SUPPLEMENTARY INFORMATION

Perceptual decision making in less than 30 milliseconds

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Key features of the model

The two dynamical variables in the race-to-threshold model should be interpreted as competing motor plans that may be informed by sensory evidence. This is consistent with neurophysiological studies indicating (1) that saccades are triggered after oculomotor cells reach a threshold level of activity (Hanes and Schall, 1996; Roitman and Shadlen, 2002; Lo and Wang, 2008), and (2) that even when a saccadic choice results from the slow accumulation of sensory evidence over time, the effect of this sensory information is observed on the rate at which the oculomotor activity rises (Gold and Shadlen, 2000; Kiani et al., 2008). Indeed, the most detailed network models implementing such accumulation processes (Wang, 2002; Wong and Wang, 2006; Furman and Wang, 2008; Beck et al., 2008) replicate data from area LIP, an oculomotor area.

We have also explored drift-diffusion models (e.g., Palmer et al., 1995; Ratcliff and Rouder, 2000; Ratcliff et al., 2007) to describe our behavioral data (Shankar et al., 2007), but found that the present race model is much more computationally efficient and thus faster to simulate, and that it is similar to the more familiar diffusion models, both in spirit and interpretation.

The current race model does not need to be simulated by small time steps, as a diffusion model or a spiking network would. The equations are such that, given the initial accumulation rates drawn in a trial, \( r_0^R \) and \( r_0^L \), and the rest of the parameters, which are constant across trials, the time to threshold can be calculated from a quadratic formula. This turns into a speed-up factor of approximately 20 over simulations of the exact same model but with time running in steps of \( \Delta t = 1 \) ms.

Generally speaking, the essence of the model is that each race (or trial) has two parts, one in which there is no cue information available, and thus the ‘winning’ motor plan is randomly determined, followed by another in which the sensory cue boosts one of the motor plans and suppresses the other. Any model, whether it involves a single diffusing variable or thousands of spiking neurons, would need to have this structure, because it is imposed by the structure of the compelled-saccade (CS) task. Within this structure, we chose as a basis for the model a simple dynamical description known to capture saccadic RT distributions reasonably well (Carpenter and Williams, 1995; Reddi and Carpenter, 2000; Nakahara et al., 2006; Brown and Heathcote, 2008).

Plausibility of \( T_{ND} \)

In our model the parameter \( T_{ND} \), which represents afferent + efferent delay, is important for obtaining good fits to the data. But note that \( T_{ND} \) does not fundamentally alter the analyses of the experimental results, because its effect is simply to shift the x-axis of the tachometric curve by a constant amount. In our study, as in many others, the non-decision time, or residual time, is very close to the minimum RT observed in the corresponding task (e.g., Palmer et al., 2005; Ratcliff and...
However, it is still interesting to ask whether the $T_{ND}$ values in our model are realistic in terms of known oculomotor neurophysiology.

The race model represents the development of a motor plan in an oculomotor structure, so it corresponds approximately to neuronal activity at the level of the FEFs or area LIP. Therefore, the relevant questions are, how long does it take for a highly-discriminable sensory signal meant to guide a saccade to have an impact on these structures? and, how long after this activity reaches threshold is a saccade observed? A high-contrast potential target appearing in a neuron’s receptive field produces a sharp increase in activity that starts about 60–70 ms after target onset, both in FEF and LIP (Thompson et al., 1996; Churchland et al., 2008). At the other end, in our own population of 30 FEF neurons we found that when a saccade is made toward the movement field, the peak of activity occurs 30–45 ms before saccade onset (data not shown), which is in agreement with previous reports (Elsley et al., 2007; Churchland et al., 2008). The sum of these two delays gives a total of 90–115 ms, which is indeed consistent with the $T_{ND}$ values of 103 and 112 ms found for monkeys S and G in the standard CS task.

**Match between experimental and predicted RT distributions**

Having fit the model parameters for each monkey, simulated RT distributions were generated for each gap value, as shown in Figure 3e. Gap-specific differences between the RT distributions in error and correct trials were not used to fit the model; only the proportion of errors at each gap was used. Therefore, any features in the shapes of the RT distribution functions produced by the model served as predictions. To compare the predicted and experimental distributions we did the following.

First, the RTs for each gap were converted to z scores by subtracting the mean and dividing by the s.d. of all trials for that gap. Experimental and simulated data were treated identically. This transformation left the shapes of the RT distributions intact but removed any mean dependencies on the gap. Then we computed the mean ($\mu_z$), the s.d. ($\sigma_z$), and the skewness coefficient ($\omega_z$) of the z scores separately for correct and error trials (at each gap), and compared the monkeys’ results with the simulated ones. Because the data were de-trended, any systematic differences between correct and error trials in the simulated z scores constitute true predictions that are independent of the fitted data.

The results of this analysis are shown in Supplementary Figure 1. The high correlation values between simulations and experiments obtained with the three statistics indicate that, overall, the model approximates the shapes of the monkey RT distributions quite accurately, and accounts for the observed differences between correct and error trials. To appreciate these results it is useful to realize that, in this analysis, a model that generated identical RT distributions for correct and error trials in each gap would only produce small and nonsignificant correlations.

**What happens if the monkeys wait?**

A potential concern with the compelled-response design is that, rather than responding immediately after the go signal, the monkeys could try to wait for the cue before initiating their responses. Intuitively, such behavior might seem problematic because it could bias the RT values of the subjects in a non-uniform way. There are, however, three points to consider about this issue: (1) the
**Supplementary Figure 1:** Comparison between monkey data and model predictions for correct and error trials. RTs at each gap were first converted to z scores and then separated between correct and error trials.

(a) Mean z score ($\mu_z$) as a function of gap for monkey S correct trials (blue bars), model correct trials (black bars), monkey S error trials (red bars), and model error trials (gray bars). (b) Monkey $\mu_z$ versus model $\mu_z$ at each gap, for correct (black points) and error trials (red points). Same data as in a. Dotted line indicates equality. Spearman’s correlation coefficient $\rho$ is indicated at the bottom. (c) Standard deviation of the z scores ($\sigma_z$) as a function of gap. Same conventions as in a. (d) Monkey $\sigma_z$ versus model $\sigma_z$ at each gap, for correct (black points) and error trials (red points). (e) Skewness coefficient of the z scores ($\omega_z$) as a function of gap. Skewness coefficient is equal to $3(\mu_z - \text{median}(z))/\sigma_z$. (f) Monkey $\omega_z$ versus model $\omega_z$ at each gap, for correct (black points) and error trials (red points). (g–l) As in a–f but for monkey G. All correlation coefficients were significantly different from zero ($p < 0.00001$, permutation test).

Conditions of the task make it difficult for the subjects to wait beyond the go signal, (2) there is no evidence in the data indicating that the subjects wait for the cue, and (3) unless such waiting were extremely exaggerated, it would have no impact whatsoever on the measurement of sensory processing speed.

First, to prevent the monkeys from waiting or predicting when the cue is revealed, gap intervals were always delivered pseudo-randomly, and responses that took more than 600 ms were not rewarded. It is unclear whether this time deadline was necessary or not, because trials with RT longer than 600 ms were always rare ($< 1\%$). Still, these measures do not completely rule out the possibility that, within the allotted time, the monkeys could gamble about how long to wait for the cue and still execute the saccade in time.

If the monkeys waited, however, this would become apparent in two ways. First, their RTs would likely change in proportion to the gap duration, because they would need to wait more at
long gaps than at short gaps to obtain an equivalent advantage in cue exposure. Second, and more importantly, the percentage of correct responses would tend to stay considerably above 50%, even at the longest gaps. Figures 3a,b and 5b,c show no evidence for either of these effects. Our subjects' performance was always near 50% at the longest gaps, and although their RTs did increase slightly as functions of gap, this ∼30 ms change was fully accounted for by the model, which did not include any such waiting. Thus, the observed trend was entirely consistent with the subjects responding to the go signal as instructed, without any knowledge of the waiting times.

Finally, upon closer examination, one sees that the waiting strategy is a problem only if the monkeys are able to completely hold back their responses until the cue is revealed, which would produce near-perfect performance and a difference in RT of 200 ms between the longest and shortest gaps. If the waiting is such that overall performance remains significantly below 100% correct, then it is harmless. How is this possible?

This is illustrated in Supplementary Figure 2. The left side of the figure replots simulation results shown in Figure 3, which replicate the behavior of monkey S assuming that the oculomotor choice process starts at the go signal. In comparison, the right side of the figure shows the results of another simulation, with identical parameters, in which the model was programmed to wait beyond the go signal. The implemented waiting strategy was such that, in effect, it reduced each gap longer than 50 ms by about 30%. This had the expected consequences: the psychometric curve moved closer to the 100% border (Sup. Fig. 2a), and the chronometric curve developed an

Supplementary Figure 2: Invariance of the tachometric curve to waiting strategies. Results are shown for two simulations of the CS task, a standard one in which the oculomotor choice process was always initiated at the onset of the go signal (left side; same model parameters as in Fig. 3, monkey S), and another one in which the process started an additional amount of time $\Delta T_W$ after the go signal, but was otherwise identical (right side). Waiting time as a function of gap was $\Delta T_W = 0.48 (\text{gap} - 50)$, in ms. (a) Psychometric curves. (b) Chronometric curves. (c) ePT distributions for correct (black) and incorrect (orange) trials. (d) Tachometric curves. The two curves were computed exactly in the same way, without any knowledge of the waiting times.
increasing trend in which the mean RTs between longest and shortest gaps differed markedly, by about 130 ms in this example (Sup. Fig. 2b). Crucially, however, note that the resulting tachometric curves were identical (Sup. Fig. 2d). The only difference between them was that, without waiting, more points were sampled from the left side of the curve, at negative ePTs, whereas with the waiting strategy more points were sampled from the right side, at positive ePTs (see Sup. Fig. 2c). Importantly, both curves were calculated in the same way, using Eqn. 1 and assuming that there was no waiting involved.

Other versions of this simulated experiment in which somewhat different waiting strategies were implemented produced very similar results. For example, drawing the waiting time randomly in each trial from a uniform distribution between 0 and gap ms again had no effect on the tachometric curve (not shown).

These results may seem surprising, but they have a straightforward algebraic explanation. Suppose that, in a particular trial, the monkey waits an amount $\Delta T_W$ beyond the go signal before initiating the choice process. His measured RT in this trial is thus artificially lengthened by $\Delta T_W$ ms with respect to what it would have been if he had not waited, which we will call $\text{RT}_{\text{true}}$. On the other hand, the gap value used by the experimenter to compute rPT in this trial is just the nominal value presented in the trial, but because the monkey waited, the effective gap value was actually shorter by an amount $\Delta T_W$. That is, $\text{gap}_{\text{true}} = \text{gap} - \Delta T_W$. Therefore, the measured rPT is

$$rPT = \text{RT} - \text{gap} = \text{RT}_{\text{true}} + \Delta T_W - (\text{gap}_{\text{true}} + \Delta T_W) = \text{RT}_{\text{true}} - \text{gap}_{\text{true}}.$$  

This last expression gives the rPT that the experimenter would have measured if he had set the gap equal to $\text{gap}_{\text{true}}$ in this trial and the monkey had not waited at all. Thus, in the end, the waiting times always cancel out, and over the course of many trials their effect is simply to shorten the effective range of gaps used to sample the monkey’s behavior. So, if the experimenter uses gaps of 50–250 ms and the monkey on average waits, say, 50 ms, the resulting tachometric curve is identical to one obtained without any waiting but sampled with gaps of 0–200 ms. This becomes a problem only if the effective gap range is shortened to the point where very few errors are made; otherwise, the resulting tachometric curve is the same.

In summary, there is no evidence suggesting that the monkeys wait for the cue, but even if they did so to some extent, this would not affect the inferred processing-time values themselves, nor their relationship to perceptual performance, only the way in which they are sampled. In this sense, the measurement of processing speed derived from the tachometric curve is maximally robust to variations in strategy. This result emphasizes that, individually, neither the observed variable (the RT) nor the explicitly controlled experimental parameter (the gap) is highly correlated with the signal that is perceptually relevant, but their difference is.

**Additional results in the motor-bias experiment**

Experimental conditions were identical for monkeys S and G during the motor-bias experiment. Supplementary Figure 3 shows the data obtained with monkey G, in the same format as Figure 5 in the main text. Of course, for the simulations in this supplementary figure, model parameters were adjusted so that the results matched the behavior of monkey G.
**Supplementary Figure 3:** Psychophysical performance of monkey G in the motor-bias experiment. Trials are sorted according to choices, either toward the high-reward side (black) or the low-reward side (orange). (a) Fractions of saccades made to the high- and low-reward sides as functions of gap (226 ≤ n ≤ 280 trials per gap). (b) Percentages of correct choices as functions of gap. (c) Mean RTs ± 1 s.d. as functions of gap. (d) Distributions of ePT values for correct (black bars) and incorrect responses (gray lines) toward the high-reward side. (e) Distributions of ePT values for correct (orange bars) and incorrect responses (gray lines) toward the low-reward side. (f) Percentages of correct responses as functions of ePT for high- (black lines) and low-reward (orange lines) trials. (g) For each ePT, the curves show the fraction of all saccades (orange lines) or of all correct saccades (gray lines) made to the low-reward side. * indicates p < 0.0001, binomial test. ePT bin size is 20 ms.

Overall, psychophysical results were similar with both monkeys, but there were a couple of differences. First, at the shortest gaps, monkey S chose the high- and low-reward sides with almost equal frequency (Fig. 5a), whereas monkey G did not (Sup. Fig. 3a). And second, whereas monkey S made no errors for ePT > 65 ms (Fig. 5f), monkey G did, occasionally, make mistakes at relatively long ePTs; furthermore, he made significantly more mistakes in this range when the high-reward side was chosen than when the low-reward side was chosen (Sup. Fig. 3f). We speculate that these mistakes may reflect a momentary lapse in attention or motivation, because they occurred at a point at which perceptual performance did not increase any further with cue exposure time.

Besides this significant difference in maximum performance level seen in monkey G, there were only minor differences between the tachometric curves for high- and low-reward choices in either monkey. The tachometric curves plotted as functions of rPT were slightly shifted with respect to each other. The center points of the curves were $T^{\text{low }}_{\text{cfr}} = 108$ and $T^{\text{high }}_{\text{cfr}} = 123$ ms for monkey S, and $T^{\text{low }}_{\text{cfr}} = 144$ and $T^{\text{high }}_{\text{cfr}} = 164$ ms for monkey G. Here, $T_{\text{cfr}}$ is the rPT value at which the tachometric curve reaches the midpoint between 0.5 and its maximum (the midpoint is usually 75%, but not if the maximum performance is below 100%). According to these numbers, then, the curves for monkeys S and G shift to the right by 15 and 20 ms, respectively, when the high-reward
side rather than the low-reward one is chosen. Both shifts were significant \( p = 0.01 \) for monkey S, \( p = 0.007 \) for monkey G, permutation tests), and were consistent with the slightly different \( T_{ND} \) values found by the model for low- and high-reward choices: in both animals, \( T_{ND} \) was larger by 14 ms in the latter case. These differences are consistent with the subjects reacting slightly more slowly or slightly faster to the go signal depending on the chosen side, and thus on the potential reward — which is not surprising.

The crucial quantity, however, is the steepness of the tachometric curve, because it indicates how fast the perceptual discrimination proceeds. We compared the steepness of the curves for low- and high-reward choices and found that they were statistically identical in both monkeys \( (p = 0.18 \) for monkey S, \( p = 0.53 \) for monkey G, permutation tests). Furthermore, for each monkey, the experimental data in both reward conditions were replicated accurately by the model using a single value of \( \tau \), the parameter that controls most strongly the slope of the tachometric curve. We interpret these findings to mean that the perceptual processing speeds of the two monkeys were not affected by the reward contingencies of the task.

**Lack of transient cue-related activity in FEF movement cells**

The 30 FEF neurons used in this study were selected from a population of 130 cells recorded from the two monkeys. As mentioned in the main text, 23/30 units were from recording sites in which saccade-like eye movements were evoked with low-current \(< 50 \mu A\) microstimulation. Also, all movement fields (MFs) were characterized using a single-target delayed-saccade task, which revealed strong presaccadic activity and weak or no responses linked to the appearance of the target — as is typical of so-called movement cells in FEF (Bruce and Goldberg, 1985; Hanes and Schall, 1996). In addition to these tests and to the standard CS task trials, 21/30 cells were further studied on an easy version of the task in which the cue was revealed at varying times before the go signal (Sup. Fig. 4a). We include neuronal responses in this easy-choice task to further confirm that these cells did not respond directly to the color changes of the spots placed in their MFs. These data are relevant because the color change that occurs when the cue is revealed is equally informative in the CS task and the easy-choice task; the only difference is that, in the former, the saccadic choice process is already ongoing, because the go signal is given earlier.

Supplementary Figure 4b shows the mean activity of the 21 movement-related FEF neurons tested with the easy-choice task. Most tellingly, when the target was outside of the cell’s MF (green trace), the firing rate was virtually the same before and after the cue. The change in color did not evoke a substantial stimulus-locked response.

When the target was in the cell’s MF (red trace), activity started ramping up about 110 ms after the cue. To better characterize this build-up, we divided the trials into two groups, one with short delays \( (10-50 \text{ ms}) \) and another with long delays \( (200-250 \text{ ms}) \). As expected, there was no difference across groups when the target was outside the MF (Sup. Fig. 4d). And when the saccade was into the cell’s MF, the activity developed faster in short- than in long-delay trials (Sup. Fig 4c), which is not surprising either. What is interesting in this case is that the initial rise in activity was the same regardless of when the go instruction occurred: at the point marked by the arrow (Sup. Fig 4c), the go signal had had enough time to reach these cells in short-delay trials, but for long-delay trials the go signal had not been given yet. Thus, we interpret the early rise in firing rate around that point as anticipating the upcoming saccade.
Supplementary Figure 4: Insensitivity of the movement neurons to the sensory cue. (a) Schematic of the easy-choice task. (b) Activity of 21/30 movement-related FEF neurons during easy-choice trials as a function of time. All spikes trains were synchronized on cue presentation (triangle and vertical line). Firing rates were obtained by convolving the spikes with a Gaussian function with $\sigma = 6$ ms, and were normalized before averaging across cells. Red and green traces are for trials into ($n = 988$) and away from ($n = 911$) the MF, respectively. Light colors indicate ± 1 s.e.m. (c) Neuronal responses to saccades into the MF. Traces for short-delay trials (10–50 ms, black curve) and long-delay trials (200–250 ms, blue curve) are shown separately. Arrow marks a point in time at which the go signal is already in effect for all short-delay trials but has not been delivered yet for any long-delay trials. (d) As in c, but for saccades away from the neuron’s MF.

In summary, in the selected FEF neurons, the color changes from yellow to green and from yellow to red do not evoke the brisk, transient fluctuations in activity that are typically associated with responses to sensory stimuli. Rather, in the easy-choice task this information allows the system to quickly start planning a subsequent response.

Estimating the transition point of a curve

The transition point at which a curve starts rising or falling was estimated by fitting the data to a threshold-linear function, as explained in the Methods section. The results are illustrated in Supplementary Figure 5, which includes the same data in Figures 7c,d–f together with the best-fitting threshold-linear functions.
Supplementary Figure 5: Estimation of a curve’s transition point based on linear-threshold fitting. Each graph plots a curve (black trace) and the best-fitting approximation using a linear-threshold function (magenta trace). Each fit is drawn for the range of data values included in the fitting procedure. Arrows mark the transition points at which the linear-threshold functions become non-flat. Horizontal lines on the arrows indicate ± 1 s.e. in the transition points (by jackknife). (a) Psychometric curve, as in Figure 7d. $x_{\text{trans}} = 131 \pm 2.7$ ms; significance of slope, $p = 0$, from permutation test. (b) Mean convexity in trials away from the MF, from the race model, as in Figure 7c. $x_{\text{trans}} = 131$ ms. (c) Mean convexity in trials into the MF, from the FEF data, as in Figure 7e. $x_{\text{trans}} = 124 \pm 27$ ms; significance of slope, $p = 0.002$. (d) Mean convexity in trials away from the MF, from the FEF data, as in Figure 7f. $x_{\text{trans}} = 138 \pm 15$ ms; significance of slope, $p = 0.0004$.

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