiani, M. N. Shadlen, *Nat. Neurosci.* **11**, 693–702 (2008).
12. M. L. Meister, J. A. Hennig, A. C. Huk, *J. Neurosci.* **33**, 2254–2267 (2013).
13. R. Kiani, T. D. Hanks, M. N. Shadlen, *J. Neurosci.* **28**, 3017–3029 (2008).
14. V. de Lafuente, M. Jazayeri, M. N. Shadlen, *J. Neurosci.* **35**, 4306–4318 (2015).

28 August 2015; accepted 4 February 2016
10.1126/science.aad3242



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Science **351** (6280), 1406. [doi: 10.1126/science.aad3242]

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