From spike rates to simple decisions:
stochastic ODEs as models for evidence accumulation in
cortical circuits.

Philip Holmes, Princeton University.
Eric Brown (U Wash), Rafal Bogacz (Bristol), Jeff Moehlis (UCSB), Juan Gao (Stanford),
Patrick Simen, Sam Feng & Jonathan Cohen (Princeton), Miriam Zacksenhouse
(Technion), Alan Rorie & Bill Newsome (Stanford).
[Long-term collaboration with Jonathan Cohen (Psych & Neurosci)]

Thanks to: NIMH and AFOSR.
Psychology Dept., Tel Aviv University, March 17th, 2009.
The overall idea: Making the most of a random world.

Underlying hypothesis: Human and animal behaviors have evolved to be (near) optimal.

(e.g., Bialek et al., 1990-2009: Fly vision & steering.)

Optimal signal processing & information transmission theory provides normative accounts with which to compare actual behaviors. Given such a theory, we don’t just fit the data, but, if it deviates significantly from optimality, we investigate and try to explain why.

Big problem: What’s being optimized? What’s the right objective function?
Contents


2: The speed accuracy tradeoff and optimal performance on a free response task.

3: Information gap theory: an account for sub-optimal behavior.

4: Incorporating biases and priors: top-down vs. bottom-up information; a cued response task, psychometric functions and two almost optimal monkeys.

Message: Simple stochastic differential equations can help understand brain function.
1: A simple perceptual decision task

“On each trial you will be shown one of two stimuli, drawn at random. You must identify the direction (L or R) in which the majority of dots are moving.” The experimenter can vary the coherence of movement (% moving L or R) and the delay between response and next stimulus. Correct decisions are rewarded. “Your goal is to maximize rewards over many trials in a fixed period.” You must be fast, and right!

30% coherence 5% coherence

Courtesy: W.T. Newsome

Behavioral measures: reaction time distributions, accuracy; speed-accuracy tradeoff.
An optimal decision procedure for noisy data: the Sequential Probability Ratio Test

Mathematical idealization: During the trial, we draw noisy samples from one of two fixed distributions $p_L(x)$ or $p_R(x)$ (left or right-going dots).

The SPRT works like this: set up two thresholds $1/B$ and $B$ and keep a running tally of the ratio of likelihood ratios:

$$R_n = \left( \frac{p_L(x_n)}{p_R(x_n)} \right) \times \ldots \times \left( \frac{p_L(x_2)}{p_R(x_2)} \right) \times \left( \frac{p_L(x_1)}{p_R(x_1)} \right)$$

When $R_n$ first exceeds $B$ or falls below $1/B$, declare victory for $R$ or $L$.

**Theorem:** (Wald, Barnard) Among all fixed sample or sequential tests, SPRT minimizes expected number of observations $n$ for given accuracy.

For fixed $n$ & $B=1$ SPRT maximizes accuracy (Neyman-Pearson lemma).
The continuum limit is a **DD** process

Take logarithms: multiplication in $R_n$ becomes addition.
Take a continuum limit: addition becomes integration.

The SPRT becomes a drift-diffusion (DD) process (a cornerstone of 20th century physics, and perhaps the simplest stochastic ODE):

$$dx = A \, dt + c \, dW$$

(\text{drift rate} \quad \text{noise strength})

Here $x(t) = \log R$ is the accumulated evidence (the log likelihood ratio). When $x(t)$ reaches either threshold, $Z = \log B$ or $-Z$, declare R or L the winner.

But do humans (or monkeys, or rats) drift and diffuse?
Evidence comes from three sources: behavior, neural recordings, and mathematical models.
Behavioral evidence: RT distributions

Human reaction time data in free response mode can be fitted to the first passage threshold crossing times of a DD process.

Prior or bias toward one alternative can be implemented by setting starting point $x(0) \neq 0$. Extended DD: variable drift & starting point. Simple expressions for mean RT, accuracy.

Ratcliff et al., Psych Rev. 1978, 1999, 2004
Neural evidence 1: neural firing rates

Spike rates of neurons in oculomotor areas rise during stimulus presentation, monkeys signal their choice after a threshold is crossed.


Neural evidence 2: spiking neuron models

Working hypothesis: motion sensitive cells in visual cortex MT pass noisy signals on to LIP, FEF, ... where integration occurs.

Experimental observations:

Simulation & analysis of spiking neurons:
Stochastic averaging over populations: A. Saxe.
Reduced model evidence: integration of noisy signals

We can reduce the spiking neuron model to a pair of leaky competing accumulators (LCAs):

\[
\begin{align*}
\frac{dy_1}{dt} &= (-\gamma y_1 + f(-\beta y_2) + s_1)dt + \sqrt{D}dW_1 \\
\frac{dy_2}{dt} &= (-\gamma y_2 + f(-\beta y_1) + s_2)dt + \sqrt{D}dW_2 
\end{align*}
\]

(Usher & McClelland, 1995, 2001)

Subtracting the accumulated evidence yields a DD process for \( x = y_1 - y_2 \).

2: Optimal decisions: a speed-accuracy tradeoff

The task: maximize rewards for a succession of trials in a fixed period:

Reward Rate: \[ RR = \frac{1 - ER}{RT + D} \] (\% correct / average time for resp.)

• Threshold too low

• Too high

• Optimal
Explicit optimum thresholds

How fast to be? How careful? The DDM delivers an explicit solution to the speed-accuracy tradeoff in terms of just 3 parameters: normalized threshold and signal-to-noise ratio $\alpha = Z/A$, $\beta = (A/c)^2$ and $D$.

\[
\begin{align*}
RT &= \alpha \tanh(\alpha \beta) \\
ER &= 1/[1 + \exp(2\alpha \beta)] \\
RR &= \frac{1 - ER}{RT + D}
\end{align*}
\]

Setting the threshold $\alpha = \alpha^*(\beta)$, we can express RT in terms of ER and calculate a unique, parameter-free Optimal Performance Curve:

\[
RT/D = F(ER)
\]
A behavioral test

Do people adopt the optimal strategy? Some do; some don’t.

Is this because they are optimizing a different function, e.g. weighting accuracy more?

Or are they trying, but unable to adjust their thresholds appropriately?

The theory delivers quantitative predictions. Its successes and failures generate precise questions, suggest new experiments.

A problem: What’s the right objective function?
A modified reward rate function with a penalty for errors gives a family of OPCs with an extra parameter: the weight placed on accuracy. (It fits the whole dataset better, but what’s explained?)

Too much accuracy is bad for your bottom line. (Princeton undergrads don’t like to make mistakes.)
Suboptimality: taking necessary care?

Q: Suboptimal behavior could be reckless (threshold too low) or conservative (threshold too high)? Why do most people tend to be conservative? Could it be a rational choice? Which type of behavior leads to smaller losses?

A (simple): Examine the RR function. Slope on high threshold side is smaller than slope on low threshold side, so for equal magnitudes, conservative errors cost less.

A (complicated): Appeal to a rational theory of uncertainty.
3: Information gaps: another view of what’s best

Info-gap theory allows uncertainties in parameter estimates, and can also be applied to DD process models of forced choice tasks; e.g. suppose that response-to-stimulus interval \( D_{\text{actual}} \in [D - \varepsilon, D + \varepsilon] \).

There are two approaches.

**Robust satisfy:** Maximize the uncertainty \( \varepsilon \) for which a given (and necessarily suboptimal) RR can be guaranteed. (How little work can I do and still get a B?)

**Maximin:** Choose the threshold \( \alpha \) that maximizes the worst RR over a given uncertainty uncertainty range \( \varepsilon \).

Similar treatment for uncertainties in \( \text{SNR} \beta \).

Uncertainties in response-to-stimulus interval treated via the maximin strategy appear to match the overall pattern of the data best:

Uncertain RSIs: maximin perf curves predict higher thresholds for poorer timers.

M. Zacksenhouse, PH & R. Bogacz (in review, 2009)
Poor timing can account for suboptimal behavior

Split the subjects into 3 groups, based on total scores over all conditions. Fit Info-gap maximin perf curves, allowing each 1 uncertainty parameter.

All fit the top 30% well, but MMPCs fit all groups best; signif. better than accuracy weight theory.

The shapes of the curves, and the data histogram, are decisive here!

M. Zacksenhouse, PH & R. Bogacz (in review, 2009)
4: Fixed viewing time (cued response) tests

can also be modeled by DD/OU processes (focus on accuracy, ignore RTs). One considers the PDF of sample paths of the SDE, which is governed by the forward Fokker-Planck or Kolmogorov PDE:

$$dx = [A(t) + \lambda x] dt + cdW \Rightarrow \frac{\partial p}{\partial t} = -\frac{\partial}{\partial x} ([A(t) + \lambda x] p) + \frac{c^2}{2} \frac{\partial^2 p}{\partial x^2}$$

Interrogate solution at cue time $T$: is $x > 0$ or $< 0$? [Neyman-Pearson]

General solutions for time-varying drift (SNR) are available, so ....
We can predict Psychometric Functions (PMFs):

Accuracy for fixed viewing time $T$, sorted by coherence.

$$P_{\text{corr}}(C, T) = \int_0^\infty p(x, T; C, \ldots) \, dx$$

DD model with variable drift, e.g.:

$$dx = a C^m \left[ d + (1 - d) e^{-\gamma t} \right] \, dt + c \, dW$$

Model fits to data from monkeys during training on the moving dots task. Animals learn to extract signal from noise.

Scale factor $a$: steady increase in SNR.  
DD can incorporate priors: reward expectations

Integrating bottom-up (stimulus) and top-down (prior expectation) inputs: a motion discrimination task with four reward conditions. Introduces reward priors (expectations).

Why monkeys? Electrophysiology!

We only model this part

DD/OU models with reward bias priors, 1

Choose a model for reward expectation. Two examples are:

1. Bias applied to drift rate throughout reward cue and motion periods:
   \[
   A(C, t) = \begin{cases} 
   b, & t \in [0, \tau) \\
   b + aC, & t \in [\tau, T + \tau] 
   \end{cases} \quad \text{reward cue period}
   \]
   \[
   x(0) = 0. \quad \text{motion period.}
   \]

2. Initial condition set at start of motion period:
   \[
   A(C, t) = aC, \quad x(0) = \mu_0 \neq 0. \quad \text{motion period only.}
   \]

For \( b \neq 0 \) or \( \mu_0 \neq 0 \), predicts shifted PMFs:

\[
\frac{dx}{dt} = [A(C, t) + \lambda x]dt + \sigma dW
\]

stable OU (recency)  
\( \lambda < 0 \)

DD (optimal)  
\( \lambda = 0 \)

unstable OU (primacy)  
\( \lambda > 0 \)

DD/OU models with reward bias priors, 2

These reward expectation models both lead to PMFs that can be written in the simple form

\[
P(C; b_1, b_2) = \frac{1 + \text{erf}[b_1(C + b_2)]}{2}
\]

Where

\[
b_1 = \frac{a(e^{\lambda T} - 1)}{\sigma \sqrt{\lambda(e^{2\lambda T} - 1)}}, \quad b_2 = \frac{\mu_0 \lambda e^{\lambda T}}{a(e^{\lambda T} - 1)},
\]

or

\[
b_1 = \frac{a(e^{\lambda T} - 1)}{\sigma \sqrt{\lambda(e^{2\lambda(T+\tau)} - 1)}}, \quad b_2 = \frac{b(e^{\lambda(T+\tau)} - 1)}{a(e^{\lambda T} - 1)},
\]

depending on the model chosen. But unless we have a range of “priming” and viewing times \( \tau, T \), these models can’t be distinguished: the parameters \( a, \sigma, \lambda, \mu_0, b \) cannot be separated.

We can nonetheless compute shifts that maximize expected rewards, e.g., in simple case of fixed coherence \( \pm \bar{C} \):

\[
b_2^{\text{opt}} = \frac{1}{4b_1^2 \bar{C}} \ln \left( \frac{r_1}{r_2} \right)
\]

\(~1/\text{SNR} \) reward ratio
DD/OU models with reward bias priors, 3

Fit the model to the Rorie-Newsome behavioral data from two adult male rhesus monkeys, averaged over all sessions:

monkey A

monkey T

For fixed $\tau, T$ the PMFs all reduce to a 2 parameter family:

$$P(C; b_1, b_2) = \frac{1 + \text{erf}[b_1(C + b_2)]}{2}$$

slope  shift
Maximize expected rewards: compute optimal shifts $b_2^{opt}$ given animals’ slopes $b_1$ and compare with their actual shifts:

\[
E[r] = \frac{1}{2N+1} \left\{ r_1 \sum_{j=1}^{N} P(b_1(+C_j + b_2)) + r_2 \sum_{j=1}^{N} [1 - P(b_1(-C_j + b_2))] \\
+ \frac{r_1 P(b_1 b_2) + r_2 (1 - P(b_1 b_2))}{2} \right\}
\]

\[
\frac{r_1}{r_2} = \frac{\sum_{j=1}^{N} \frac{\partial P}{\partial b_2}(b_1(-C_j + b_2)) + \frac{1}{2} \frac{\partial P}{\partial b_2}(b_1 b_2)}{\sum_{j=1}^{N} \frac{\partial P}{\partial b_2}(b_1(+C_j + b_2)) + \frac{1}{2} \frac{\partial P}{\partial b_2}(b_1 b_2)}.
\]

They both overshift, and T prefers alternative 2 when rewards are equal. But does this cost them much? How steep is the reward hill?
Expected reward functions are rather flat, and overshifting costs less than undershifting. So they don’t lose much!
DD/OU models with reward bias priors, 6

Acuity (= slope $b_1$) and shifts ($b_2$) vary significantly from session to session, but, in spite of the “visual correlation,” the animals do not exhibit significant $b_1$ vs $b_2$ correlations. For monkey A:

Blue is optimal; magenta curves are 99% & 97% of optimal. With few exceptions, A stays inside 97% in every session.
Neural activity in simple decisions resembles a DD process: this model predicts optimal speed-accuracy tradeoffs. Some subjects are optimal, others not. Why? A bias toward accuracy?

Info gap theory allows for uncertainty in parameter estimates: robust suboptimal performance. A better account of behavior?

The DD process can also model cued responses, predict psychometric functions (PMFs): increasing SNR tracks learning.

DD processes extend to include top-down cognitive control: it can predict optimal PMFs. Two subjects tested both overshift, but garner 98 — 99% of their maximum possible rewards, in spite of significant session-to-session variability.

Future: Would like to correlate/compare indiv session and reward condition behaviors with electrophysiological data (LIP recordings).

Conclusions