

Saccadic brightness decisions do not use a difference model

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Eye movements are the most frequent (~3 per second), shortest-latency (~150–250 ms), and biomechanically simplest (1 joint, no inertial complexities) voluntary motor behavior in primates, providing a model sensorimotor decision-making system. Current computational “difference” models of choice behavior utilize a single decision variable encoding the difference between two alternate signals, often implemented as a log-likelihood ratio. Alternatively, the oculomotor literature describes a “race” mechanism, in which two separate decision variables encoding the two alternate signals race against one another independently. These two models make two qualitatively distinct predictions, which can be tested empirically with a two-alternative forced-choice task. Unlike the race model, a decision variable based upon a differencing operation predicts strong mirror image correlations between response time (RT) and the signal strengths of the selected and unselected stimuli (because differencing creates equal and opposite correlations). In a saccadic brightness discrimination task, we observed positive correlations between response rate (1/RT) and the strength of both the selected and unselected stimulus, a simple qualitative prediction of race models that applies to any 2AFC task but which is fundamentally at odds with the most basic prediction of any difference model. Our data are, however, qualitatively consistent with a mechanism in which two competing motor plans co-exist and their two corresponding neural decision variables race to a threshold to drive the saccadic decision.

concerns the computation driving decision signals. In a difference model (M. S. Stone, 1960; Figure 1A), a single decision variable that quantifies the difference between the magnitudes of the two stimuli is integrated over time until either a positive or a negative threshold is crossed (Link & Heath, 1975; Ratcliff & Rouder, 1998), a neural implementation of a log-likelihood ratio (Gold & Shadlen, 2001). In a race model (Ratcliff, Hasegawa, Hasegawa, Smith, & Segraves, 2007; Robinson, 1973; Usher & McClelland, 2001) (Figure 1B), independent competing decision variables (M. S. Stone, 1960), each representing support for one alternative (Carpenter & Williams, 1995), race each other to threshold. Both models have been used to fit response time distributions and choice proportions for a variety of single-stimulus tasks (Churchland, Kiani, & Shadlen, 2008; Niwa & Ditterich, 2008; Palmer, Huk, & Shadlen, 2005; Ratcliff et al., 2007; Ratcliff & Rouder, 1998; Usher & McClelland, 2001), and both classes of models can account for a number of well-known benchmark phenomena (Brown & Heathcote, 2005, 2008) in the response-time literature. The approach in this paper is to separate the effects of the model decision variables (Figure 1A, B) from those emanating from model noise sources (Figure 1C).

Consider a generic magnitude discrimination between two sensory signals (a and b). In the noise-free case, the difference model and the race model yield canonically equivalent decision rules (i.e., $a - b > 0 \equiv a > b$) and produce identical sets of behavioral choices. However, these two models yield qualitatively different patterns of response times. For example, by employing the common assumption made by both models that the mean rate of rise is proportional to signal strength (Grice, 1968; LaBerge, 1962; Palmer et al., 2005; Piéron, 1927), the response time predicted by the difference model will be $1/|a-b|$, whereas the response time predicted by the race model will be $1/a$ if $a > b$ and $1/b$ if $b > a$. Starting with this basic difference between model predictions in the noise-free case, we examine the impact of various model noise

Introduction

Current models for perceptual and motor choices assume that noisy neural signals accumulate toward a response threshold, allowing one to account for the proportions of behavioral choices and their respective response time distributions. In the taxonomy of these models given by Smith and Ratcliff (2004), the distinction between the two basic classes of models

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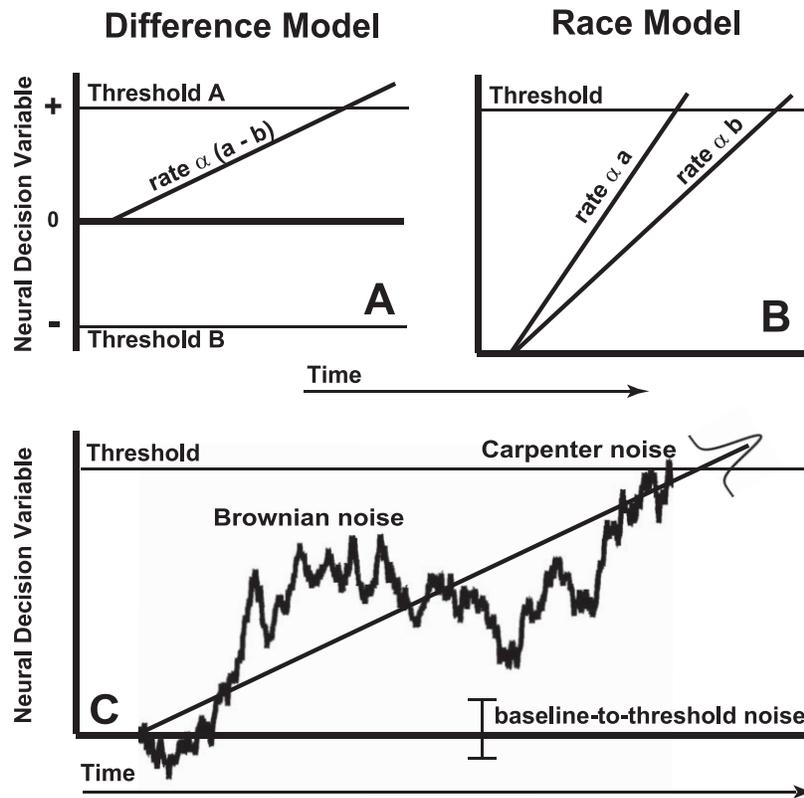


Figure 1. Model mechanisms. In A, a single neural decision variable encodes the difference between two input signals (a and b), integrated over time to reach a positive or negative threshold, triggering response A or B. In B, neural decision variables for two signals race to threshold against each other; the first signal to cross the threshold wins the race, triggering the response. In the noise-free case, these two models yield equivalent decision rules (i.e., $a - b > 0 \equiv a > b$) and predict identical choice performance, but qualitatively different patterns in response time. These generic models employ the common assumption that signal strength is proportional to rate of rise. C illustrates three well-known noise sources used to account for the proportions of behavioral choices (e.g., correct and incorrect responses) and their respective response-time distributions.

sources, and develop general qualitative predictions for both models which can be tested against response-time data from any 2AFC task.

In the present study, we use a very simple task to test predictions made by these two models regarding the relative strength and sign of the respective correlations between response time (or its reciprocal, response rate) and the signal strength of the selected and unselected stimulus. For the race model, both stimuli do not contribute equally to the timing of the response; the strength of the selected stimulus is expected to be more strongly correlated with response time than is the strength of the unselected stimulus, and the signs for both correlations are expected to match. For the difference model, because both stimuli contribute equally to the differencing operation, the strength of these two correlations (e.g., Pearson's r) will always have the same magnitude (Richards & Zhu, 1994), but opposite sign. In our task, we report significant positive correlations between response rate and both the selected and unselected stimulus strength. No difference model can account for that observed pattern in

saccadic response time and choice behavior. We conclude that humans do not drive their saccadic targeting decision in our 2AFC task using a differencing computation. Preliminary reports of our finding have been reported previously (Liston & Stone, 2009).

Materials and methods

Paradigm

To test the two models, we used a paradigm whereby observers made saccadic eye movements in a standard 2AFC brightness discrimination task that we have used before to examine the relationship between visual decision making for saccades and perception (Liston & Stone, 2008). On each trial, subjects fixated a central cross for a randomized duration (Luce, 1986; Palmer et al., 2005) drawn from a truncated exponential distribution (mean: 700 ms, minimum: 200 ms, maximum: 5000 ms) to defeat possible temporal expectation of

stimulus onset. Two bright disks appeared on a background of pixel noise, 6° to the left and right of fixation, and subjects were instructed to make a saccade to the brighter of the two disks. As two disks were presented on each trial, this stimulus allowed the signal strength and noise of each alternative to be manipulated independently. We ran seven human observers (all seven naïve, 500 trials per session, ten sessions per subject) on a task with signal strength varying over a large brightness range (i.e., both stimulus alternatives were drawn independently from a uniform distribution from 0 to 10 d' units with external noise SD of 1 d' unit). All observers provided informed consent under protocols approved by the NASA Ames Research Center Human Research Institutional Review Board, and our methods adhered to the Declaration of Helsinki.

Stochastic signal strength

We used stochastic, noisy stimuli in both tasks in this study. To create each stimulus image, we started with a full-field background of Gaussian pixel noise ($\sigma_{\text{ext}} = 8.2 \text{ cd/m}^2$) on a uniform gray background (37.6 cd/m^2). Two Gaussian-blurred ($\sigma = 1$ pixel) disks of diameter 0.6° (15 pixels) were added to the background, 6° to the right and left of the central fixation cross, each framed by a black bounding box. Both disks were scaled versions of one original “signal template,” which was normalized to have unit energy with respect to the external background noise (i.e., detection d' for the ideal observer was 1.0). This d' value is the square root of the energy in each stimulus disk (the magnitude of the inner product of the signal template and the stimulus) divided by the standard deviation of the background pixel noise (Burgess, Wagner, Jennings, & Barlow, 1981; Eckstein, Beutter, & Stone, 2001). We used fixed background noise and a fixed uniform background level, and set the signal strength for each of the two disks independently. For each stochastic stimulus image created, the stimulus strength for each stimulus disk was computed by calculating its detectability by the ideal observer in d' units (Green & Swets, 1966).

Reward schedule

Observers from outside the laboratory were paid hourly for their participation (\$12/h), and all subjects were paid an additional monetary incentive (maximum of \$15) corresponding to rewards accumulated during the course of a session. We used a monetary reward schedule that incorporated both response time (i.e., the size of the reward decreased as latency increased) and

accuracy (i.e., only correct trials were rewarded) on individual trials (Liston & Krauzlis, 2005; Liston & Stone, 2008). After each correct trial, subjects were given an auditory tone corresponding to the magnitude of reward on that trial (100 Hz to 1000 Hz). After each experimental session, the incentives were summed and paid to subjects. This schedule encouraged subjects to establish a consistent balance point between fast and accurate responses (Green & Swets, 1966), and subjects were instructed to maximize their take-home pay.

Simulations

The purpose of these simulations was to disentangle the properties of the model decision variable (i.e., a single difference variable or a race between two independent variables) from the noise sources that perturb those variables by simulating the effect of three commonly-used noise sources in psychophysical and response-time models of decision-making for both models. First, Brownian noise describes normally-distributed variability in the decision signal as a function of time within a trial (Link & Heath, 1975; Palmer et al., 2005; Ratcliff & Rouder, 1998), consistent with a Weiner diffusion process (i.e., $\text{var} = \sigma_{\text{brownian}}^2 \cdot t$). Second, Carpenter(ian) noise describes normally-distributed across-trial variability (Carpenter, 1981) in the rate of rise of the decision variable (Carpenter, 2002; Carpenter & Williams, 1995; Ratcliff & Rouder, 1998), giving rise to the “Recinormal” shape of response time distributions (i.e., the reciprocal of latency follows a normal distribution). Last, baseline-to-threshold noise describes across-trial variability in the distance between the starting position and the response threshold, distributed uniformly in these simulations, equivalent to either starting-point (Laming, 1968) or threshold (Grice, 1968; Hallett, 1969; Ratcliff & Rouder, 1998; Wickelgren, 1968) variability.

We ran four separate discrete (temporal resolution of 1 ms) Monte Carlo simulations of the models shown in Figure 1A, B, using Matlab (MathWorks, Natick, MA). First, to generate smooth choice-triggered response-rate color plots in Figure 2A, B, we simulated 1 million trials of our task (completely independent, uniformly-distributed brightness values) with a fixed level of Brownian noise (1.5 s^{-1}). Second, to illustrate the basic predictions for the choice-triggered correlations, we simulated 1 million trials of our task under three different noise conditions, varying the noise level in 200 steps: Brownian noise, 0 to 4 s^{-1} ; Carpenter noise, 0 to 30 s^{-1} ; baseline-to-threshold noise, 0 to 1.99. Third, to show that the predictions of the fully elaborated difference model (Ratcliff & Rouder, 1998; Smith & Ratcliff, 2004) remain consistent with the basic prediction of all difference models as far as the

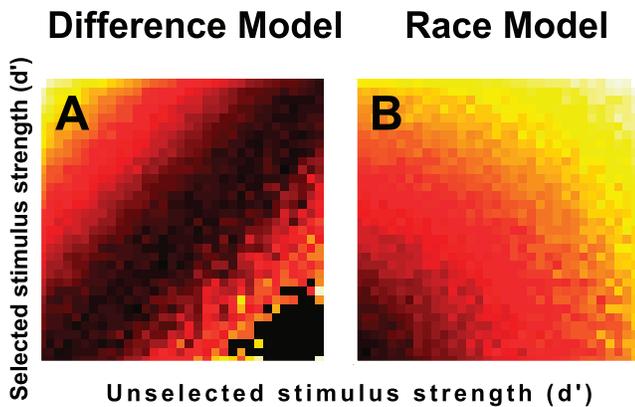


Figure 2. Model simulations. Simulated choice-triggered response time data in A, B are shown as color plots, faster responses being lighter (orange-yellow-white) and slower responses being darker (red-brown-black). The difference model (A) predicts that the selected and unselected stimulus contribute equally to response time, giving rise to iso-RT lines along the diagonal and the symmetry about the major diagonal corresponds to the predicted equality between correct and error response times with Brownian noise (Laming, 1968; M. S. Stone, 1960). Limited sampling of incorrect responses (below the major diagonal) gives rise to more noise (and an empty region) in the bottom right-hand corner. A race between signals (B) predicts that the selected stimulus will have a stronger relationship than the unselected, and that, due to competition between racing signals (Raab, 1962), RTs tend to become faster (not slower) as the strength of the unselected stimulus increases. The strength of the relationship between response rate and the selected and unselected stimuli differs because the motor response is triggered by the winning decision signal (plus whatever noise in that signal); the losing decision signal (plus whatever noise in that signal) influences response time only indirectly by driving movements toward faster responses in close races.

oppositely-signed RT correlations with the selected and unselected stimulus strength, we ran discrete simulations that sampled the space of each of the seven parameters in four steps (i.e., 4^7 simulations): starting position, -0.9 to 0.9 , threshold, 0.001 to 1 , fixed nondecision delay 0 to 500 ms, and nondecision delay variability, 0 to 100 ms. The Results section describes these simulations in this order.

Behavioral performance measurements

On each trial we measured the direction of the first saccadic eye movement with amplitude greater than 0.5° , and defined the saccadic decision as the direction of the horizontal eye movement. We discarded trials with anticipatory (latency < 100 ms, 1.4% of trials) or errant saccades (saccade direction $> 45^\circ$ from hori-

zontal, or endpoint $> 4^\circ$ off target, 3.8% of trials). We computed response rate as the simple reciprocal of saccadic latency. A binary “oculometric” saccadic choice was deemed “correct” if its horizontal component (leftward or rightward direction) was toward the brighter disk (Eckstein et al., 2001). On average across subjects, the proportion of correct saccades for the 2AFC saccadic brightness task was 0.72 (range: 0.65 – 0.77). The median saccade latency averaged across subjects was 224 ms (range: 202 – 240), consistent with normal visually-guided human saccadic response behavior (Leigh & Zee, 2006; Robinson, 1965). Both correct and incorrect trials were included in all analyses.

Results

To examine the qualitative predictions of the two models, we first ran Monte Carlo simulations of the two generic decision models (Figure 1A, B) perturbed by three well-known sources of internal noise (Figure 1C). The general qualitative prediction for the difference and race models is illustrated in the choice-triggered response-rate color plots (Figure 2A, B). The difference model (Figure 2A) always generates response times that vary systematically along the minor diagonal with faster responses associated with larger signal strength in the selected stimulus and lower signal strength in the unselected stimulus. Due to the differencing operation, the model predicts no change in response time along lines parallel to the major diagonal (i.e., a fixed signal-strength difference at varying pedestal levels), and the strength of the correlation between response rate and the selected and unselected stimuli will always be equal in magnitude but opposite in sign. The race model (Figure 2B) generates the same strong relationship between response time and the strength of the selected stimulus, but a much smaller effect of the strength of the unselected stimulus (typically a small increase for higher unselected strength). The observation that simultaneous quasi-independent stimuli contribute to faster responses (Todd, 1912) has been studied in the context of the race model for some time (Diederich, 1992; Miller, 1982; Raab, 1962).

Systematic simulations illustrate the basic qualitative differences between the two model mechanisms. The difference model predicts that the correlation between response rate and the strength of the selected stimulus (Figure 3A) will be of equal magnitude (but opposite sign) compared to the correlation with the unselected stimulus (Figure 3B), and that these points fall along the line of slope equals -1 when plotted against each other (Figure 3C). The race model predicts that the

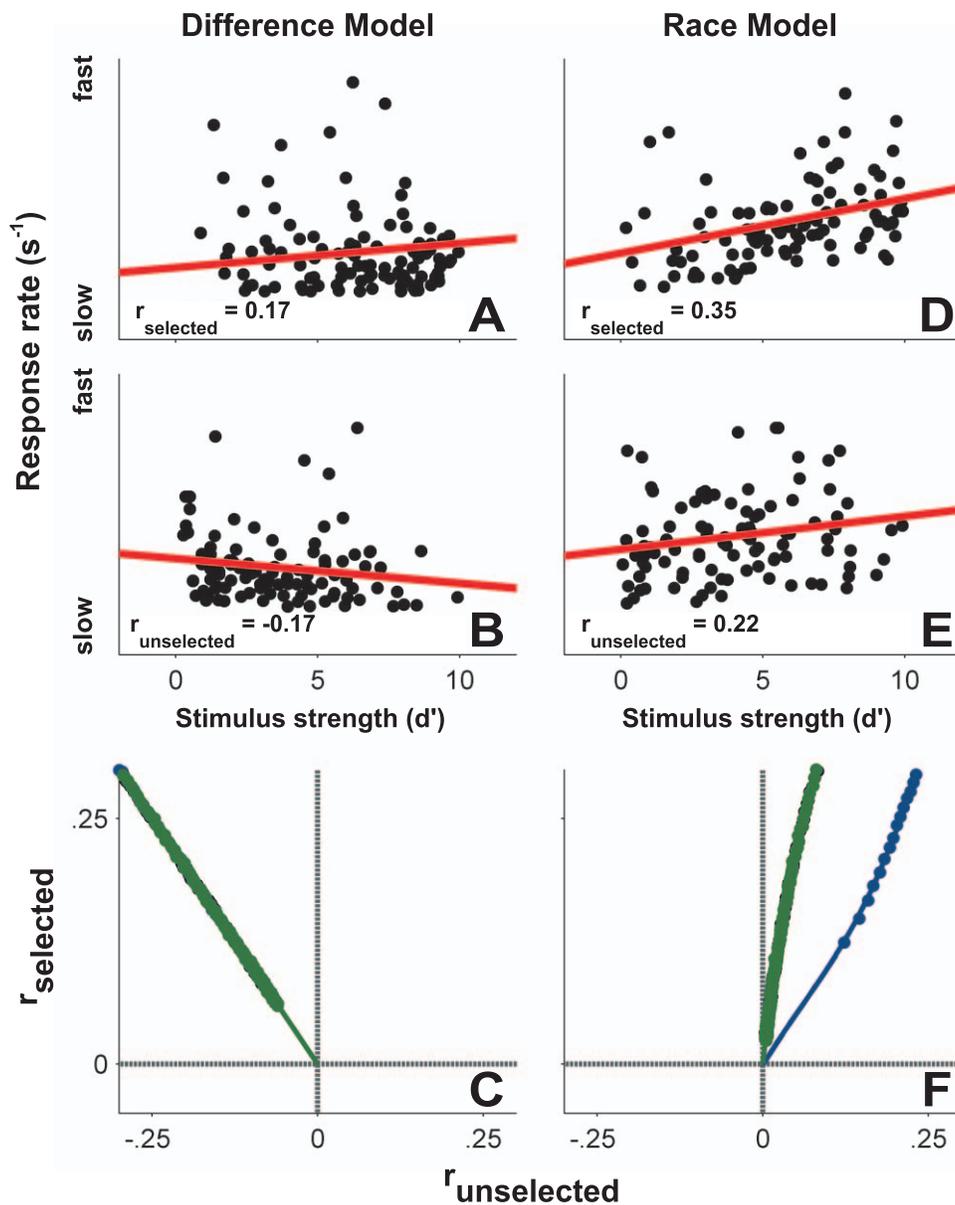


Figure 3. Correlation strength predictions. Each filled circle in the top four panels plots response rate (reciprocal latency) for one stimulated trial as a function of signal strength of the selected (A, D) or the unselected (B, E) stimulus, using the simulation data shown in Figure 2. The difference model predicts that the selected and unselected stimulus contribute equally to response time, giving rise to correlation strengths that are equal in magnitude and opposite in sign (A, B). A race between signals predicts that the selected stimulus (D) will have a stronger relationship than the unselected stimulus (E), and that the competition between racing signals drives RTs toward faster responses as the strength of the unselected stimulus increases (E). Panels C and F plot simulated Pearson's r values between response rate and the selected (ordinate) and unselected (abscissa) stimulus for the three common noise sources of internal noise (Figure 1C). Each filled circle plots the average correlation strength with one source of internal noise (black, Brownian noise; green, Carpenter noise; blue, baseline-to-threshold noise), at one noise level. Solid lines in F show polynomial regression through the origin for simulated data within the range of our observations ($r < 0.3$); starting-point variability between the origin and the first simulation point was assumed to be linear. The difference model (C) always predicts that the correlation with signal strength will have equal magnitude and opposite sign for the selected and unselected stimulus; the predictions of all three noise sources fall along the line of slope equals -1 . The race model (F) predicts a weak positive correlation between response rate and the unselected stimulus, with the predictions for Brownian and Carpenter noise following overlapping trajectories. Clearly the noise sources in the race model (blue vs. green in F) generate a minor second-order effect compared to the major qualitative difference between the difference and race models.

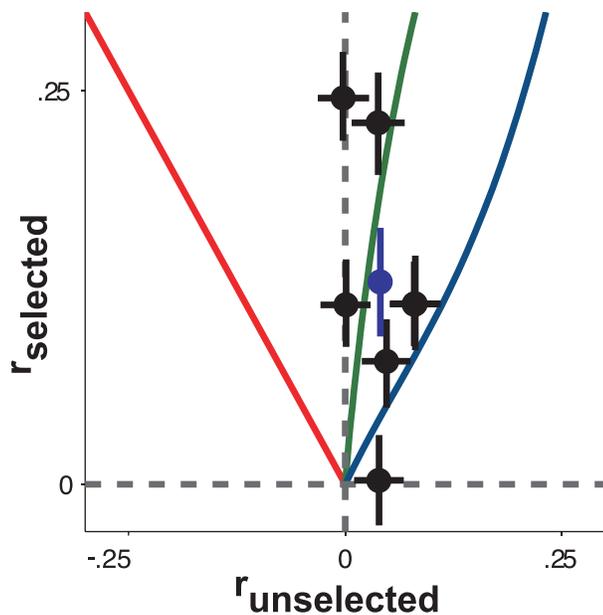


Figure 4. Observed correlation strength. Each black circle plots Pearson's r for the correlation with the selected stimulus against the corresponding correlation with the unselected stimulus, for one of the seven observers (two subjects' data very nearly overlap at the rightmost point). Error bars represent the central 95% of the distribution of bootstrapped values. The solid green (Brownian and Carpenter noise) and blue (baseline-to-threshold noise) lines delimit the range of correlation strength predictions for the race model plotted in Figure 3, and the solid red line shows the difference model prediction (with Brownian, Carpenter, and baseline-to-threshold noise superimposing). The blue circle represents the average across observers, and the error bars represent the across-observer *SEM*.

strength of the selected stimulus is expected to be more strongly correlated with response rate (Figure 3D) than is the strength of the unselected stimulus (Figure 3E), and the signs for both correlations are expected to match (Figure 3F). We also ran discrete simulations of the full diffusion model (Ratcliff & Rouder, 1998) that sampled the space of the seven parameters, and found results which conformed to the qualitative predictions shown in Figure 3C.

To test these predictions, we compared the correlations between response rate and the strength of the selected and unselected stimuli (Figure 4). We observed a weak positive correlation between response rate and the unselected stimulus (mean \pm *SD*: 0.04 ± 0.03 , t test across observers, $p < 0.05$) averaged across observers, inconsistent with the difference model, but consistent with a race model. Furthermore, the positive r -value for the correlation with the selected stimulus (mean \pm *SD*: 0.13 ± 0.08 , t test across observers, $p < 0.01$) had a significantly different magnitude than that with the unselected stimulus (paired t test across observers, $p < 0.05$). To make within-subject comparisons, we boot-

strapped a distribution of 1000 r -values for each subject by resampling our data with replacement (Efron & Tibshirani, 1993). The correlations were significantly different ($p < 0.05$) than that predicted by the difference model in all cases (i.e., significantly off the red simulated difference-model performance line with slope of -1).

The average correlation with the selected and unselected signal strength is, however, well predicted by a purely independent race model perturbed by noise (see filled blue circle in Figure 4). However, a within-subject analysis shows that the simplest race model cannot account for two of the seven observers (i.e., outside of the region bounded by the simulated noise sources in Figure 3F). Clearly, some of the intersubject variance still needs to be accounted for, perhaps by weak inhibitory, facilitatory, or auto-excitatory interactions within or between the decision variables (Boucher, Palmeri, Logan, & Schall, 2007; Usher & McClelland, 2001; Wang, 2002).

Discussion

By comparing the empirical trends in response times to model predictions, our method provides a simple test to distinguish between difference (M. S. Stone, 1960) and race (Robinson, 1973) models of 2AFC sensorimotor decisions. We observed a pattern of correlations between response rate and stimulus strength (Figure 4) that is qualitatively inconsistent with difference models. We conclude that a difference model cannot explain human saccadic behavior in our 2AFC brightness discrimination task.

Our results are, however, generally consistent with a race model although a purely independent race model cannot fully account for our data. First, two of our seven observers showed a significant deviation from our independent race model predictions. Second and more importantly, across all observers, we did not observe a positive relationship between the selected and unselected r -values given an independent race model with a single source of internal noise (solid lines in Figure 4). Thus, we propose that any race-model explanation of human performance in our task will require some interaction between the two racing decision variables (mutual facilitation or inhibition) and/or additional sources of variability (e.g., baseline-to-threshold noise), which could act to obscure the expected positive relationship between r -values and more fully explain the range of observed intersubject variability. Lastly, our data do not rule out the possibility that a neural mechanism altogether different from a race model underlies our observations.

Accounting for choice proportions

Both the race and the difference model make testable predictions about the proportion of correct and incorrect responses. In the noise-free case, both models predict an identical set of behavioral choices, although this behavior is not particularly realistic because all choices are correct. With a fixed level of Carpenter noise, and no other noise, both models make an identical set of behavioral choices (taking into account that differencing will alter the noise level by the square root of two). With a fixed level of Brownian noise, and no other noise, this remains true (also taking into account that the differencing operation will alter the timepoint-by-timepoint noise level by the square root of two). Those noise situations are straightforward, and can give rise to plausible distributions of choice proportions, but do not distinguish between the two model mechanisms. For the difference model, starting-point variability alone will still yield perfect performance. For the race model, the amount of starting point variability would have to be set to an unreasonably high level to cause incorrect responses. To produce plausible distributions of choice responses, another noise source (either Brownian or Carpenter) must be added. Thus, the two models could theoretically be distinguished using the proportions of correct and incorrect choices, although quantitative percent-correct predictions depend heavily on assumed interactions between model noise sources whereas our qualitative response rate approach is robust to noise assumptions (Figure 3).

Caveat regarding previous psychophysical studies

One potential reason that the correlation prediction resolved in this paper has not yet been tested is that it is critical to use a true 2AFC paradigm to examine models of 2AFC decisions. The structure of the race and difference models highlight the important distinction between single-stimulus “yes-no” and 2AFC psychophysical tasks (Green & Swets, 1966; Macmillan & Creelman, 1991). Both tasks require the subject to make one of two possible responses, thus seemingly “two-alternative forced-choice” tasks, although the word “alternative” refers to the two independent stimuli/signals rather than the two possible response choices. The critical difference between the task types is that in a “yes-no” paradigm, a single stimulus drawn from one of two classes is presented on each trial whereas in the two-alternative forced-choice paradigm, two statistically-independent stimulus alternatives are presented on every trial. The single stimulus in a “yes-no” task itself directly encodes the difference

between the two alternatives (e.g., in the commonly used random-dot motion paradigm, the net motion energy in the single stimulus is the simple difference between the superimposed opponent motion alternatives). Thus, any observed behavioral correlation with a difference variable may not be indicative of any actual neural differencing operation, an important point which has been noted recently (Churchland et al., 2011).

Furthermore, we must highlight the fact that simply having two stimuli does not guarantee a true “2AFC” decision. The degree of statistical dependence between the two stimuli could transform a “2AFC” task into a “yes-no” task. For example, with a stimulus like ours, if a “target” stimulus of strength $d' = 10$ were placed in one of the two locations with equal probability and a “distractor” stimulus of $d' = 1$ were always placed opposite, there would be a complete dependence between the signal alternatives, and the observer need only monitor one location in order to perform the task (thus, effectively a “yes-no” task). This fact prompted our use of two statistically-independent choice stimuli to force our observers to perform a true 2AFC task.

Indeed, if one revisits the noise-free case described in the Introduction (Figure 1) under the conditions of a YES-NO task (e.g., $b = -a$), it becomes clear that the choices of both model mechanisms always concur (i.e., $a > b \equiv a - b > 0$), and that the response time predictions are linearly related (i.e., $1/|a - b| = 1/[2a]$ for the difference model, and $1/a$ for the race model). In this context, the YES-NO task is a degenerate case of the 2AFC task because the “alternatives” are perfectly anticorrelated within a single signal and bona fide differencing is not possible. Thus, this stimulus offers no power to distinguish between the two models and fits of the difference model to YES-NO behavioral data (Palmer et al., 2005; Ratcliff et al., 2007; Ratcliff & Rouder, 1998; Usher & McClelland, 2001) are not determinative of the underlying decision mechanism.

Motor versus perceptual choices

Perceptual judgments involve the transformation of a sensory stimulus into a categorical response (Gold & Shadlen, 2001), usually communicated via a motor action (e.g., a button-press, eye-movement, verbal response). This motor action serves as a simple surrogate for the categorical interpretation of the stimulus, and has been modeled as a fixed downstream output process with no impact on the decision signal and no additional response-time variability (Liston & Krauzlis, 2005; M. S. Stone, 1960). In the present task, the brightness discrimination required a short latency

(~250 ms) saccadic motor response, a semireflexive ballistic action whose metrics are naturally linked to the spatial properties of the stimulus and whose onset does not necessarily wait for the completion of any high-level perceptual or conscious decision. Thus, while there is much evidence for shared visual processing for perception and oculomotor action (L. S. Stone, Beutter, Eckstein, & Liston, 2009) and our previous report has indeed revealed linked effects of brightness on both perception and saccades (Liston & Stone, 2008), our current oculomotor study is silent on this issue although preliminary reports have revealed similar effects in perceptual brightness decisions (Liston & Stone, 2011, 2012).

In conclusion, our data show that 2AFC decision models based on the differencing of stimulus decision variables cannot account for the observed pattern of human saccadic response times in our correlation analysis. In the present study, our 2AFC stimuli were drawn independently from two uniform distributions (0–10 d' with external noise SD of 1 d' unit and mean d' difference of 3.5); in a previous study (Liston & Stone, 2008), we used two Gaussian distributions with a smaller average signal strength difference (target signal strength of 5.5, distractor strength of 4.2 d' , both with external noise SD of 1.0 d' unit and mean d' difference of 1.3) and our correlation analysis showed the same outcome, with eight out of eight subject-cases being significantly different than the difference model prediction (Liston & Stone, 2009). Our data also show that a race model with some interaction term (Boucher et al., 2007; McPeck, 2006; Usher & McClelland, 2001; Wang, 2002) between the two alternatives cannot be ruled out. We would further argue for one theoretical advantage of the race model over the difference model in biological decision-making systems. Although the difference model can theoretically be extrapolated to N -alternatives (Gold & Shadlen, 2001; Green & Swets, 1966; Laming, 1968), in practice, it would be computationally awkward to compute all the pairwise ratios and then require a complex decision rule to sort them all out. A simple race model however naturally extrapolates to N independent alternatives running in parallel towards a finish line (Edwards, 1972). Perhaps more importantly, retaining and monitoring the entire set of N decision variables (McPeck, Han, & Keller, 2003; Robinson, 1973) appears evolutionarily advantageous as it allows possible alternative motor plans to drive behavior quickly and decisively, maintains the flexibility to incorporate costs, rewards, and prior probabilities into each decision variable independently and in real time, and permits a just-in-time “change of mind” with no added cost.

Keywords: response time, decision model, choice behavior

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References

- Boucher, L., Palmeri, T. J., Logan, G. D., & Schall, J. D. (2007). Inhibitory control in mind and brain: An interactive race model of countermanding saccades. *Psychological Review*, *114*(2), 376–397.
- Brown, S. D., & Heathcote, A. (2005). A ballistic model of choice response time. *Psychological Review*, *112*(1), 117–128.
- Brown, S. D., & Heathcote, A. (2008). The simplest complete model of choice response time: Linear ballistic accumulation. *Cognitive Psychology*, *57*(3), 153–178.
- Burgess, A. E., Wagner, R. F., Jennings, R. J., & Barlow, H. B. (1981). Efficiency of human visual signal discrimination. *Science*, *214*(4516), 93–94.
- Carpenter, R. H. S. (1981). Oculomotor procrastination. In D. F. Fisher, R. A. Monty & J. W. Senders (Eds.), *Eye movements: Cognition and visual perception* (pp. 237–246). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Carpenter, R. H. S. (2002). Choice and chance: Saccadic randomness and its implications. *NIH VideoCasting*. Retrieved from <http://www.videocast.nih.gov>.
- Carpenter, R. H. S., & Williams, M. L. L. (1995). Neural computation of log likelihood in control of saccadic eye movements. *Nature*, *377*(6544), 59–62.
- Churchland, A. K., Kiani, R., Chaudhuri, R., Wang, X. J., Pouget, A., & Shadlen, M. N. (2011). Variance as a signature of neural computations during decision making. *Neuron*, *69*(4), 818–831.
- Churchland, A. K., Kiani, R., & Shadlen, M. N.

- (2008). Decision-making with multiple alternatives. *Nature Neuroscience*, 11(6), 693–702.
- Diederich, A. (1992). Probability inequalities for testing separate activation models of divided attention. *Perception & Psychophysics*, 52(6), 714–716.
- Eckstein, M. P., Beutter, B. R., & Stone, L. S. (2001). Quantifying the performance limits of human saccadic targeting during visual search. *Perception*, 30(11), 1389–1401.
- Edwards, A. W. F. (1972). *Likelihood: An account of the statistical concept of likelihood and its application to scientific inference*. Cambridge, UK: University Press.
- Efron, B., & Tibshirani, R. (1993). *An introduction to the bootstrap*. New York: Chapman & Hall.
- Gold, J. I., & Shadlen, M. N. (2001). Neural computations that underlie decisions about sensory stimuli. *Trends in Cognitive Sciences*, 5(1), 10–16.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Grice, G. R. (1968). Stimulus intensity and response evocation. *Psychological Review*, 75(5), 359–373.
- Hallett, P. E. (1969). Quantum efficiency and false positive rate. *Journal of Physiology*, 202(2), 421–436.
- LaBerge, D. (1962). A recruitment theory of simple behavior. *Psychometrika*, 27(4), 375–396.
- Laming, D. R. J. (1968). *Information theory of choice-reaction times*. London: Academic Press.
- Leigh, R. J., & Zee, D. S. (2006). *The neurology of eye movements*. Philadelphia: F.A. Davis.
- Link, S. W., & Heath, R. A. (1975). A sequential theory of psychological discrimination. *Psychometrika*, 40, 77–105.
- Liston, D. B., & Krauzlis, R. J. (2005). Shared decision signal explains performance and timing of pursuit and saccadic eye movements. *Journal of Vision*, 5(9):3, 678–689, <http://www.journalofvision.org/content/5/9/3>, doi:10.1167/5.9.3. [PubMed] [Article]
- Liston, D. B., & Stone, L. S. (2008). Effects of prior information and reward on oculomotor and perceptual choices. *Journal of Neuroscience*, 28(51), 13866–13875.
- Liston, D. B., & Stone, L. S. (2009). Evidence for a race model. *Society for Neuroscience Abstracts*, 35(405.4).
- Liston, D. B., & Stone, L. S. (2011). Perceptual brightness decisions do not use a difference model. *Society for Neuroscience Abstracts*, 37(17.04).
- Liston, D. B., & Stone, L. S. (2012). Quantifying the relationship between perceptual and motor variability. *Society for Neuroscience Abstracts*, 38(370.15).
- Luce, R. D. (1986). *Response times: Their role in inferring elementary mental organization*. New York: Oxford University Press.
- Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. New York: Cambridge University Press.
- McPeck, R. M. (2006). Incomplete suppression of distractor-related activity in the frontal eye field results in curved saccades. *Journal of Neurophysiology*, 96(5), 2699–2711.
- McPeck, R. M., Han, J. H., & Keller, E. L. (2003). Competition between saccade goals in the superior colliculus produces saccade curvature. *Journal of Neurophysiology*, 89(5), 2577–2590.
- Miller, J. (1982). Divided attention: Evidence for coactivation with redundant signals. *Cognitive Psychology*, 14(2), 247–279.
- Niwa, M., & Ditterich, J. (2008). Perceptual decisions between multiple directions of visual motion. *Journal of Neuroscience*, 28(17), 4435–4445.
- Palmer, J., Huk, A. C., & Shadlen, M. N. (2005). The effect of stimulus strength on the speed and accuracy of a perceptual decision. *Journal of Vision*, 5(5):1, 376–404, <http://www.journalofvision.org/content/5/5/1>, doi:10.1167/5.5.1. [PubMed] [Article]
- Piéron, H. (1927). L'influence de l'intensité sur le temps de réaction à la cessation du stimulus lumineux [Translation: The influence of intensity on reaction time to the cessation of a light stimulus]. *Compte Rendu de la Société de Biologie*, 97, 1147–1149.
- Raab, D. H. (1962). Statistical facilitation of simple reaction times. *Transactions of the New York Academy of Sciences*, 24, 574–590.
- Ratcliff, R., Hasegawa, Y. T., Hasegawa, R. P., Smith, P. L., & Segraves, M. A. (2007). Dual diffusion model for single-cell recording data from the superior colliculus in a brightness-discrimination task. *Journal of Neurophysiology*, 97(2), 1756–1774.
- Ratcliff, R., & Rouder, J. N. (1998). Modeling response times for two-choice decisions. *Psychological Science*, 9(5), 347–356.
- Richards, V. M., & Zhu, S. (1994). Relative estimates of combination weights, decision criteria, and internal noise based on correlation coefficients. *Journal of the Acoustical Society of America*, 95(1), 423–434.
- Robinson, D. A. (1965). The mechanics of human smooth pursuit eye movement. *Journal of Physiology*, 180(3), 569–591.

- Robinson, D. A. (1973). Models of the saccadic eye movement control system. *Kybernetik*, *14*, 71–83.
- Smith, P. L., & Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends in Neurosciences*, *27*(3), 161–168.
- Stone, L. S., Beutter, B. B., Eckstein, M. P., & Liston, D. B. (2009). Perception and eye movements. In L. R. Squire (Ed.), *Encyclopedia of Neuroscience* (Vol. 7). (pp. 503–511). Oxford, England: Academic Press.
- Stone, M. S. (1960). Models for choice-reaction time. *Psychometrika*, *25*(3), 251–260.
- Todd, J. W. (1912). *Reaction to multiple stimuli*. New York: The Science Press.
- Usher, M., & McClelland, J. L. (2001). The time course of perceptual choice: The leaky, competing accumulator model. *Psychological Review*, *108*(3), 550–592.
- Wang, X. J. (2002). Probabilistic decision making by slow reverberation in cortical circuits. *Neuron*, *36*(5), 955–968.
- Wickelgren, W. A. (1968). Unidimensional strength theory and component analysis of noise in absolute and comparative judgments. *Journal of Mathematical Psychology*, *5*, 102–122.