

Optimal decisions: From neural spikes, through stochastic differential equations, to behavior*

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SUMMARY There is increasing evidence from in vivo recordings in monkeys trained to respond to stimuli by making left- or rightward eye movements, that firing rates in certain groups of neurons in oculo-motor areas mimic drift-diffusion processes, rising to a (fixed) threshold prior to movement initiation. This supplements earlier observations of psychologists, that human reaction-time and error-rate data can be fitted by random walk and diffusion models, and has renewed interest in optimal decision-making ideas from information theory and statistical decision theory as a clue to neural mechanisms.

We review results from decision theory and stochastic ordinary differential equations, and show how they may be extended and applied to derive explicit parameter dependencies in optimal performance that may be tested on human and animal subjects. We then briefly describe a biophysically-based model of a pool of neurons in locus coeruleus, a brainstem nucleus implicated in widespread norepinephrine release. This neurotransmitter can effect transient gain changes in cortical circuits of the type that the abstract drift-diffusion analysis requires. We also describe how optimal gain schedules can be computed in the presence of time-varying noisy signals. We argue that a rational account of how neural spikes give rise to simple behaviors is beginning to emerge.

key words: *Stochastic differential equations, drift-diffusion process, dynamical systems, phase oscillators, decision-making models.*

1. Introduction: Optimal decisions

Here we summarize a considerable body of work carried out in our group over the past five years. We are variously applied mathematicians, neuroscientists, and cognitive psychologists, and our goal is develop a series of linked models describing the collective neu-

ral computations involved in decision making and their behavioral outcomes. Much of our thinking is guided by the notion that computably optimal strategies provide limits to, and may even guide, human and animal performance. Here we focus on mathematical methods and modeling strategies, involving stochastic differential equations, dynamical systems and signal processing theory. We also sketch the behavioral and neurobiological background to this work, and we provide many references.

We start with a phenomenological drift diffusion (DD) model for the identification of a noisy stimulus drawn at random from a pair of options: the two-alternative forced choice task (2AFC). We derive optimal operating conditions for this process, presuming that certain DD parameters, describing cortical function, may be adjusted to suit the stimuli and task at hand. Neurotransmitter release provides a mechanism for such adjustments, and we continue by sketching how a biophysically-based model of spiking noradrenergic neurons in the locus coeruleus (LC) can be simplified and their response to stimuli analyzed. This brainstem area is believed to modulate gain in cortical circuits. We conclude by outlining the derivation of optimal gain schedules for a DD-type process with variable signal, noise and feedback, and comparing these to direct recordings of LC activity.

The drift diffusion (DD) process, governed by the SDE

$$dx = \pm adt + \sigma dW, \text{ with thresholds } \pm z, \quad (1)$$

where σ is the standard deviation of a Wiener (white noise) process $W(t)$ and $\pm a$ denote the drift rates corresponding to the two stimuli, has been used since the 1960's to model human reaction time and error statistics in the 2AFC and other tasks [1]. Not only is it the continuum limit of the sequential probability ratio test (SPRT), known to be the optimal decision-maker for 2AFC tasks with accumulating noisy data [2], [3], but its threshold-crossing behavior closely matches human behavioral data [4], [5]. Moreover, direct neural recordings from oculomotor brain areas of monkeys performing choice tasks has recently shown that firing rates of groups of neurons selective for the response corresponding to the chosen alternative rise toward a threshold that signals the onset of motor response in a manner

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that seems to match sample DD paths [6]–[8]. Eqn. (1) can also be derived from “high level” leaky competing accumulator (artificial neural network) models of neural function, as noted in §§2-3 below.

In this application a is the mean growth rate of the log likelihood ratio and $x(t)$ its accumulated value. If the stimuli are presented with equal frequency, sample paths are started at $x(0) = 0$ and a response is recorded when $x(t)$ first exceeds $+z$ or falls below $-z$, thus defining the *reaction time* (RT) on that trial. For drift $+a$, crossing $+z$ denotes correct responses and $-z$ errors, and vice versa. First passage time distributions yielding mean RTs, and error rates (ER) are readily computed for (1) from the backward Kolmogorov or Fokker-Planck equation associated with it [9]:

$$\text{RT} = \frac{z}{a} \tanh\left(\frac{az}{\sigma^2}\right); \quad \text{ER} = \frac{1}{1 + \exp\left(\frac{2az}{\sigma^2}\right)}. \quad (2)$$

For fixed signal to noise ratio (SNR) a/σ , as z increases, ER decreases but at the expense of longer RTs: this *speed-accuracy tradeoff* is well-known in psychology [1]. However, as suggested by Gold and Shadlen [10], one can explicitly compute thresholds that maximize the average *reward rate*:

$$\text{RR} = \frac{1 - \text{ER}}{\text{RT} + D + D_{\text{pen}} \cdot \text{ER}}; \quad (3)$$

here the numerator represents the average fraction of correct responses and the denominator denotes the average time between responses: the sum of RT, an experimenter-imposed response-to-next-stimulus interval (RSI) D , and possibly an additional penalty delay D_{pen} incurred by errors. (In applying this formula to data gathered from human or animal subjects, one must further subdivide RT into the “decision time” that represents information processing, and an “overhead time” due to visual processing and motor response latencies [11]. The latter tends to remain fixed for a given subject, and may be combined with D .)

Substituting Eqn. (2) into (3) gives:

$$\text{RR} = \left[\frac{z}{a} + D + \left(D + D_{\text{pen}} - \frac{z}{a} \right) \exp\left(-\frac{2az}{\sigma^2}\right) \right]^{-1}. \quad (4)$$

Of the original DD parameters in Eqns. (2) and (4) only the two ratios $\tilde{z} = z/a$ and $\tilde{a} = (a/\sigma)^2$ (\sim SNR) appear. Regarding \tilde{a} , D and D_{pen} as fixed and differentiating with respect to \tilde{z} , one finds that the unique maximum of RR as a function of threshold for fixed SNR and delays occurs when the following condition holds:

$$\exp(2\tilde{a}\tilde{z}) - 1 = 2\tilde{a}(D + D_{\text{pen}} - \tilde{z}); \quad (5)$$

note that only the sum $D_{\text{tot}} = D + D_{\text{pen}}$ appears in this expression. We may solve for \tilde{z} and \tilde{a} in terms of RT and ER from (2) to obtain

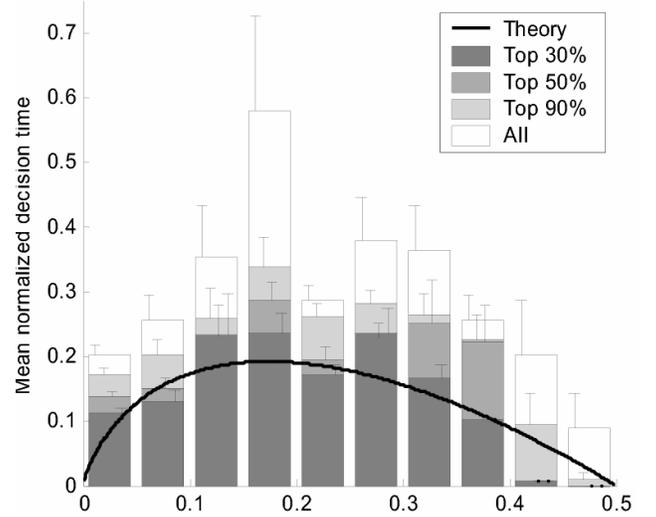


Fig. 1 Thick curve shows the optimal performance curve given by Eqn. (7), and histogram bars show data collected from 80 human subjects, sorted according to total rewards accrued. White bars: all subjects; light gray bars: lowest 10% excluded; medium gray bars: lowest 50% excluded; dark gray bars: lowest 70% excluded. Error bars indicate standard error.

$$\tilde{z} = \frac{\text{RT}}{1 - 2\text{ER}}, \quad \tilde{a} = \frac{1 - 2\text{ER}}{2\text{RT}} \log\left(\frac{1 - \text{ER}}{\text{ER}}\right), \quad (6)$$

and substituting Eqns. (6) into (5) yields a speed-accuracy tradeoff that corresponds to maximizing RR:

$$\frac{\text{RT}}{D_{\text{tot}}} = \left[\frac{1}{\text{ER} \log\left(\frac{1 - \text{ER}}{\text{ER}}\right)} + \frac{1}{1 - 2\text{ER}} \right]^{-1}. \quad (7)$$

This *optimal performance curve* (OPC) uniquely relates the normalised reaction time ($\text{RT} / [D + D_{\text{pen}}]$) to ER: no other parameters appear. Hence data collected for different subjects (who may exhibit differing SNRs, even when viewing the same stimuli), and for differing RSIs and penalty delays, can be pooled and compared with the theory. See [11] for full details.

Fig. 1 shows the OPC of Eqn. (7) as a bold curve, the form of which may be understood by noting that the left hand end, where error rates and normalised reaction times are both low, corresponds to high SNRs (decisions are quick and accurate), while at the right hand end the SNR approaches zero, and the optimum strategy is to guess without spending time to examine the stimulus, also giving a small reaction time. In between, the curve describes the optimal speed/accuracy compromise.

Fig. 1 also shows a histogram of behavioral data compiled from human subjects indicating that those who score in the top 30% overall on a series of tests with differing delays and SNRs follow the optimal curve remarkably closely. More detailed data analysis [11] reveals that, in each block of trials for which stimulus recognition difficulty (\sim SNR) and RSI are held constant, these subjects rapidly adjust their thresholds to achieve this. However, other subjects, and especially

the lowest-scoring 10%, display suboptimal behavior, with significantly longer reaction times and correspondingly lower ERs. Previous studies have shown that humans often favor accuracy over reward [12]–[14], and alternative objective functions have been proposed to account for this behavior.

For example, one can propose a modified reward rate, weighted toward accuracy by additionally penalizing errors, as suggested by the proposal that human subjects experience a competition between reward and accuracy (COBRA) [13], [14]:

$$RA = RR - \frac{q}{D_{total}}ER; \quad (8)$$

here the factor q specifies the additional weight placed on accuracy, and the characteristic time D_{total} is included in the second factor, so that the units of both terms in RA are consistent.

Maximizing RA as above we obtain a family of OPCs parameterized by q :

$$\frac{RT}{D_{total}} = \frac{\mathcal{E} - 2q - \sqrt{\mathcal{E}^2 - 4q(\mathcal{E} + 1)}}{2q}, \quad (9)$$

where

$$\mathcal{E} = \left\{ \frac{1}{ER \log\left(\frac{1-ER}{ER}\right)} + \frac{1}{1-2ER} \right\}. \quad (10)$$

If rewards are monetary, one can also postulate a situation in which errors are rewarded (albeit less lavishly than correct responses), or penalized by subtraction of previous winnings:

$$RR_m = \frac{(1-ER) - qER}{RT + D_{total}} \quad (11)$$

This leads to the following OPC family:

$$\frac{RT}{D_{total}} = (1+q) \left\{ \frac{\frac{1}{ER} - \frac{q}{1-ER}}{\log\left(\frac{1-ER}{ER}\right)} + \frac{1-q}{1-2ER} \right\}^{-1}. \quad (12)$$

Both Eqns. (9) and (12) reduce to (7) for $q = 0$, as expected. Fig. 2 shows an example of the second family (12). Eqn. (9) gives a similar family, but the maxima move leftwards with increasing q rather than rightwards as in Fig. 2.

Both of these proposals involve a weight parameter q , which will typically be subject-dependent, since different people may place a greater or lesser weight on accuracy, even if they understand that a specific balance is implied, as in Eqn. (12). Values of q should then be fitted to individuals or subgroups of subjects, and the theory becomes descriptive rather than prescriptive. We are currently assessing such theories against our original behavioral data [11], and carrying out additional experiments, but in Fig. 2 we show that an average weight ($= 0.62$) may be assigned to the entire group.

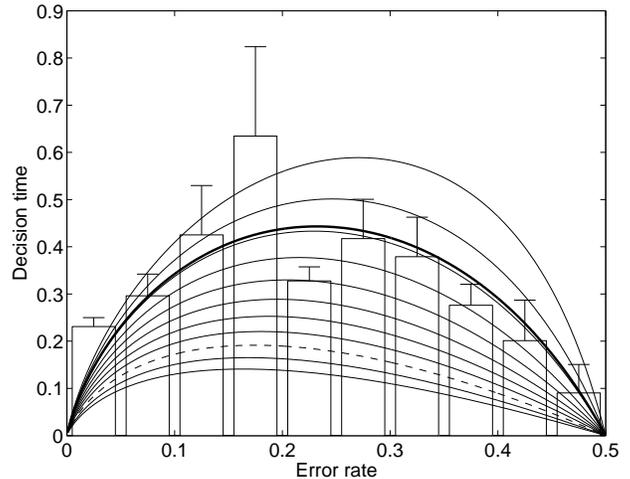


Fig. 2 Optimal performance curves of (12) for the modified reward rate function RR_m of (11) with q varied in steps of 0.1 between -0.2 (lowest curve) and 0.8 (highest curve). The dashed curve corresponds to $q = 0$ (Eqn. (7)) and the bold solid curve to $q = 0.62$: the best fit to *all* the subjects in the study (white bars). Error bars indicate standard error.

2. A biophysically-based neural model

The DD decision theory sketched above, based on the SDE (1), is an example of a ‘high level’ cognitive model. By themselves such models can be helpful in formalising questions in cognitive psychology and brain science more generally [15], but it is of course desirable to connect them with biophysically detailed models of the neural substrates involved in specific behaviors. We now review a recent example of such a model, emphasising the mathematical ideas used to simplify it so that analyses are possible.

As shown in [11], the DD process (1) can be derived in suitable limits from artificial neural network (connectionist) models of neural activity (see [16]–[18] and §3 below), which are in turn related to firing rate models that may be derived from biophysically-detailed, spiking, ionic current equations [19], [20] describing single cell activity, and “integrate-and-fire” simplifications thereof [21]–[24].

We have begun studies of specific cortical neural groups involved in the decision process, as well as others that, via neurotransmitter release, are responsible for control and attention selection. As described in the forthcoming review paper [25], the brainstem nucleus *locus coeruleus* (LC) plays an important role in the latter [26], [27], releasing norepinephrine (NE) widely in the cortex when its cells fire action potentials. Direct recordings in monkeys and pupillometry in humans reveal that the LC displays two operational modes: a “tonic” state in which the baseline firing rate in the absence of salient external stimuli is relatively high and transient responses to stimuli are relatively small,

and a “phasic” state in which baseline rates are lower but transient responses significantly larger [25]. Tonic modes are associated with poor performance on choice tasks and phasic modes with good performance [27]. This has led to the proposition that, while average levels of NE are important in tuning cortical circuits, the transient dynamics also plays a major role [25].

We model LC with a heterogeneous set of single-compartment, periodically spiking, ionic current neurons, originally proposed by Connor et al. [28], and subsequently reduced to a planar system by Rose and Hindmarsh [29] by assuming that the fast currents are equilibrated. Details of this specific case are given in [30]; here we describe the general strategy. Ionic current models, pioneered by Hodgkin and Huxley [31] in their Nobel Prize winning work, take the general form:

$$C\dot{v} = I_{\text{ion}}(v, w_1, \dots, w_N) + I_{\text{ext}}(t), \quad (13)$$

$$\dot{w}_i = \frac{\gamma_i}{\tau_i(v)} (w_{i\infty}(v) - w_i); \quad i = 1, \dots, N, \quad (14)$$

where Eqn. (13) describes the voltage dynamics, with C denoting cell membrane capacitance, I_{ion} the multiple ionic currents, and $I_{\text{ext}}(t)$ synaptic and external inputs. Eqns. (14) describe the dynamics of the gating variables w_i , each of which represents the fraction of open channels in the cell membrane that pass ions of type i , and γ_i is a positive parameter. At steady state, gating variables approach voltage-dependent limits $w_{i\infty}(v)$, usually described by sigmoidal functions [19], [20].

One can appeal to time scale separation to set fast gating variables, for which $\gamma_i/\tau_i(v)$ is large, at their equilibrium values, thereby eliminating the corresponding variables w_i . Similarly, very slow variables can be taken constant in studying mid range dynamics. In this way the relatively high $(N + 1)$ -dimensional dynamics of Eqns. (13-14) can be reduced to a phase space spanned by v and a few mid-range w_i 's. This procedure may be justified via geometric singular perturbation theory [32].

As noted, Rose and Hindmarsh [29] had already reduced the Connor model to two variables, v and a single representative channel variable w . This planar system may be further reduced to a one-dimensional oscillator via the phase response curve (PRC) method [33], [34]. This reduction, which can also be applied in higher dimensional cases and to more complex bursting neurons [35], [36], relies on the existence of an attracting, normally hyperbolic limit cycle Γ [37] (representing the periodic spikes in isolation). One defines a non-uniform “angular” coordinate ϕ along the limit cycle and complementary “radial” coordinates that span isochronal (= equal time or equal phase) surfaces transverse to Γ and assumes that external inputs and coupling are sufficiently weak that the original voltage and gating variables can be written as functions $v(\phi)$, $w_i(\phi)$, with values determined by phase on the isolated limit cycle. The isochronal foliation enables one to determine

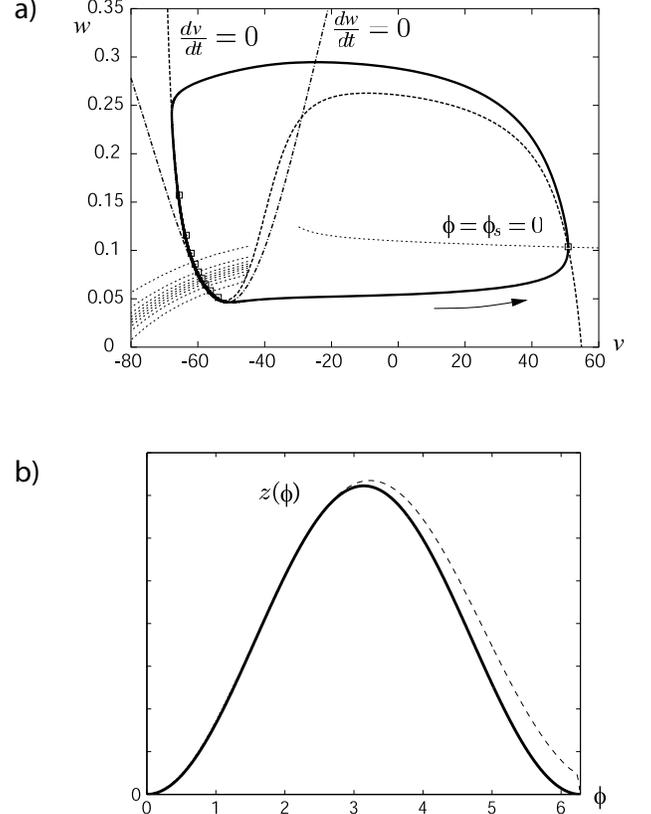


Fig. 3 (a) Phase space structure for the two-variable Rose-Hindmarsh model, showing attracting limit cycle and isochrons. The thick dashed and dash-dotted lines are nullclines for $\dot{v} = 0$ and $\dot{w} = 0$, respectively, and squares show points on the perturbed limit cycle, equally spaced in time, under small constant input current I_{ext} . (b) PRCs for the Rose-Hindmarsh model: asymptotic form $z(\phi) \sim [1 - \cos \phi]$ shown solid, and numerical computations dashed. Adapted from [30].

the effects of instantaneous (delta function), infinitesimal perturbations in voltage due to external or synaptic inputs in terms of a single PRC function $Z(\phi)$ that encodes the phase shift due to such a perturbation in terms of the phase at which it is applied. This function captures and summarizes much of the detailed ionic dynamics. Moreover, in cases in which the limit cycle Γ is close to a bifurcation, analytical expressions for $Z(\phi)$ in terms of parameters in the original equations (13-14) can be derived [33], [38], [39]. Fig. 3 illustrates the procedure for the Rose-Hindmarsh model.

Applied to a heterogeneous coupled LC network subject to independent additive white noise in external currents, this yields a set of SDEs each of the form:

$$d\phi_i = \left[\omega_i + Z(\phi_i)(I(t) + \sum_j f(\phi_i, \phi_j)) \right] dt + \sigma Z(\phi_i) dW(t) + \mathcal{O}(\sigma^2), \quad (15)$$

where $I(t)$ and $f(\phi_i, \phi_j)$ denote inputs due to external stimuli and from synaptic and electrotonic coupling

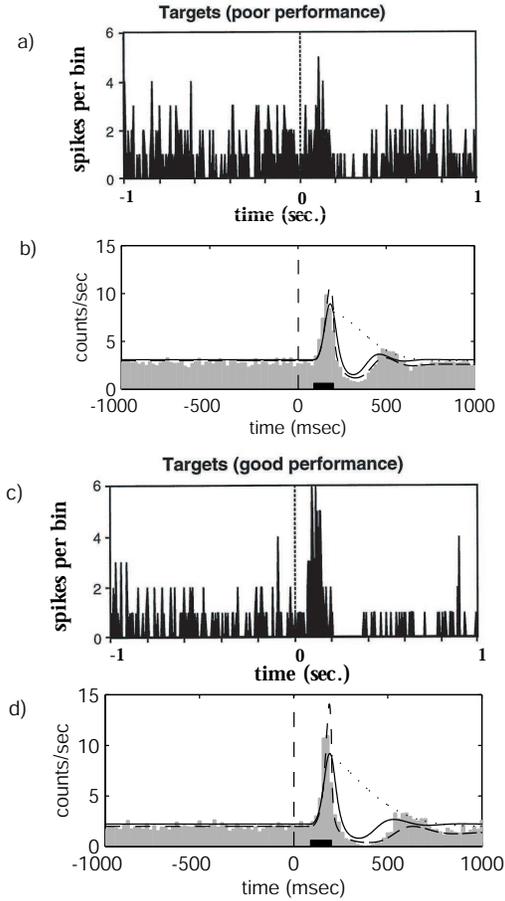


Fig. 4 Peri-stimulus time histograms of LC activity for poor (a) and good (c) performance periods during a target identification task, taken from single neurons, averaged over ~ 100 trials, from [27]. Panels (b,d) show corresponding histograms computed by simulating 100 Rose-Hindmarsh neurons (gray bars) and from Fokker-Planck equation for (15) (solid curve), with analytical decay bounds (dashed curve).

from other LC cells, and $\sigma dW(t)$ denotes a Wiener process of variance σ . Note that all inputs are “filtered” through the PRC $Z(\phi_i)$. See [30] for further details.

The probability density of phases, $p(\phi, t)$, for (15) in the weakly-coupled limit may be found from the associated forward Kolmogorov or Fokker-Planck equation [9] and (semi-) analytical expressions derived for the flux of phases through $\phi = \phi_s = 0$, corresponding to the cell firing an action potential. This, in turn allows us to compute average firing rates of (groups of) LC cells in response to stereotyped stimuli representative of simple visual recognition tasks [27], [40]. Fitting noise (σ) and oscillator frequency distributions $P(\omega_i)$ to interspike interval data in the absence of stimuli, we may then compute firing rate histograms for comparison with experimental data.

Fig. 4 illustrates the main result of [30]: that the magnitude of the transient response to stimulus, relative to baseline, is inversely proportional to baseline

spiking frequency of LC in the absence of stimuli. This partially explains the correlations between low baseline activity and strong phasic response on the one hand, and higher baseline activity and lower response on the other [25], [27].

These results, and others with different stimuli representing more complex decision tasks [30] and different neural models [39], show that analytically-tractable reduced descriptions of neural groups can be derived from biophysically detailed ion-channel models. A major challenge is to assemble such groups into ‘global’ models of interacting brain mechanisms known to be active in perception and decision-making, e.g. the medio-temporal and lateral interparietal areas, superior colliculus and frontal eye fields (MT, LIP, SC, FEF), involved in motion-detection and response saccades in monkeys [6]–[8], and to integrate other brain areas such as LC and thalamus. At the level of connectionist models, we have begun to study how gain changes such as those due to the transient increases of LC spike rates of Fig. 4 can affect cortical neurons. We briefly review this before concluding the paper.

3. Optimal gain schedules

Neurophysiological studies have shown that, among other actions, NE modulates cortical activity, making neurons relatively more responsive to synaptic inputs while decreasing their spontaneous (noisy) activity [41]. The resulting enhanced synaptic throughput was simulated in a connectionist network by increasing gain ($g(t)$, see below) [42]. This makes precise the conjecture that LC activity influences cortical function [25], and suggests how time-dependent gain effects may contribute to improved performance, as we now describe.

A firing rate model for decision-making in 2AFC takes the form:

$$dy_1 = [-\alpha y_1 + f_{g(t)}(-\beta y_2 + a_1(t))] dt + g(t)\sigma(t)dW_1, \quad (16)$$

$$dy_2 = [-\alpha y_2 + f_{g(t)}(-\beta y_1 + a_2(t))] dt + g(t)\sigma(t)dW_2, \quad (17)$$

where W_j are independent Wiener processes and the function $f_{g(t)}$ relating firing rate to inputs is typically sigmoidal:

$$f_{g(t)}(x) = \frac{1}{1 + \exp(-4g(t)(x - b))}, \quad (18)$$

or piecewise-linear, being bounded above (by 1) and below (by 0). Here we allow time-varying stimuli $a_j(t)$, noise level $\sigma(t)$ and gain $g(t)$ (the maximum slope of $f_{g(t)}$) (cf. [16], [17]).

If decay (leak) α and/or inhibition β are large, then (16-17) has a one-dimensional stochastic slow manifold [43] that attracts solutions in a probabilistic sense. Moreover, linearizing (18) at the point of

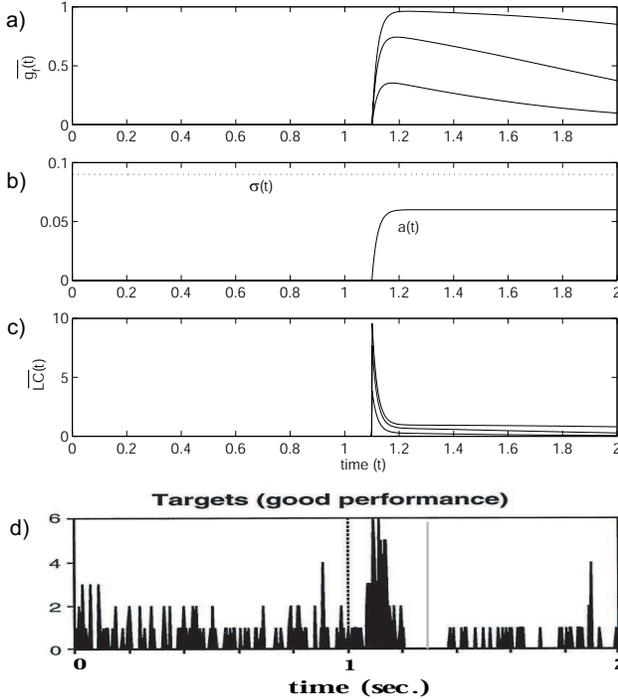


Fig. 5 Comparison of optimal gain theory with empirical data for a target detection task. (a) Optimal gain schedules for the firing rate model, with a processing time lag of 0.1 sec following sensory cue and signal that rises from 0 with constant noise, as shown in (b). (c) The corresponding optimal time course of LC firing rate. (d) Histogram of LC firing rates recorded in monkey during good performance, from [27].

maximum slope and subtracting (17) from (16) yields a scalar Ornstein-Uhlenbeck (OU) process for the difference $x = y_1 - y_2$ in firing rates:

$$dx = (\lambda x + g(t)a)dt + g(t)\sigma dW, \quad (19)$$

where $\lambda = g(t)\beta - \alpha$ and $a = a_1 - a_2$. If g is constant and the network is *balanced* in that leak rate equals inhibition ($\lambda = 0$), Eqn. (19) reduces to the DD SDE (1) with $a = a_1 - a_2$. In this case a balanced firing rate model with constant SNR closely approximates the optimal DD decision-maker [11], [18].

The SPRT optimality theory assumes that the two distributions from which samples are drawn are stationary: effectively, that a and σ are constant in (1). In practice, visual and other stimuli may vary on fast time scales, so that one is faced with decoding a signal that waxes and wanes during the decision process. In [18] we address this problem of varying SNR and, using the linearised one-dimensional OU SDE (19) with time-dependent coefficients $a(t)$ and $\sigma(t)$, we develop general expressions for optimal multiplicative gain schedules $g(t)$. These implement the matched filter strategy of signal processing [44]. We compute optimal g s for specific simple cases of stimuli that rise both slowly and rapidly and, using a linear model of norepinephrine re-

lease as a function of LC firing rate, we find that the transient LC firing rates thus predicted are qualitatively similar to experimental PSTH records such as those of Fig. 4. See Fig. 5. This lends further support to the hypothesis that LC activity, triggered by the arrival of salient stimuli in cortical decision areas, can tune those areas (as well as motor areas) to improve accuracy and speed responses [25].

4. Conclusion

We have reviewed recent work in modeling neural and behavioral responses to stimuli at both the level of biophysical detail, beginning with ion channel models of Hodgkin-Huxley type, and at that of abstracted “higher level” connectionist and drift-diffusion SDEs. While numerous gaps remain between models at these disparate spatial and temporal scales, we believe that the general outlines of an integrated theory of neural function in simple decision-making tasks are beginning to emerge.

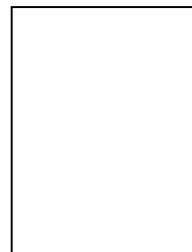
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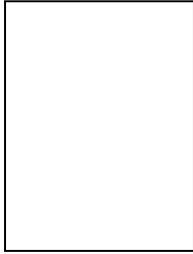
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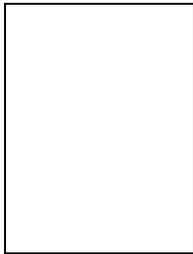


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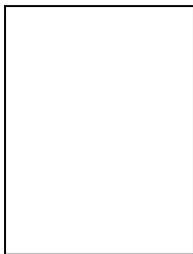
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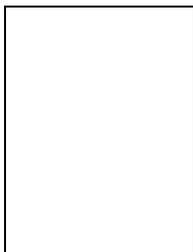
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