Different forms of variability could explain a difference between human and rat decision making

Quynh Nhu Nguyen[1], Pamela Reinagel[1]*

[1] Section of Neurobiology, Division of Biological Sciences, University of California San Diego, La Jolla, California, United States of America.

* Corresponding author

Email: preinagel@ucsd.edu (PR)

Abstract

When observers make rapid, difficult perceptual decisions, their response time is highly variable from trial to trial. In a visual motion discrimination task, it has been reported that human accuracy declines with increasing response time, whereas rat accuracy increases with response time. This is of interest because different mathematical theories of decision-making differ in their predictions regarding the correlation of accuracy with response time. On the premise that perceptual decision-making mechanisms are likely to be conserved among mammals, we seek to unify the rodent and primate results in a common theoretical framework. We show that a bounded drift diffusion model (DDM) can explain both with variable parameters: trial-to-trial variability in the starting point of the diffusion process produces the pattern typically observed in rats, whereas variability in the drift rate produces the pattern typically observed in humans. We further show that the same effects can be produced by deterministic biases, even in the absence of parameter stochasticity or parameter change within a trial.

Introduction

One might expect decision-making by humans to be quite different from that of rats. In decisions with wide-reaching long-term consequences, we expect (or at least wish) humans would avail themselves of abstract conceptual thought, logical reasoning, and culturally accumulated knowledge that would be unavailable to a rat. Yet all organisms face a continuous challenge of selecting among alternative available actions in order to pursue goals. In order to select an action, sensory information, internal knowledge, and goals are combined to assess and evaluate the likely outcomes of possible actions relative to survival needs. Often there is not enough time to acquire the evidence necessary to determine with certainty the optimal course of action, so an action must be selected despite unresolved or unresolvable uncertainty. Some mechanism is needed to ensure timely commitment and to optimize outcome on average, and this must adapt flexibly to prevailing sensory context, shifting goal priorities, the urgency of action, and the severity of consequences of errors. When it comes to the continuous sensory guidance of moment-by-moment actions, decisions about sensory evidence are made in a fraction of a second. We speculate that in this case, mechanisms are largely conserved across mammals.

A now-classic series of studies in humans and non-human primates introduced the use of a stochastic visual motion task to study decision making (Britten, Shadlen et al. 1992, Britten, Shadlen et al. 1993, Britten, Newsome et al. 1996, Shadlen, Britten et al. 1996, Shadlen and Newsome 1996, Gold and Shadlen 2001, Shadlen and Newsome 2001, Roitman and Shadlen 2002, Mazurek, Roitman et al. 2003, Huk and Shadlen 2005, Palmer, Huk et al. 2005, Gold and Shadlen 2007). In each trial a visual stimulus provides information regarding which of two available actions is associated with reward and

which is associated with non-reward or penalty. Stimulus strength is modulated by the motion coherence, which is defined as the fraction of the dots in the display that are "signal" (moving toward the rewarded response side). The remaining dots are "noise" (moving in random directions). As stimulus strength increases, accuracy increases and response time decreases for both monkeys (Roitman and Shadlen 2002) and humans (Palmer, Huk et al. 2005). This is parsimoniously explained by drift diffusion models, which postulate that noisy sensory evidence is integrated over time until the accumulated evidence reaches a decision threshold (Stone 1960, Ashby 1983, Busemeyer and Townsend 1993, Gold and Shadlen 2001, Usher and McClelland 2001, Ratcliff and Tuerlinckx 2002, Palmer, Huk et al. 2005, Gold and Shadlen 2007, Brown and Heathcote 2008, Ratcliff and McKoon 2008, Ratcliff, Smith et al. 2016). Although this class of model is highly successful, more data are needed to test model predictions and differentiate among competing versions of the model and alternative model classes (Wang 2002, Ratcliff and McKoon 2008, Pleskac and Busemeyer 2010, Purcell, Heitz et al. 2010, Rao 2010, Heathcote and Love 2012, Tsetsos, Gao et al. 2012, Huang and Rao 2013, Usher, Tsetsos et al. 2013, Scott, Constantinople et al. 2015, Ratcliff, Smith et al. 2016, Sun and Landy 2016, White, Servant et al. 2018).

For example, when monkeys or humans perform this task, among trials of the same stimulus strength the interleaved trials with longer response times are more likely to be errors (Roitman and Shadlen 2002, Palmer, Huk et al. 2005). In its simplest form the drift diffusion model does not explain this result; therefore the observation has been an important constraint for recent theoretical efforts. The result can be explained if the decision bound is not constant but instead decays as a function of time (Bowman, Kording et al. 2012, Drugowitsch, Moreno-Bote et al. 2012). A collapsing decision bound can be rationalized as an optimal strategy under some task constraints (Rao 2010, Hanks, Mazurek et al. 2011, Huang and Rao 2013, Tajima, Drugowitsch et al. 2016) though this argument has been challenged by others (Hawkins, Forstmann et al. 2015, Boehm, Hawkins et al. 2016). There are alternative ways to explain the data within the drift diffusion model framework without positing an explicit urgency signal or decaying bound (Ditterich 2006, Ditterich 2006, Ratcliff and McKoon 2008, Ratcliff and Starns 2013).

When rats performed the same random dot motion task, however, the opposite effect was found: their later decisions were more likely to be accurate (Reinagel 2013, Shevinsky and Reinagel 2019). The same has also been reported for image discriminations in rats (Reinagel 2013), for visual orientation decisions in mice (Sriram, Li et al. 2020), and in humans in some other tasks (McCormack and Swenson 1972, Ratcliff and Rouder 1998, Long, Jiang et al. 2015, Stirman, Townsend et al. 2016). This result is not readily explained by some of the models suggested to explain the late errors of primates (reviewed in (Heitz 2014, Ratcliff, Smith et al. 2016, Hanks and Summerfield 2017)). Here we explore a stochastic variant of the drift-diffusion model (Ratcliff and Tuerlinckx 2002, Ratcliff and McKoon 2008) for its ability to explain these problematic findings in both species.

In a basic drift diffusion model (DDM; also called the Decision Diffusion Model), the relative sensory evidence in favor of a decision (e.g. "motion is rightward" vs. "motion is leftward") is accumulated by an internal decision variable, resulting in a biased random walk, i.e., diffusion with drift (Fig 1A). The strength of the drift is determined by the sensory signal to noise ratio (e.g., the strength of a visual motion signal). When the decision variable reaches either decision threshold, the agent commits to a choice. The time at which the decision variable crosses a threshold (response time), and the identity of the decision threshold that is crossed (correct vs. incorrect), vary from trial to trial.

In this simple form, the drift diffusion model depends on four parameters: the threshold separation a; the non-decision-time t; the accumulator starting point z; and the average drift rate v, which is determined by the strength of the sensory stimulus. An interesting feature of this model is that for any given stimulus strength and decision threshold , errors and correct responses have identical response time distributions (Fig 1B-E, red vs. green). Therefore errors are on average the same speed as correct responses – even if the signal is so strong that errors are very rare.

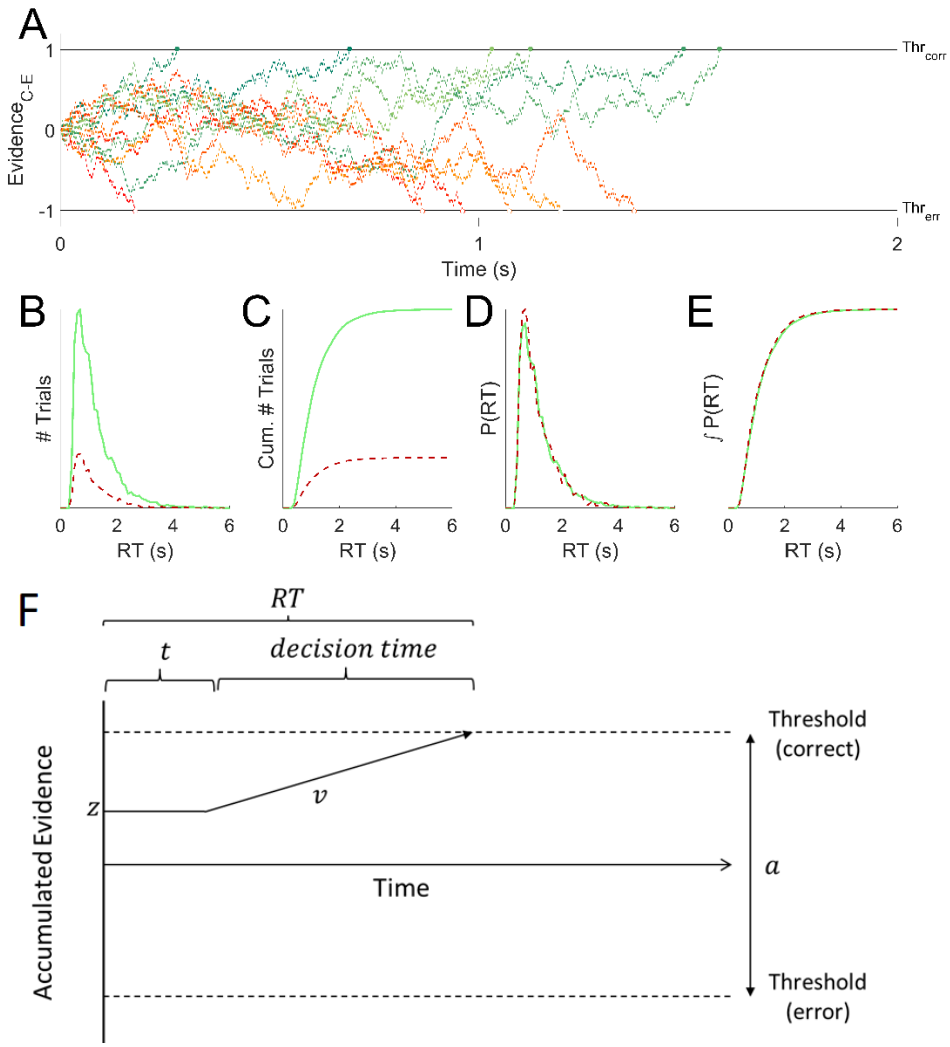


Fig 1. Illustration of a basic drift diffusion model. A. Six randomly chosen example trials that terminated in correct decisions (green shades, solid symbols) and six that terminated in error decisions (red shades, open symbols). Although an equal number of traces are shown, in the condition illustrated 80% of the traces terminated by crossing the correct boundary. **B.** Response time distributions for errors (red, dashed) vs. correct trials (green, solid) of 10^4 trials like those simulated as in A. **C.** Cumulatives of the distributions shown in B. **D-E:** Distributions in B and C normalized to the number of trials. **F.** Definition of parameters. The parameter a is the distance between the error and correct thresholds. The starting point of evidence accumulation is given by z. The average drift rate v depends on the stimulus strength. The observable outcomes are response time (RT) and decision (correct or error). The non-decision-time t reflects both sensory latency and motor latency, but is drawn at left for graphical simplicity. The simulations in A-E used parameters $a = 2$, $t = 0$, $z = 0$, $v = 0.7$.

We note that this does not, but may at first appear to, contradict two other facts. First, responses to stronger stimuli are both more accurate and faster, which in this model is explained by a

higher drift rate v. In this sense response time is negatively correlated with accuracy – but only when comparing trials of differing stimulus strengths. Second, conservative subjects take more time to respond and are more accurate, which in this model is explained by a greater threshold separation a. In this sense response time is positively correlated with accuracy – but only when comparing blocks of trials with different overall degrees of caution. Both of these facts are consistent with the fact that within a block of fixed overall caution, comparing among the trials of the same stimulus strength, response time and accuracy are uncorrelated in the basic DDM model.

Both humans and rats deviate systematically from the prediction that correct and error trials have the same mean and probability distribution, however. In the random dot motion discrimination task, for example, correct trials of rat subjects tend to have longer response times compared to errors (e.g., Fig 2A-D). Humans also violate the basic DDM model prediction, but in the opposite way. For humans, errors tend to have longer response times (e.g., Fig 2E-H).

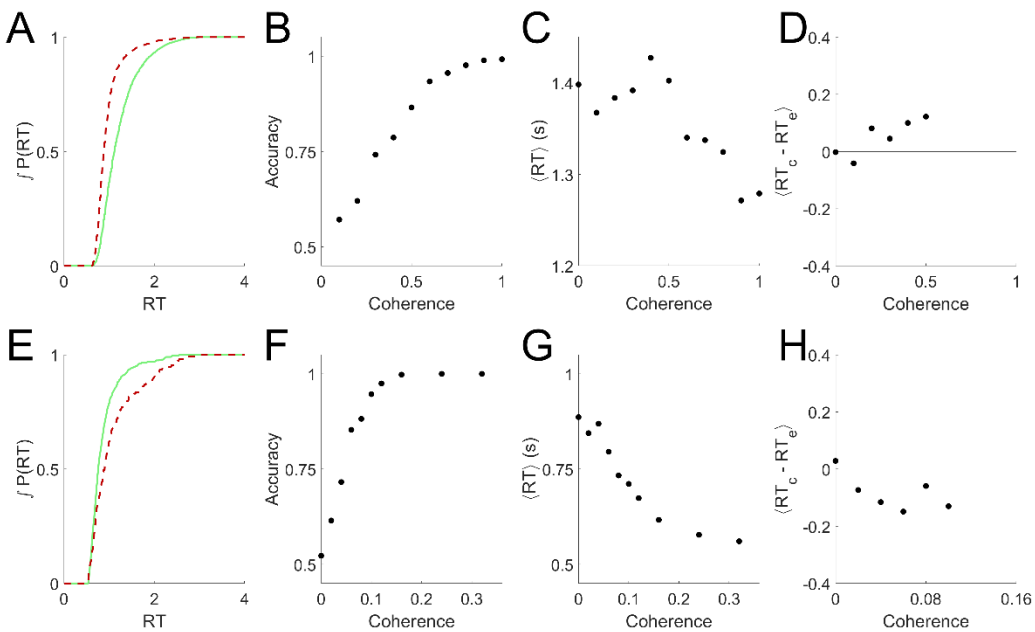


Fig 2. Example data from rats and humans inconsistent with the basic DDM. A. Cumulative probability function of response time for errors (red, dashed) and correct trials (green, solid) for one example experiment in a rat, a fixed-coherence epoch with 65% coherence, for which the rat was 82% correct. The null hypothesis that the distributions are the same can be rejected with P=2.91e-171 (N=8851,1913) by two-tailed Kolmogorov–Smirnov (KS) test. **B-D.** Analysis of an example rat psychometric experiment. **B.** Accuracy increased with coherence. **C.** Mean response time decreased with coherence. **D.** On average, the response of a correct trial is greater than that of a temporally nearby error trial of the same coherence. **E.** Like A, for an example experiment in a human, a fixed-coherence epoch with 10% coherence for which the subject was 83% correct; P= 4.69e-05 (N=745,153) by KS test. **F-H:** Like B-D, for example human psychometric epoch. Data from (Shevinsky and Reinagel 2019, Reinagel and Shevinsky 2020).

Results

Drift Diffusion Model with variable parameters

It was previously shown that adding noise to the parameters of a bounded drift diffusion model can differentially affect the error and correct response time distributions (Ratcliff and Tuerlinckx 2002, Ratcliff and McKoon 2008). The version we implemented has three additional parameters: variability in

starting point σ_z, variability in non-decision-time σ_t, and variability in drift rate σ_v (Fig 3A). By hand-tuning, we are able to find parameter sets that produce behavior qualitatively similar to either a rat (Fig B-E, c.f. Fig 2A-D) or a human (Fig3 F-I, c.f. Fig 2E-H). Removing drift rate variability and starting point variability from these simulations improved accuracy (Fig 3C,G open vs. filled symbols), increased the response time for ambiguous stimuli (Fig D,H), and eliminated the difference between correct and error response times (Fig 3 E,I).

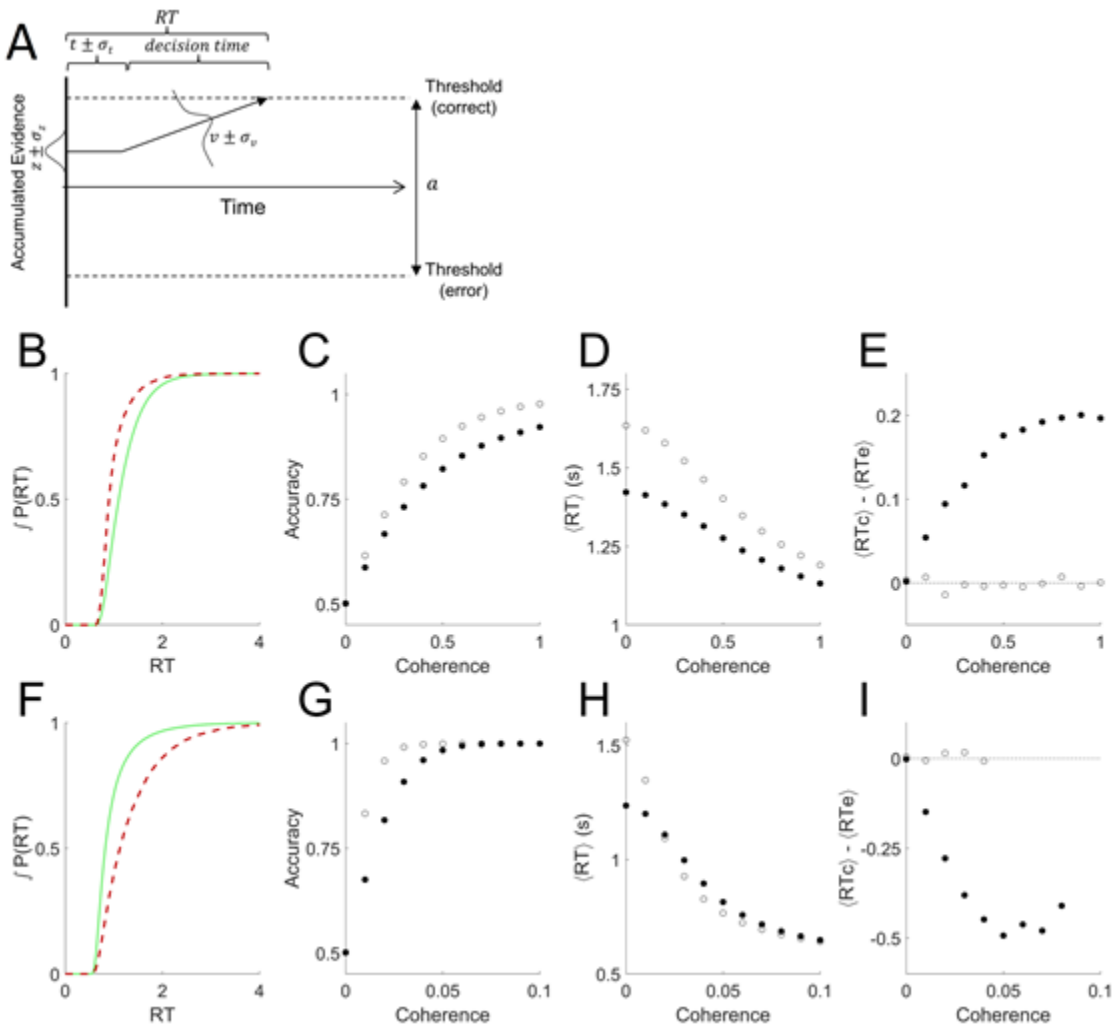


Fig 3. Addition of variability to the parameters of the drift diffusion model. A. Parameters *t*, *z*, and *v* in the drift diffusion model vary from trial to trial according to the variability parameters σ_t, σ_z, and σ_v respectively. Drift rate variability was simulated by a normal distribution around the mean parameter. Starting point variability and non-decision time variability were simulated by uniform distributions centered on the mean parameter. Diagram after (Ratcliff and McKoon, 2008). **B-E**. Analysis of trials simulated with parameters that produce qualitatively rat-like behavior: $a = 1.84$, $t = 0.74$, $\sigma_v = 0.1$, $\sigma_z = 1.5$, $\sigma_t = 0.2$, and $v = -0.5\ c^2 + 2.5c$, where c is coherence (motion stimulus strength). **B.** Cumulative probability distributions of correct vs. error trial response times, for $c = 0.8$. **C.** Psychometric curve. **D.** Chronometric curve **E.** Difference between mean response times of errors and correct trials. **F-I.** Like panels B-E but with parameters that produce qualitatively human-like behavior: $a = 2.0$, $t = 0.5$, $\sigma_v = 1.5$, $\sigma_z = 0.3$, $\sigma_t = 0.03$, and $v = -80\ c^2 + 80c$. **F.** Cumulative RT probability distributions for $c = 0.03$. For all these simulations, the mean starting point $z = 0$, timestep $\tau = 0.001$, diffusion noise $\sigma_n = 1$, $N = 10^5$ trials per coherence. Open symbols show results obtained after setting σ_z=0 and σ_v=0. Note that conditions with ~100% accuracy did not yield enough error trials to estimate RTe, so the RT difference is undefined.

In general, it is difficult or impossible to fit the parameters of this model to data (Boehm, Annis et al. 2018). Therefore we systematically varied the parameters (Fig 4) to determine all the conditions under which the mean RT of correct trials can be greater or less than the mean RT of error trials, using parameter ranges from the literature (Ratcliff and Tuerlinckx 2002, Wagenmakers, van der Maas et al. 2007, Ratcliff and McKoon 2008). Like the basic DDM, the simulations with $\sigma_z = 0$, $\sigma_v = 0$ showed no difference between correct and error RT for any drift rate (black curve is on y=0 line), in spite of the addition of non-decision time variability σ_t.

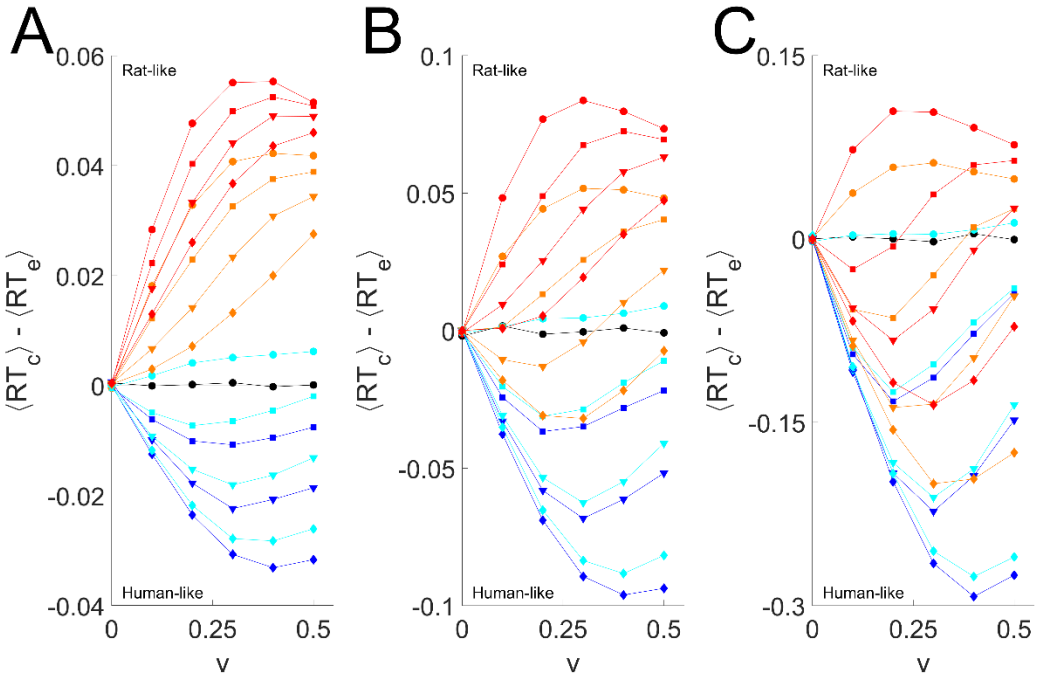


Figure 4. Parameter sweep of the variable-parameter DDM. Curves show the difference between correct and error mean response times, $\langle RT_{correct} \rangle - \langle RT_{error} \rangle$, as a function of drift rate parameter $v = [0.0, 0.1, 0.2, 0.3, 0.4, 0.5]$. Colors indicate starting point variability $\sigma_z = [0.0, 0.02, 0.07, 0.10]$, in spectral order from low (dark blue) to high (red). Symbols indicate drift rate variability $\sigma_v = [0.0, 0.08, 0.12, 0.16]$, increasing in the order: circle, square, triangle, diamond. Black curve with circles represents the special case of $\sigma_v = 0$, $\sigma_z = 0$. **A.** Simulations with threshold separation $a = 0.08$. **B.** Simulations with $a = 0.11$. **C.** Simulations with $a = 0.16$. For all the simulations shown, $z = 0$, $t = 0.3$, $\sigma_t = 0.2$, $\tau = 0.001$, and $\sigma_n = 0.1$. We classified models "human-like" when the RT difference was negative and "rat-like" when it was positive, in reference to the empirical findings in (Shevinsky and Reinagel 2019).

We never observed a positive RT difference in this model unless the starting point was variable (the dark blue or black curves, $\sigma_z = 0$, lie entirely on or below the abscissa). Whenever $\sigma_z > 0$ and σ_v=0, the RT difference was positive (circles other than black). We never observed a negative RT difference in the absence of drift rate variability (the circles, $\sigma_v = 0$, lie entirely on or above the abscissa). Whenever $\sigma_v > 0$ and σ_z=0, the RT difference was negative (blue curves). Holding other parameters constant, the RT difference always increased (more positive, or less negative) with increasing σ_z (red > orange > cyan > blue) and decreased with increasing σ_v (circle > square > triangle > diamond). When both starting point variability and drift rate variability are present simultaneously, these effects trade off against one another quantitatively, such that there are many parameter combinations consistent with any given sign and amplitude of effect. This explains why parameter fits to data are generally degenerate. Nevertheless the simulations show that human-like pattern is generally associated with dominance of σ_v and the rat-like

pattern with dominance of σ_z. The nondecision time t and its variability σ_t were explored in separate simulations and did not impact the effect of interest in either species (not shown).

Variability need not be random

We have defined decision thresholds as "correct" vs. "error" rather than "left" vs. "right" (Fig 3A). Therefore it is impossible for the mean starting point z to be biased, because the agent cannot know *a priori* which side is correct. If a subject's starting point were systematically biased to one response side, the starting point would be closer to the correct threshold on half the trials (when the preferred side was the correct response), but further on the other half of the trials (when the non-preferred response was required). Thus the mean starting point would be $z = 0$, but the distribution of z would be binary (or at least bimodal), and thus high in variance. This could mimic a model with high σ_z, even in the absence of stochastic parameter variability.

We confirmed by simulation that adding a fixed response side bias to the standard DDM was sufficient to produce longer RT in correct trials than error trials, as commonly seen in rodents (Fig 5A-C). What if such static or dynamic response biases were computationally implemented not as shifts in the starting point of evidence accumulation, but rather as assymetries in the drift rate for leftward vs. rightward motion: $v_{c,R} \neq v_{c,L}$? Again, this would bias toward or away from the correct response with equal probability, resulting in a binary or bimodal distribution in v, and producing effects equivalent to high drift rate variability σ_v (Fig 5 D-F).

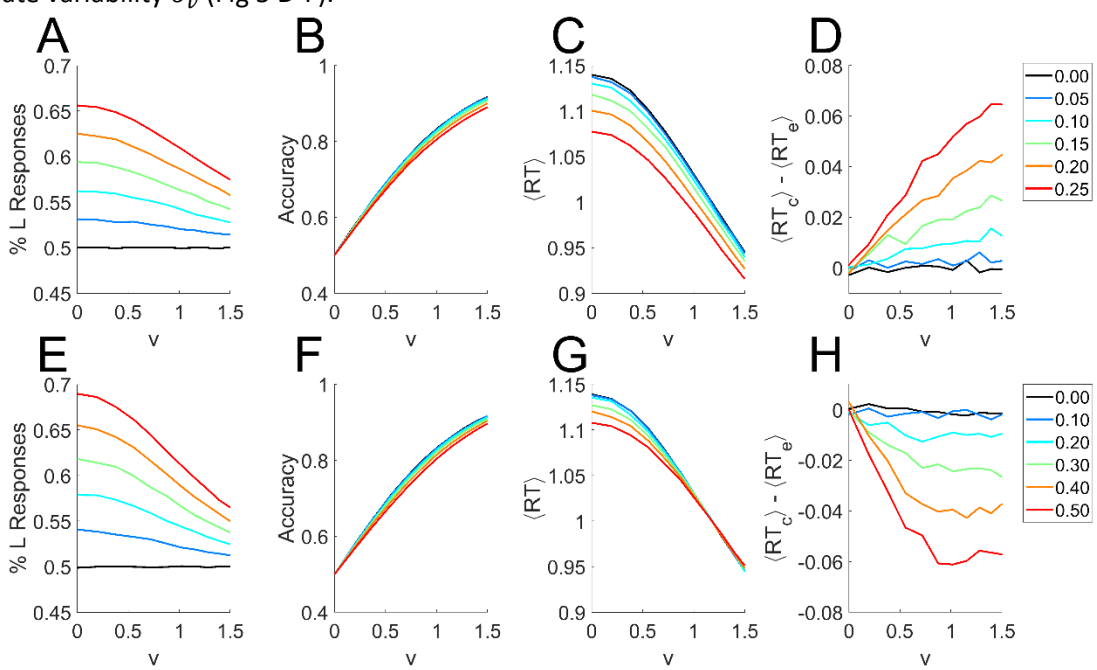


Figure 5. Bias is sufficient to produce either effect within the standard DDM. Simulations were performed with $\sigma_v = 0$, $\sigma_z = 0$, $\sigma_t = 0$ (i.e. the basic model in Fig 1) but with different forms of bias added. Trials were simulated with 50% Left targets. **A-C**. A Left side bias was simulated by displacing the starting point towards the correct boundary on Left-target trials, or towards the error boundary for Right-target trials, by the amount indicated by color key at right. **A.** Average accuracy of the response as a function drift rate v (sensory stimulus strength). **B.** Average response time as a function of v. **C.** Difference between correct and error mean response times, $\langle RT_{correct} \rangle - \langle RT_{error} \rangle$, as a function v. **D-E:** like A-C but here bias was simulated by increasing the drift rate v on L-target trials, or decreasing it on R-target trials, by the amount indicated in color key at right.

The simulations in Fig 5 only require that a bias to one side (L or R) exists in each trial. It does not matter if that bias is fixed or varying from trial to trial, only that it is uncorrelated with the correct response. If the starting point or drift rate were biased in individual trials based on the recent trial history, for example, this would also bias the decision towards or away from the correct response with equal probability in each trial. Therefore history-dependent bias could mimic high σ_z or high σ_v, even in the absence of an overall left or right side bias.

In principle, therefore, systematic response biases could be sufficient to explain the observed dependence of accuracy on response time in both species, even in the absence of overt bias, random variability of parameters, or within-trial parameter change. More generally, the observed effects could be explained by a combination of fixed bias, contextual biases, and noise impacting both starting point and drift rate in both species. On this model, the difference between rats and humans would be explained by assuming that noise and/or biases have a stronger effect on drift rate in humans and a stronger effect on starting point in rats.

Discussion

The impetus for this study was an observed difference between human and rat decision-making: for humans correct decisions are on average faster than errors, whereas for rats correct decisions are on average slower than errors. Both observations violate the predictions of the standard drift diffusion model. This species difference was seen even when sensory task was matched such that rats were just as accurate and just as fast as humans in the task (Shevinsky and Reinagel 2019).

We do not presume that the difference in response time of correct vs. error trials is functionally significant for either species; the difference is small and accounts for a small fraction of the variance in response time. The reason this effect is interesting is because it is places constraints on the underlying decision-making algorithms, and in particular, because it is inconsistent with DDM in its basic form.

Decreasing accuracy with response time has been widely reported in both humans and nonhuman primates (Roitman and Shadlen 2002, Palmer, Huk et al. 2005) and has been explained by a number of competing models (Ditterich 2006, Ditterich 2006, Ratcliff and McKoon 2008, Rao 2010, Hanks, Mazurek et al. 2011, Huang and Rao 2013, Ratcliff and Starns 2013, Tajima, Drugowitsch et al. 2016). It was only recently appreciated that accuracy increases with response time in this type of task in rats (Reinagel 2013, Reinagel 2013, Shevinsky and Reinagel 2019, Sriram, Li et al. 2020), and it remains unclear which of those models can accommodate this observation as well. We used a simple drift diffusion model with parameter noise (Ratcliff and Tuerlinckx 2002, Ratcliff and McKoon 2008) to illustrate that trial-to-trial parameter variability could explain the observed interaction between reaction time and accuracy in either species. While this was demonstrated in a simple DDM, similar effects might be found in other DDM-based decision-making models.

Can context account for variability?

Although stochastic trial-by-trial variability of parameters could explain the effects of interest (Fig 4), systematic variations can also do so. We demonstrate this for the simple case of response side bias (Fig 5). Response bias is more prevalent in rats than in humans, but correct trials have longer RT than errors even in rats with no bias (Shevinsky and Reinagel 2019). In any case, response side bias

would only produce the rat-like pattern (e.g., Fig 2D) if that bias impacted starting point to a greater degree than drift rate.

It is known that decisions in this type of task can be biased by the previous trial's stimulus, response, and outcome in mice (Busse, Ayaz et al. 2011, Hwang, Dahlen et al. 2017, Roy, Bak et al. 2021), rats (Lavan, McDonald et al. 2011, Roy, Bak et al. 2021), non-human primates (Sugrue, Corrado et al. 2004), and humans (Goldfarb, Wong-Lin et al. 2012, Roy, Bak et al. 2021), reviewed in (Frund, Wichmann et al. 2014). Such history-dependent biases can be strong without causing an average side preference or an observable lapse rate (errors on strong stimuli). Species differ in the strength of such biases (Roy, Bak et al. 2021), but a difference in strength of bias does not determine whether accuracy increases or decreases with response time (c.f. 2D vs. 2H). This requires a difference in the computational site of action of bias.

Fluctuations in arousal, motivation, satiety or fatigue could conceivably modulate decision thresholds or drift rates from trial to trial independently of either response side or trial history. (Note that in the model of Figure 3-4, fluctuations in the threshold separation parameter a are referred to the starting-point variability parameter σ_z (Ratcliff and Tuerlinckx 2002, Ratcliff and McKoon 2008)). Such sources of variation might be correlated with measurable states, such as alacrity (e.g., latency to trial initiation, or in rodents the number or frequency of request licks), arousal (e.g., assessed by pupillometry), fatigue (the number of trials recently completed), satiety (amount of reward recently consumed), or frustration/success (fraction of recent trials penalized/rewarded). It would be of interest to determine how much of the observed behavioral variability is reducable to such deterministic components in each species, and whether those effects can be attributed differentially to starting point vs. drift rate effects in either decision-making models or neural recordings.

Is parameter variability a feature or a bug?

To the extent that parameter variability is attributable to systematic influences rather than noise, a separate question would be whether this variability is adaptive or dysfunctional, in either species. It is possible that non-sensory influences shift the decision-making computation from trial to trial in a systematic and reproducible fashion that would be functionally adaptive in the context of natural behavior, even though we have artificially broken natural spatial and temporal correlations to render it maladaptive in our laboratory task.

For example, in nature some locations may be intrinsically more reward-rich, or very recent reward yields may be informative about the expected rewards at each location. In the real world, recently experienced visual motion might be highly predictive of the direction of subsequent motion stimuli. Therefore biasing either starting point or drift rate according to location or recent stimulus or reward history may be adaptive strategies under ecological constraints, for either or both species.

Conclusions

It has been argued that neural computations underlying sensory decisions could integrate comparative information about incoming sensory stimuli (e.g., left vs. right motion signals), internal representations of prior probability (frequency of left vs. right motion trials) and the expected values (rewards or costs) associated with correct vs. incorrect decisions, in a common currency (Gold and

Shadlen 2001, Gold and Shadlen 2007). On the premise that basic mechanisms of perceptual decision-making are likely to be conserved, fitting a single model to data from multiple species – especially where they differ – is a powerful way to develop and distinguish among alternative computational models, and enables direct comparison of species.

Methods

Experimental data

No experiments were reported in this manuscript. Example human and rat data shown in Fig 2 were previously published (Shevinsky and Reinagel 2019, Reinagel and Shevinsky 2020). Specifically, Fig 2A used rat fixed-coherence epoch 256; 2B-D used rat psychometric epoch 146. Fig 2E used human fixed-coherence epoch 63, and 2F-H used human psychometric epoch 81 from that data set.

To summarize the experiment briefly: the task was random dot coherent motion discrimination. When subjects initiated a trial, white dots appeared at random locations on a black screen and commenced to move. Some fraction of the dots ("signal") moved at the same speed toward the rewarded response side. The others ("noise") moved at random velocities. Subjects could respond at any time by a left vs. right keypress (human) or lick (rat). Correct responses were rewarded with money or water; error responses were penalized by a brief time-out. Stimulus strength was varied by the motion coherence (fraction of dots that were signal dots). Other stimulus parameters (e.g. dot size, dot density, motion speed, contrast) were chosen for each species to ensure that accuracy ranged from chance (50%) to perfect (100%) and response times ranged from ~500-2500ms for typical subjects of the species. The psychometric parameters with respect to coherence could be, but were not, matched.

Computational methods

The drift diffusion process was simulated according to the equation $X(t) = X(t\text{-}1) \pm \delta$ with probability p of increasing and $(1\text{-}p)$ of decreasing. Here t is the time point of the process, with time step τ in seconds; $\delta = \sigma \cdot \sqrt{\tau}$ denotes the step size, where σ is the standard deviation of the Gaussian white noise of the diffusion; $p = 0.5 \cdot \left(1 + v \cdot \frac{\sqrt{\tau}}{\sigma}\right)$, where v is the drift rate. The values for τ and σ were fixed at 0.1 msec and 1, respectively. For any trial, the process starts at a starting position z, sampled from a uniform distribution of range σ_z, assumes a constant drift rate v, sampled from a normal distribution of standard deviation σ_v, and continues until $X(t)$ exceeds either threshold boundary. The non-decision-time t, sampled from a uniform distribution of range σ_t, is added to the elapsed time to obtain the final RT associated with that trial.

In Fig 2D,H we measured the interaction between accuracy and response time using the temporally local measure $\langle RT_{correct} - RT_{error} \rangle$ introduced in (Shevinsky and Reinagel 2019). This method is preferred for real data because it is robust to non-trending non-stationarities that are commonly present in both human and rat data, not detected by traditional stationarity tests, and that could confound estimation of the effect of interest. The response time of each error trial is compared to a temporally adjacent correct trial of the same coherence, requiring a minimum distance of 3-5 trials to avoid sequential effects. For simulated data, where stationarity is guaranteed, the temporally local measure $\langle RT_{correct} - RT_{error} \rangle$ and global measure $\langle RT_{correct} \rangle - \langle RT_{error} \rangle$ are numerically equivalent.

The data and code required to replicate all results in this manuscript are archived in a verified replication capsule (Reinagel and Nguyen 2021).

References

Ashby, F. G. (1983). "A Biased Random-Walk Model for 2 Choice Reaction-Times." Journal of Mathematical Psychology **27**(3): 277-297.

Boehm, U., J. Annis, M. J. Frank, G. E. Hawkins, A. Heathcote, D. Kellen, A. M. Krypotos, V. Lerche, G. D. Logan, T. J. Palmeri, D. van Ravenzwaaij, M. Servant, H. Singmann, J. J. Starns, A. Voss, T. V. Wiecki, D. Matzke and E. J. Wagenmakers (2018). "Estimating across-trial variability parameters of the Diffusion Decision Model: Expert advice and recommendations." Journal of Mathematical Psychology **87**: 46-75.

Boehm, U., G. E. Hawkins, S. Brown, H. van Rijn and E.-J. Wagenmakers (2016). "Of monkeys and men: Impatience in perceptual decision-making." Psychonomic bulletin & review **23**(3): 738-749.

Bowman, N. E., K. P. Kording and J. A. Gottfried (2012). "Temporal integration of olfactory perceptual evidence in human orbitofrontal cortex." Neuron **75**(5): 916-927.

Britten, K. H., W. T. Newsome, M. N. Shadlen, S. Celebrini and J. A. Movshon (1996). "A relationship between behavioral choice and the visual responses of neurons in macaque MT." Vis Neurosci **13**(1): 87-100.

Britten, K. H., M. N. Shadlen, W. T. Newsome and J. A. Movshon (1992). "The analysis of visual motion: a comparison of neuronal and psychophysical performance." J Neurosci **12**(12): 4745-4765.

Britten, K. H., M. N. Shadlen, W. T. Newsome and J. A. Movshon (1993). "Responses of neurons in macaque MT to stochastic motion signals." Vis Neurosci **10**(6): 1157-1169.

Brown, S. D. and A. Heathcote (2008). "The simplest complete model of choice response time: linear ballistic accumulation." Cognitive psychology **57**(3): 153-178.

Busemeyer, J. R. and J. T. Townsend (1993). "Decision field theory: a dynamic-cognitive approach to decision making in an uncertain environment." Psychological review **100**(3): 432-459.

Busse, L., A. Ayaz, N. T. Dhruv, S. Katzner, A. B. Saleem, M. L. Scholvinck, A. D. Zaharia and M. Carandini (2011). "The Detection of Visual Contrast in the Behaving Mouse." Journal of Neuroscience **31**(31): 11351-11361.

Ditterich, J. (2006). "Evidence for time-variant decision making." The European journal of neuroscience **24**(12): 3628-3641.

Ditterich, J. (2006). "Stochastic models of decisions about motion direction: behavior and physiology." Neural networks : the official journal of the International Neural Network Society **19**(8): 981-1012.

Drugowitsch, J., R. Moreno-Bote, A. K. Churchland, M. N. Shadlen and A. Pouget (2012). "The cost of accumulating evidence in perceptual decision making." The Journal of neuroscience : the official journal of the Society for Neuroscience **32**(11): 3612-3628.

Frund, I., F. A. Wichmann and J. H. Macke (2014). "Quantifying the effect of intertrial dependence on perceptual decisions." Journal of Vision **14**(7).

Gold, J. I. and M. N. Shadlen (2001). "Neural computations that underlie decisions about sensory stimuli." Trends Cogn Sci **5**(1): 10-16.

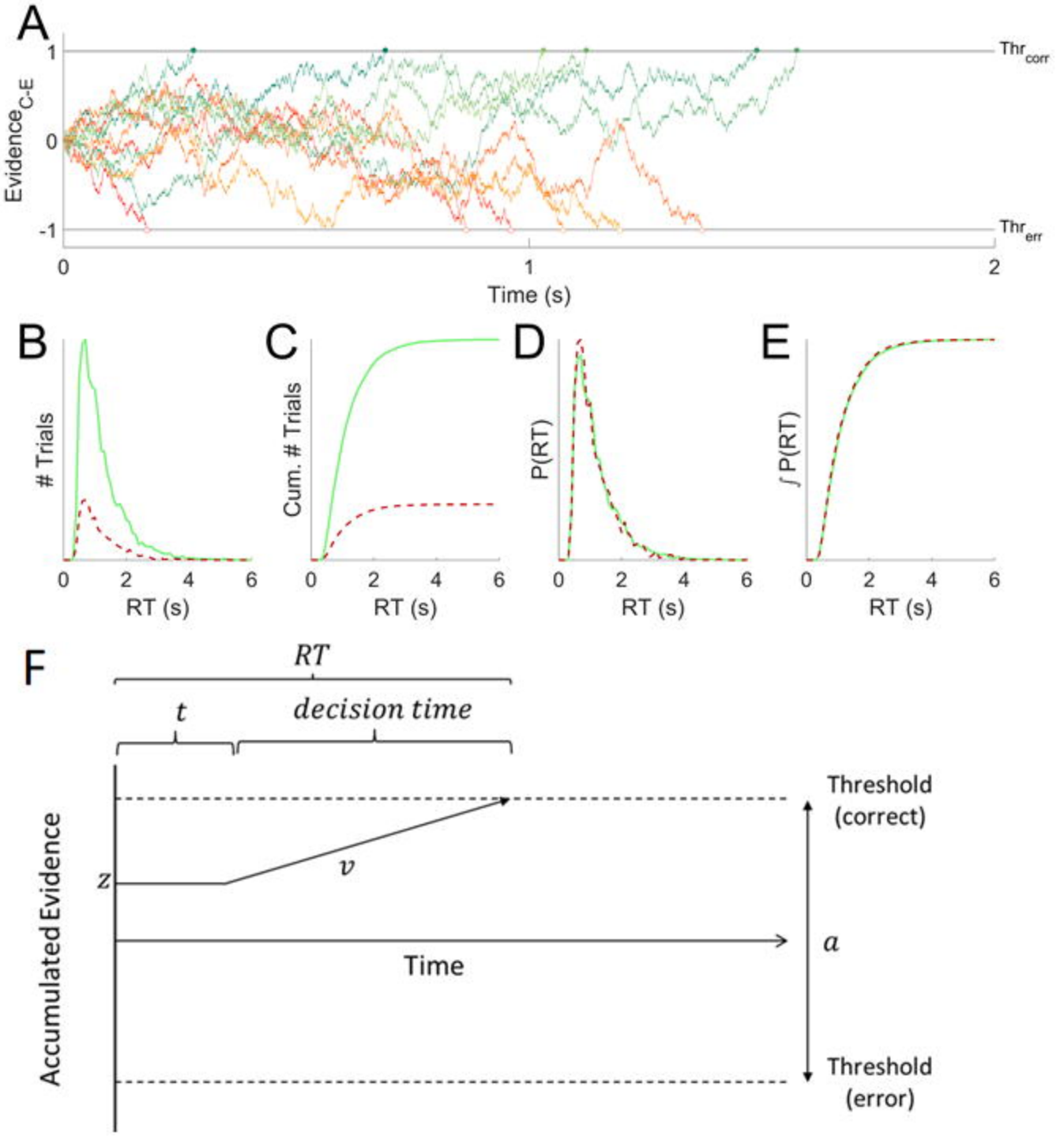
Gold, J. I. and M. N. Shadlen (2007). "The neural basis of decision making." Annu Rev Neurosci **30**: 535-574.

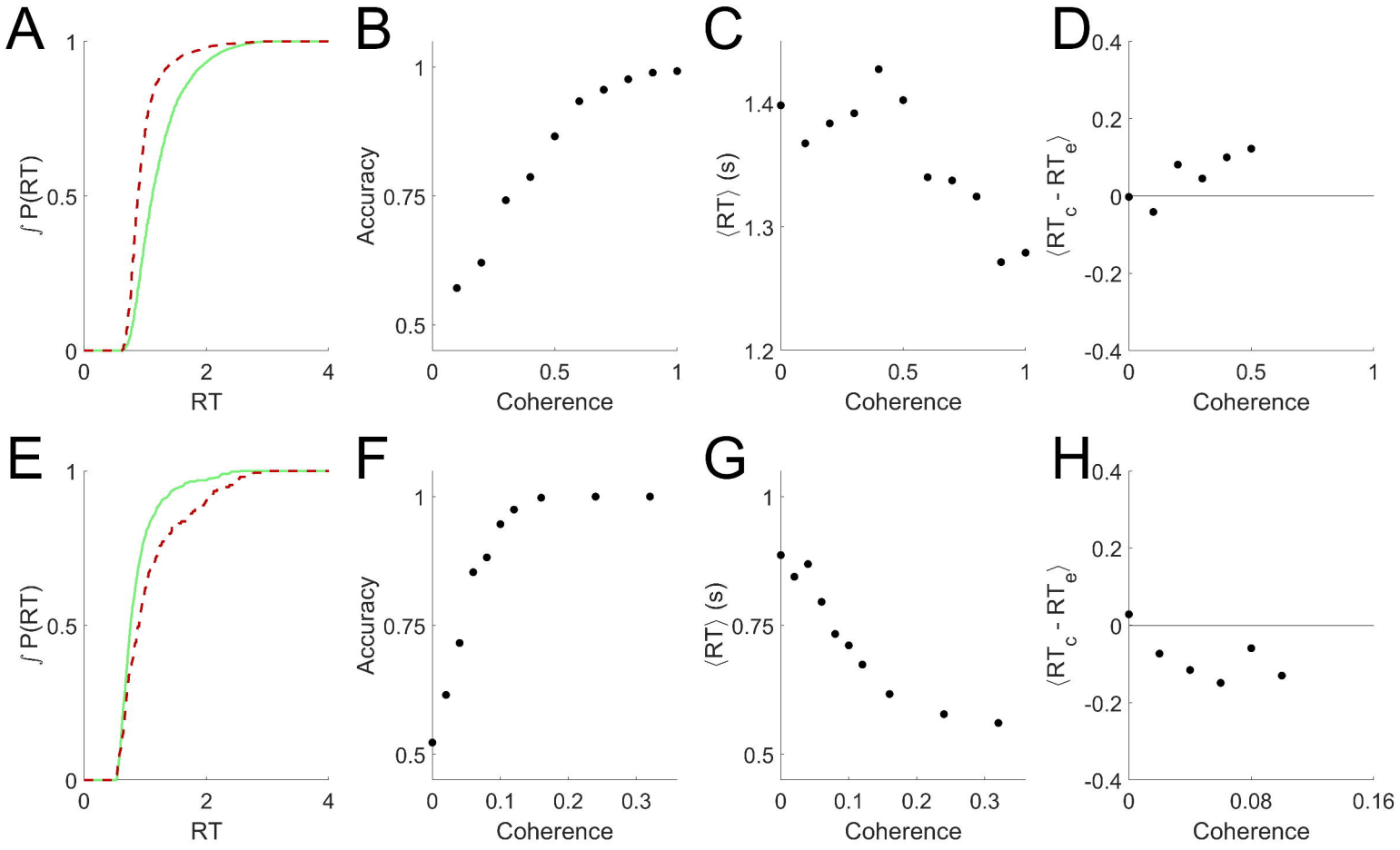
Goldfarb, S., K. Wong-Lin, M. Schwemmer, N. E. Leonard and P. Holmes (2012). "Can post-error dynamics explain sequential reaction time patterns?" Frontiers in Psychology **3**.

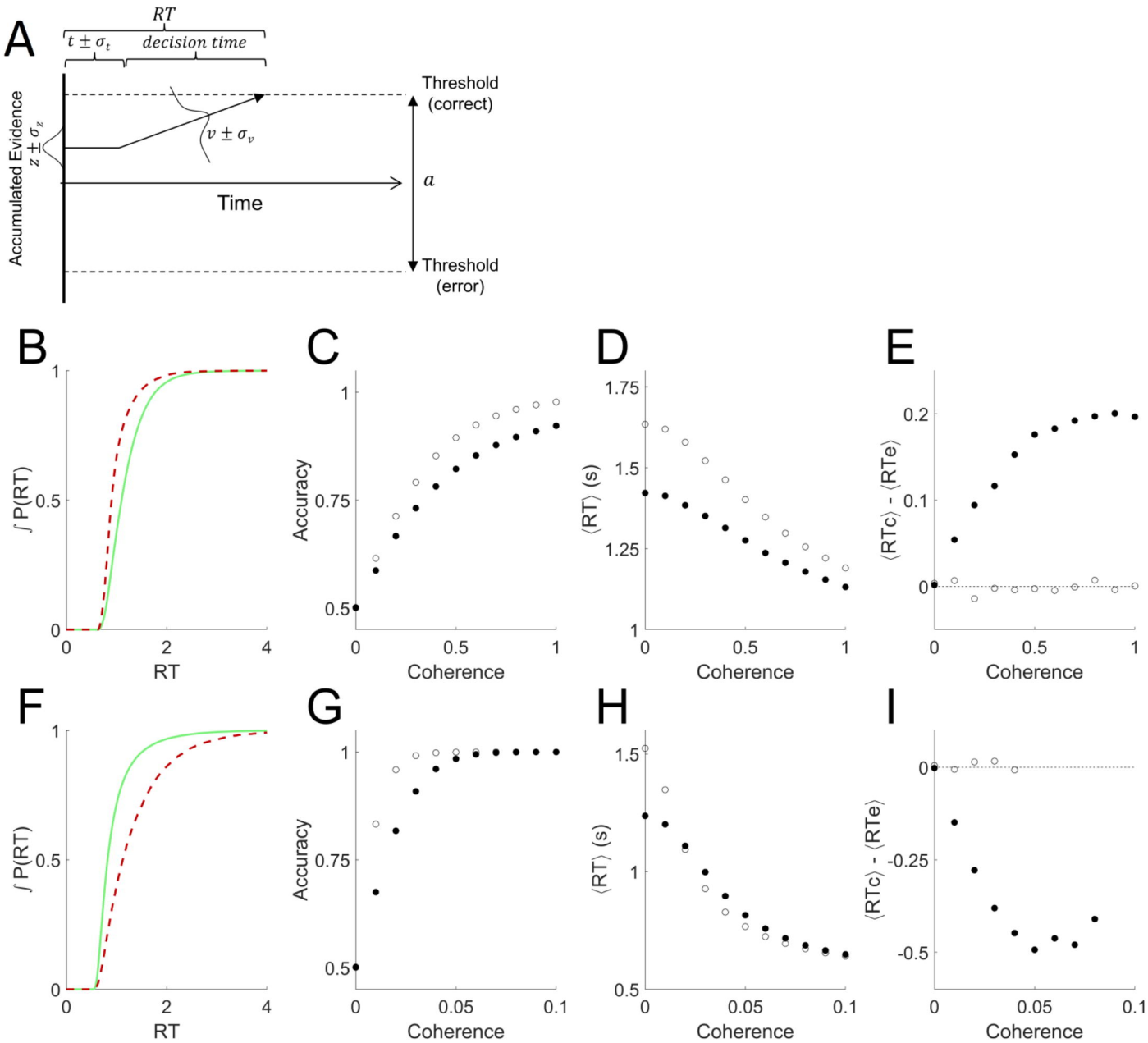
Hanks, T. D., M. E. Mazurek, R. Kiani, E. Hopp and M. N. Shadlen (2011). "Elapsed decision time affects the weighting of prior probability in a perceptual decision task." The Journal of neuroscience : the official journal of the Society for Neuroscience **31**(17): 6339-6352.

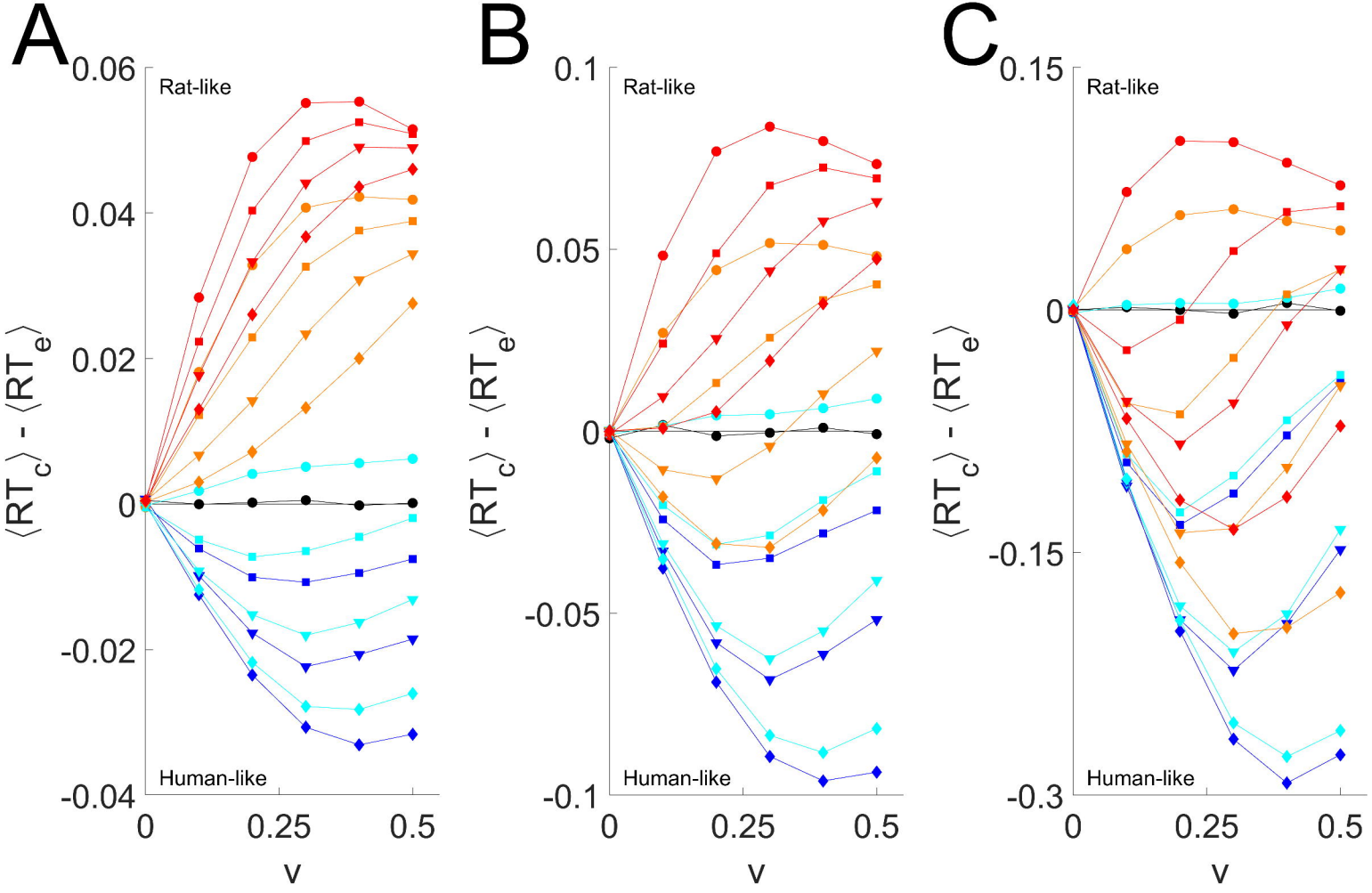
Hanks, T. D. and C. Summerfield (2017). "Perceptual Decision Making in Rodents, Monkeys, and Humans." Neuron **93**(1): 15-31.
Hawkins, G. E., B. U. Forstmann, E. J. Wagenmakers, R. Ratcliff and S. D. Brown (2015). "Revisiting the evidence for collapsing boundaries and urgency signals in perceptual decision-making." J Neurosci **35**(6): 2476-2484.
Heathcote, A. and J. Love (2012). "Linear deterministic accumulator models of simple choice." Frontiers in psychology **3**: 292.
Heitz, R. P. (2014). "The speed-accuracy tradeoff: methodology, and behavior." Frontiers in Neuroscience **8**.
Huang, Y. and R. P. Rao (2013). "Reward optimization in the primate brain: a probabilistic model of decision making under uncertainty." PLoS One **8**(1): e53344.
Huk, A. C. and M. N. Shadlen (2005). "Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making." J Neurosci **25**(45): 10420-10436.
Hwang, E. J., J. E. Dahlen, M. Mukundan and T. Komiyama (2017). "History-based action selection bias in posterior parietal cortex." Nat Commun **8**(1): 1242.
Lavan, D., J. S. McDonald, R. F. Westbrook and E. Arabzadeh (2011). "Behavioural Correlate of Choice Confidence in a Discrete Trial Paradigm." Plos One **6**(10).
Long, M. H., W. Q. Jiang, D. C. Liu and H. S. Yao (2015). "Contrast-dependent orientation discrimination in the mouse." Scientific Reports **5**.
Mazurek, M. E., J. D. Roitman, J. Ditterich and M. N. Shadlen (2003). "A role for neural integrators in perceptual decision making." Cereb Cortex **13**(11): 1257-1269.
McCormack, P. D. and A. L. Swenson (1972). "Recognition memory for common and rare words." Journal of experimental psychology **95**(1): 72-77.
Palmer, J., A. C. Huk and M. N. Shadlen (2005). "The effect of stimulus strength on the speed and accuracy of a perceptual decision." J Vis **5**(5): 376-404.
Pleskac, T. J. and J. R. Busemeyer (2010). "Two-stage dynamic signal detection: a theory of choice, decision time, and confidence." Psychological review **117**(3): 864-901.
Purcell, B. A., R. P. Heitz, J. Y. Cohen, J. D. Schall, G. D. Logan and T. J. Palmeri (2010). "Neurally constrained modeling of perceptual decision making." Psychological review **117**(4): 1113-1143.
Rao, R. P. N. (2010). "Decision making under uncertainty: a neural model based on partially observable markov decision processes." Frontiers in computational neuroscience **4**: 146.
Ratcliff, R. and G. McKoon (2008). "The diffusion decision model: theory and data for two-choice decision tasks." Neural Comput **20**(4): 873-922.
Ratcliff, R. and J. N. Rouder (1998). "Modeling response times for two-choice decisions." Psychological Science **9**(5): 347-356.
Ratcliff, R., P. L. Smith, S. D. Brown and G. McKoon (2016). "Diffusion Decision Model: Current Issues and History." Trends Cogn Sci **20**(4): 260-281.
Ratcliff, R. and J. J. Starns (2013). "Modeling confidence judgments, response times, and multiple choices in decision making: recognition memory and motion discrimination." Psychol Rev **120**(3): 697-719.
Ratcliff, R. and F. Tuerlinckx (2002). "Estimating parameters of the diffusion model: approaches to dealing with contaminant reaction times and parameter variability." Psychon Bull Rev **9**(3): 438-481.
Reinagel, P. (2013). "Speed and accuracy of visual image discrimination by rats." Frontiers in neural circuits **7**: 200.
Reinagel, P. (2013). "Speed and accuracy of visual motion discrimination by rats." PloS one **8**(6): e68505.
Reinagel, P. and Q. Nguyen (2021). Differential effects of variability could explain distinct human and rat deviations from DDM, Code Ocean.

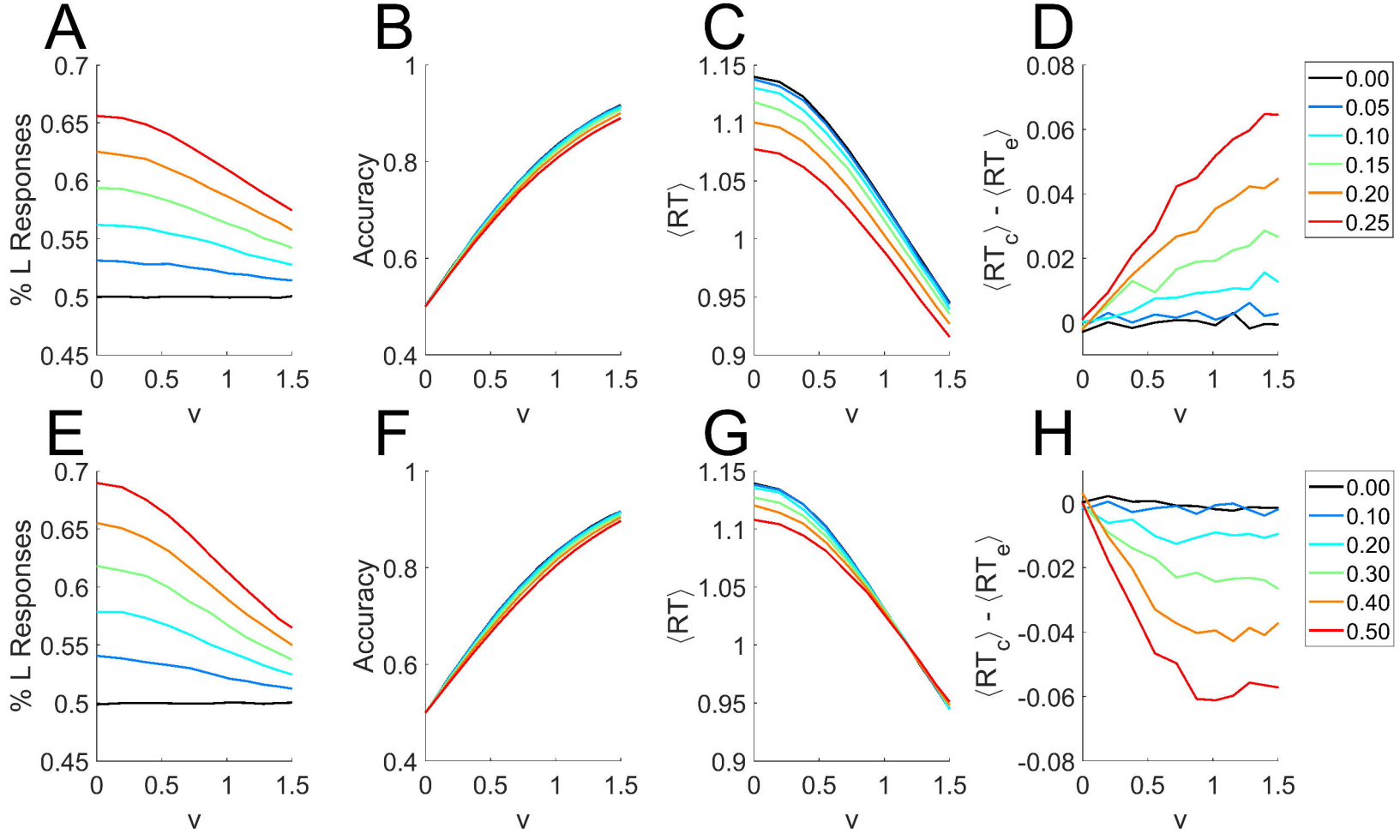
Reinagel, P. and C. A. Shevinsky (2020). Human and Rat Motion Discrimination Reaction Time Task Data. Harvard Dataverse.
Roitman, J. D. and M. N. Shadlen (2002). "Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task." J Neurosci **22**(21): 9475-9489.
Roy, N. A., J. H. Bak, L. International Brain, A. Akrami, C. D. Brody and J. W. Pillow (2021). "Extracting the dynamics of behavior in sensory decision-making experiments." Neuron **109**(4): 597-610 e596.
Scott, B. B., C. M. Constantinople, J. C. Erlich, D. W. Tank and C. D. Brody (2015). "Sources of noise during accumulation of evidence in unrestrained and voluntarily head-restrained rats." eLife **4**: e11308.
Shadlen, M. N., K. H. Britten, W. T. Newsome and J. A. Movshon (1996). "A computational analysis of the relationship between neuronal and behavioral responses to visual motion." J Neurosci **16**(4): 1486-1510.
Shadlen, M. N. and W. T. Newsome (1996). "Motion perception: seeing and deciding." Proc Natl Acad Sci U S A **93**(2): 628-633.
Shadlen, M. N. and W. T. Newsome (2001). "Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey." J Neurophysiol **86**(4): 1916-1936.
Shevinsky, C. A. and P. Reinagel (2019). "The Interaction Between Elapsed Time and Decision Accuracy Differs Between Humans and Rats." Frontiers in neuroscience **13**: 1211.
Sriram, B., L. Li, A. Cruz-Martin and A. Ghosh (2020). "A Sparse Probabilistic Code Underlies the Limits of Behavioral Discrimination." Cerebral cortex (New York, N Y : 1991) **30**(3): 1040-1055.
Stirman, J. N., L. B. Townsend and S. L. Smith (2016). "A touchscreen based global motion perception task for mice." Vision Research **127**: 74-83.
Stone, M. (1960). "Models for choice-reaction time." Psychometrika **25**: 251-226.
Sugrue, L. P., G. S. Corrado and W. T. Newsome (2004). "Matching behavior and the representation of value in the parietal cortex." Science **304**(5678): 1782-1787.
Sun, P. and M. S. Landy (2016). "A Two-Stage Process Model of Sensory Discrimination: An Alternative to Drift-Diffusion." The Journal of neuroscience : the official journal of the Society for Neuroscience **36**(44): 11259-11274.
Tajima, S., J. Drugowitsch and A. Pouget (2016). "Optimal policy for value-based decision-making." Nature communications **7**: 12400.
Tsetsos, K., J. Gao, J. L. McClelland and M. Usher (2012). "Using Time-Varying Evidence to Test Models of Decision Dynamics: Bounded Diffusion vs. the Leaky Competing Accumulator Model." Frontiers in neuroscience **6**: 79.
Usher, M. and J. L. McClelland (2001). "The time course of perceptual choice: the leaky, competing accumulator model." Psychological review **108**(3): 550-592.
Usher, M., K. Tsetsos, E. C. Yu and D. A. Lagnado (2013). "Dynamics of decision-making: from evidence accumulation to preference and belief." Frontiers in psychology **4**: 758.
Wagenmakers, E. J., H. L. van der Maas and R. P. Grasman (2007). "An EZ-diffusion model for response time and accuracy." Psychon Bull Rev **14**(1): 3-22.
Wang, X.-J. (2002). "Probabilistic decision making by slow reverberation in cortical circuits." Neuron **36**(5): 955-968.
White, C. N., M. Servant and G. D. Logan (2018). "Testing the validity of conflict drift-diffusion models for use in estimating cognitive processes: A parameter-recovery study." Psychonomic bulletin & review **25**(1): 286-301.


A
Evidence C-E
1
0
-1
Thr corr
Thr err
0
1
2
Time (s)
B
Trials
0
2
4
6
RT (s)
C
Cum. # Trials
0
2
4
6
RT (s)
D
P(RT)
0
2
4
6
RT (s)
E
∫ P(RT)
0
2
4
6
RT (s)
F
RT
t
decision time
Threshold
(correct)
z
v
Accumulated Evidence
Time
a
Threshold
(error)


A
B
C
D
E
F
G
H
∫ P(RT)
RT
Accuracy
Coherence
⟨RT⟩ (s)
⟨RT_c - RT_e⟩


A
RT
$t \pm \sigma_t$
decision time
Threshold (correct)
$v \pm \sigma_v$
Accumulated Evidence
$z \pm \sigma_z$
a
Time
Threshold (error)
B
∫ P(RT)
RT
C
Accuracy
Coherence
D
⟨RT⟩ (s)
Coherence
E
⟨RTc⟩ - ⟨RTe⟩
Coherence
F
∫ P(RT)
RT
G
Accuracy
Coherence
H
⟨RT⟩ (s)
Coherence
I
⟨RTc⟩ - ⟨RTe⟩
Coherence


A
B
C
Rat-like
Human-like
⟨RT_c⟩ - ⟨RT_e⟩
v
0.06
0.04
0.02
0
-0.02
-0.04
0.1
0.05
-0.05
-0.1
0.15
-0.15
-0.3
0.25
0.5


A
B
C
D
E
F
G
H
% L Responses
Accuracy
⟨RT⟩
⟨RT_c⟩ - ⟨RT_e⟩
v
0.00
0.05
0.10
0.15
0.20
0.25
0.00
0.10
0.20
0.30
0.40
0.50