Evidence against perfect integration of sensory information during perceptual decision-making

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Abstract

Perceptual decision-making is often modeled as perfect integration of sequential sensory samples until the accumulated total reaches a fixed decision bound. In that view, the build-up of neural activity during perceptual decision-making is attributed to temporal integration. However, an alternative explanation is that sensory estimates are computed quickly using a low-pass filter and combined with a growing signal reflecting the urgency to respond, and it is the latter that is primarily responsible for neural activity build-up. These models are difficult to distinguish empirically because they make similar predictions for tasks in which sensory information is constant within a trial, as in most previous studies. Here, we presented subjects with a variant of the classic constant-coherence motion discrimination (CMD) task in which we inserted brief motion pulses. We examined the effect of these pulses on reaction times (RTs) in two conditions: 1) when the CMD trials were blocked and subjects responded quickly; and 2) when the same CMD trials were interleaved among trials of a variable motion coherence task that motivated slower decisions. In the blocked condition, early pulses had a strong effect on RTs but late pulses did not, consistent with both models. However, when subjects slowed their decision policy in the interleaved condition, later pulses now became effective while early pulses lost their efficacy. This last result contradicts models based on perfect integration of sensory evidence and implies that motion signals are processed with a strong leak, equivalent to a low-pass filter with a short time constant.

Keywords: Decision-making, drift-diffusion model, urgency
Introduction

Many models of decision-making posit that the brain arrives at a decision by accumulating evidence in favor of competing choices until the accumulated total for one of the choices reaches a fixed decision bound (Laming 1968; Ratcliff 1978; Bogacz et al. 2006; Gold & Shadlen 2007). In this view, the rate of accumulation corresponds to the quality of sensory information while the bound controls tradeoffs between decision speed and accuracy (Reddi and Carpenter 2000). The most common of these models, the drift-diffusion model (DDM; Ratcliff, 1978), assumes perfect integration of sensory samples to a fixed bound. This simple and elegant model replicates reaction time (RT) distributions and error rates across a variety of tasks (Ratcliff 2002; Ratcliff et al. 2004), and has been used to explain the build-up of neural activity to a threshold in many brain regions (Kim & Shadlen 1999; Gold & Shadlen 2000, 2003; Roitman & Shadlen 2002; Palmer et al. 2005; Ratcliff et al. 2007).

While such models capture the intuition that one should accumulate evidence until the accumulated total satisfies some criterion of accuracy, an important question concerns what constitutes evidence in a given situation. In particular, during the kinds of perceptual discrimination tasks usually studied, sequential samples of a static stimulus are increasingly redundant; taking a second look may be useful, but taking a tenth or eleventh is less so. This motivates one to only integrate information that is novel. Furthermore, in many natural scenarios the world can suddenly change, and the decision-making system must be quick to respond to such changes. For these reasons, several alternatives to the DDM have been proposed. In particular, it has been suggested that integration is leaky, with old information gradually being discounted as new information arrives (Busemeyer & Townsend, 1993; Roe, Busemeyer & Townsend, 2001; Usher & McClelland, 2001). This is consistent with the observation that decisions are dominated by information from a limited time window (Cook & Maunsell 2002; Luna et al. 2005; Uchida et al. 2006; Yang et al. 2008; Chittka et al. 2009), emphasizing novel information. It has also been suggested that the decision bound is not fixed but decreases over time, possibly due to a growing “urgency” signal that pushes neural activity toward commitment as time passes (Ditterich 2006; Churchland et al. 2008; Cisek et al. 2009; Hanks et al. 2014). This proposal is motivated by analyses showing that for tasks in which subjects are allowed to respond at any time, a decreasing decision bound yields higher reward rates than any setting of a fixed bound (Drugowitsch et al. 2012; Thura et al. 2012).

Importantly, if an urgency signal is present, then most existing data can be explained even if the integration is highly leaky (Ditterich 2006; Cisek et al. 2009), equivalent to a low-pass filter with a relatively short time constant (e.g. 200ms). This is called the “urgency-gating model” (UGM). Crucially, in nearly all previous experiments the sensory information provided to subjects was constant within each trial, and under such conditions a perfect integrator with fixed bound behaves very similarly to a leaky integrator with an urgency signal (Cisek et al. 2009; Thura et al. 2012; Hawkins, Wagenmakers, Ratcliff & Brown 2015). Thus, data from experiments featuring constant evidence tasks can support either model, and even sophisticated comparisons of model fits (Hawkins, Forstmann, Wagenmakers, Ratcliff & Brown 2015) do not produce consistent answers across tasks, subjects, or modeling assumptions. Part of the reason is that these models are relative extremes on a wide continuum of parameters, whereby the DDM assumes zero leak and a fixed accuracy bound, while the UGM proposes a strong leak and a growing urgency signal that implements a decreasing accuracy bound. Deciding on the appropriate settings of these parameters, even for a specific subject, is difficult using data that can be fit with a wide range of parameter combinations. The purpose of the present experiment is to place bounds on the
values that these parameters may take, and therefore to constrain the set of possible models that may
be used to account for behavior during perceptual decision-making tasks.

We recently conducted two behavioral studies (Cisek et al. 2009; Thura et al. 2012) and one neural
recording study (Thura & Cisek 2014) featuring tasks in which sensory information changed over the
course of each trial. In such conditions, different settings of leak and urgency parameters produce
clearly divergent predictions that are easy to distinguish empirically. Indeed, the results of those studies
were incompatible with perfect integration, and instead supported a UGM with a filter time constant of
200ms or less. However, it could be argued that those results were task-dependent and do not
generalize to the kinds of constant-evidence perceptual discrimination tasks usually studied.
Consequently, here we aim to distinguish among perfect- versus leaky integration by observing the
effect of brief motion pulses on subjects’ reaction times during the classic random-dot motion
discrimination task. Previous studies using motion pulses have shown that they can influence RTs (Huk &
Shadlen, 2005) – but the critical test examined here is how the effects of these pulses change as subjects
modify their decision policy.

The logic of our experimental design is illustrated in Figure 1. As in a typical random-dot motion
discrimination task, subjects are presented with a noisy coherent motion stimulus that remains constant
within a given trial and are asked to respond as soon as they detect the direction of motion. Unknown to
the subjects, some trials contain a brief 100ms increase of motion coherence at various times following
motion onset. If decisions are made using a perfect integrator such as the DDM (Fig. 1a,b), then motion
pulses presented prior to the time of decision will briefly increase the rate of integration and result in
decisions that are made earlier, on average, than those made in no-pulse trials. Pulses that appear later
in the trial will have no effect if the decision bound is low (Fig. 1a, blue line), because they occur too late
to affect the decision process. If the decision bound is high (Fig. 1b), then both early and late pulses (red
and blue lines) will affect response times. In other words, as subjects slow down their decision policy,
the time window during which pulses can have an effect on reaction times is predicted to expand.
Critically, this model predicts that early pulses will always be at least as effective as late pulses in
reducing reaction times.

If the perfect integrator is replaced with a low-pass filter (a highly leaky integrator) and combined with
an urgency signal, then early pulses will still have a stronger effect than late pulses under fast decision
policies, i.e. when the urgency signal grows quickly (see Fig. 1c). However, the reverse will be true under
slower decision policies, i.e. when urgency grows more slowly (Fig. 1d), because the information
provided by early pulses will have leaked away by the time the decision bound is crossed. Thus as
subjects slow down, the time window in which pulses are effective is predicted to shift, and later pulses
will become effective while early pulses will lose efficacy.

Our approach for testing these predictions is to present subjects with an identical set of pulse trials in
two different contexts: one in which they are motivated to respond quickly, and another in which they
are motivated to slow down. Some of this data has previously appeared in abstract form (Carland et al.
2013).

Methods

Subjects and apparatus
Forty-four right-handed participants (24 female, ages 19-37) with normal- or corrected-to-normal vision provided written consent and were naïve to the purpose of our experiment. Participants were seated in front of a large digitizing tablet placed at arm-level for recording movements of a handheld cordless stylus embedded within a vertical plastic handle (125Hz sample rate with 0.013 cm accuracy). Stimuli, targets and cursor position feedback were projected by an LCD monitor onto a half-silvered mirror positioned 16cm above and parallel to the digitizer surface, and thus appeared to float on the plane of the digitizing tablet. The subjects’ task was to report the direction of motion of the stimulus by completing reaching movements toward one of two targets whose locations corresponded to the potential motion directions. The task and data collection was programmed in LabView (National Instruments, Austin TX), stored in a database (Microsoft SQL Server 2005, Redmond WA), and analyzed using custom MATLAB scripts (MathWorks, Natick MA). The experimental protocol was approved by the university ethics committee. The data presented in this report are available upon request from the corresponding author.

Behavioral task

Each trial began when subjects moved the cursor into a small circular target (1cm in diameter) near the center of a white display. After 500ms, two circular targets (3cm in diameter) appeared 6cm to each side of the stimulus display area, separated by 180°. The targets were projected to appear oriented along the natural direction of single-joint elbow movements, thereby minimizing any potential difference in biomechanical cost between the two peripheral targets (Figure 2a). 300ms after the start target was entered, 200 black dots appeared in a borderless circular area (3cm diameter) in the center of the display between the two targets. Each of the dots was re-drawn in a new location 2 pixels away from its previous location on each frame (60Hz). While most dot movements were random, a subset of the dots was re-drawn along a vector corresponding to the location of one of the two targets. While the individual dots assigned to the coherently-moving subset changed from frame to frame, the resulting percept was of a persistent motion signal, whose direction subjects could reliably and accurately report with a degree of difficulty inversely related to the percentage of coherently-moving dots (Newsome et al. 1989; Kim & Shadlen, 1999).

Subjects were given up to 3000ms to report the direction of the coherent motion by moving from the initial start target to one of the two choice targets, and were free to respond at any time. Movements had to be completed in less than 1000ms, and had to land within the chosen target circle. The motion stimulus continued until the cursor crossed a target circle’s border. The cursor had to remain within the chosen target for 500ms, at which point the outline of the target turned green or red to indicate a correct or incorrect choice, respectively. After a brief inter-trial interval of 500ms, all on-screen objects disappeared except for the starting target, and a new trial began.

In the analyses reported here, response times (RTs) for each trial were obtained post hoc by determining the precise moment at which the cursor’s velocity began to increase from a point of rest within the start target. However, an ad hoc estimate of RT based on the time at which the cursor exited the boundary of the start target was used to obtain session-specific estimates of subjects’ mean reaction times; these were then used to provide on-line feedback during the experimental sessions, as described below.

Before each session began, we presented the subject with 40 very easy motion-discrimination trials in which the motion coherence was 50%, and instructed them to respond as rapidly as possible. The average RT from these trials was then stored as a session-specific estimate of “non-decision time”
comprising both sensory and motor delays (mean=475ms, std=103ms). This measurement was used to classify correct and incorrect responses for trials in which the motion signal could change directions over the course of a single decision (see below). Importantly, these initial 40 trials were the only ones for which subjects were ever provided with explicit instructions about how quickly to respond: for the main experimental task, subjects were informed of the 3-second time limit but were told that they could make their decision whenever they liked, though most of our subjects very rarely took more than 1800ms to make their decision.

For any experimental session, subjects completed one of two session types: “blocked” or “interleaved”. “Blocked” sessions consisted entirely of trials with a single, common baseline motion coherence value of 3%; we refer to these as “constant-motion discrimination” (CMD) trials. In 40% of such trials there were no additional changes to the stimulus, and we refer to these as “no-pulse” trials. The remaining 60% of the CMD trials contained brief motion “pulses” during which the coherence of the motion stimulus was doubled (to 6%) for 100ms. Such brief coherence manipulations have previously been shown to affect response timing in motion discrimination tasks (Huk & Shadlen, 2005; Wong et al. 2007), even though they are not consciously detectable by our subjects (confirmed by post-experiment interview and consistent with similar studies; see Kiani et al. 2008). Thus, as far as the subjects were aware, the motion coherence for all CMD trials appeared to remain constant throughout each trial, regardless of whether a pulse was or was not actually shown. These pulses could occur 100, 200, or 400ms following stimulus onset, and we refer to such trials collectively as “pulse” trials. Each of these pulse timing conditions thus comprised 20% (60% total) of the total number of trials in the “blocked” condition.

“Interleaved” sessions consisted of a mix of trial types. Twenty percent of the trials in these sessions were CMD trials – including both pulse- and no-pulse trials – identical in every respect to those presented in the blocked sessions. Each of the 4 CMD trial types comprised 5% of the total number of trials encountered during these sessions. These CMD trials were randomly interleaved among “variable-motion discrimination” (VMD) trials, which comprised the remaining 80% of the interleaved session. These trials began with a net motion coherence of +/-3%, and this motion signal was adjusted either up or down in 3% steps every 200ms (sometimes reversing the direction of motion; see Figure 2b). Of the VMD trials, 60% were random, such that each motion coherence change was given an independent and equal probability of favoring either of the two possible targets. The remaining 40% of trials were divided among a number of pre-generated trial types similar to those featured in previous studies (Cisek et al. 2009; Thura et al. 2012) – these included “easy” and “ambiguous” trial types, as well as a variety of “bias” trials. These trials were included to test whether effects previously reported (Thura et al. 2012) were still observed in our subjects. In brief, “easy” trials were those in which the motion signal reached >=9% within the first 800ms and remained at or above 9% for the remainder of the trial; “ambiguous” trials were those in which the absolute motion signal remained within 6% of zero throughout the trial. “Bias” trials included brief biases (800ms or 1000ms) either for or against the final motion direction and then resembled easy trials (see Thura et al. 2012 for details). Since the previously reported effects were indeed confirmed, we do not analyze these further and refer the reader to Thura et al. (2012).

Each session type consisted of a single pseudorandom, predefined sequence of trials that was the same for all subjects. Subjects had to achieve a total of 560 correct trials to complete one “blocked” session, or 500 to complete an “interleaved” session. Correct trials were always defined with respect to whether the net direction of the motion signal indicated the chosen target at the time of the subject’s decision. Decision accuracy classification was straightforward for CMD trials in which the motion signal always favors one of the two targets; in contrast, the motion signal in VMD trials could sometimes indicate
different targets over the course of a single trial. We therefore determined decision accuracy for VMD trials by subtracting each subject’s estimated non-decision time from the approximate time of the start of the movement with which they reported their decision. The trial was counted as correct if the motion signal at this time indicated the chosen target, even if the signal had changed directions between the effective decision time and the offset of the motion stimulus. Both session types took approximately 50 minutes on average to complete, depending on an individual subject’s speed and accuracy on that day. Importantly, however, subjects were paid the same amount per session ($20 CAD) regardless of how long it took for them to reach the required quota of correct trials. Thus, while we otherwise provided no explicit penalty for wrong answers, the structure of the task nonetheless implicitly motivated subjects to minimize the total session duration by finding a decision policy that maximized success rate for each experimental session.

Crucially, our two session types differed with respect to the value of stimulus observation time. In blocked sessions, the average success rate was not appreciably improved with longer observation times because the motion in CMD trials was essentially constant; in other words, all relevant decision information was fully present from the start of each trial and therefore motivated relatively rapid decisions. In contrast, the interleaved sessions predominantly featured VMD trials. In these trials, not only does the motion signal itself change over time, but – crucially – the range over which it may vary increases in direct proportion to elapsed time. Thus the more one prolongs their decision, the greater the chance that the motion signal will reach a value of larger magnitude. Because this tendency is unique to the VMD trials, which only appear in interleaved sessions, we expected that subjects would exploit this by generally adopting a slower decision policy during the interleaved sessions relative to the blocked sessions. With respect to the two models being tested, this difference in decision policy can be achieved either by increasing the decision bound, as per figures 1a-b, or decreasing the urgency signal’s slope, as per figures 1c-d.

Consequently, we expected that this difference in decision policy between task conditions would result in systematically different response times during the otherwise identical CMD trials common to both session types. Note that while subjects were generally able to discern that some sessions were different from others, post-experiment interviews revealed that they could not specify the precise nature of the differences in the stimuli across sessions; nor could they detect the presence of the pulses in CMD trials or specific types of VMD trials. Furthermore, even had they been able to tell the difference between session types, the fact that trial sequences were randomized would preclude them from being able to know in advance what type a given trial would be. Thus we can be confident that any differences in our subjects’ decision policies in CMD trials across session types indicated adaptations to the implicit reward structure inherent to each session type as a whole, rather than specific strategies adopted on a trial-by-trial basis.

Most importantly, this contextual manipulation of decision policy, if successful, would allow for an empirical discrimination of the divergent predictions of the DDM and UGM by comparing trials in which evidence is identical and only the effective decision policy differs (as per Figure 1). Specifically: if early pulses have an effect on reaction times that is always at least as strong as late pulses, then this would support a pure integration model such as the DDM. If, instead, early pulses lose their efficacy as decisions are slowed while late pulses become more effective, then this would support models in which evidence is not integrated over time, but instead low-pass filtered with a highly leaky integrator.
To test these predictions, we initially ran 39 subjects for three sessions each (1 blocked, 2 interleaved), thereby allowing across-subject analyses (total trials=90,302). Then, to obtain enough data to perform within-subject analyses we ran 4 of these subjects plus an additional 5 new subjects for 10 to 24 sessions each (total trials=71,736).

**Modeling**

To implement the drift-diffusion model, we use the following equation

\[
\frac{dx}{dt} = aE + N
\]

where evidence \(E\) is set to 1 to simulate 3% coherent motion and increased to 2 for 100ms to simulate the motion pulse. The variable \(N\) denotes 1000Hz intra-trial Gaussian noise with mean zero and standard deviation \(\theta\). The variable \(a\) denotes an “attentional gain” that varied from trial to trial with mean 1 and standard deviation 1.5, effectively implementing endogenous variations in the signal-to-noise ratio that differed across trials but was constant within each trial (negative assignments to parameter \(a\) were redrawn from the source distribution until it was positive, and thus this parameter was never permitted to be negative). The decision was made when the variable \(x(t)\) reached a threshold +/- \(T\), and a non-decision delay of \(t_0 = 300\)ms was added to yield the total reaction time. The \(T\) and \(\theta\) parameters were adjusted to fit the data separately in the blocked and interleaved conditions, using an exhaustive grid-search to find the pair that minimized the mean squared error between the model’s estimate of the median RT in no-pulse trials and its estimate of the effect of the 100, 200, and 400ms pulses on median RT (the latter three error terms were multiplied by 10 to emphasize the importance of these effects). After finding the best parameters using a grid search, we fine-tuned them by hand to further improve the fit. The purpose of all of our fitting procedures was to capture the qualitative differences among the various pulse conditions (e.g. relative effect of early versus late pulses), with less emphasis placed on precise quantitative fits. For reasons explained below, in some simulations we also allowed the model extra parameters to implement a delay between the onset of motion and the start of integration.

To implement the urgency-gating model, we first low-pass filter the sensory information using a first-order linear differential equation

\[
\tau \frac{dx}{dt} = -x + (aE + N)
\]

where the time constant was set to \(\tau = 167\)ms. Note that the precise value of the time constant is difficult to establish with confidence from behavioral data, because any changes of the time constant can be “traded-off” with changes to the inter-trial variability of the urgency signal or other potential variance parameters. Thus, not knowing the precise value of these parameters ahead of time necessitates either the introduction of an intractably large number of free parameters, or else calls for assumptions about what these parameters may be. Consequently, we assumed a time constant of 167ms on the basis of a number of previous behavioral and physiological studies which have suggested that it must be at least 100ms (Cisek et al. 2009; Thura et al. 2012) and at most 200ms (Thura & Cisek, 2014). The evidence \((E)\) and attentional gain \((a)\) parameters were exactly the same as in the DDM, and intra-trial noise was 60Hz with mean zero and standard deviation set to \(\theta=5\).

The resulting variable \(x(t)\) is then combined with an urgency signal as
where $U(t)$ is the urgency signal that rises from zero with a slope that varies from trial to trial according to a log-normal distribution with parameters $\mu$ and $\sigma$. While our analyses of monkey behavior suggest that the urgency signal has a non-zero baseline value that can vary with speed-accuracy tradeoffs (Thura, Cos, Trung & Cisek, 2014), here we simply set its baseline to zero so as to avoid introducing another free parameter. The decision was made when the variable $y(t)$ reached a threshold of $T = \pm 300$, and a non-decision delay $t_0=300$ms was added to yield a reaction time. To simulate each of the conditions (blocked and interleaved), we picked values of $\mu$ and $\sigma$ that produced the best fit to the mean and standard deviation of the RT distribution from 3% coherence no-pulse CMD trials in each condition. We then used the same parameter settings when simulating pulse trials, trusting the effects of our different pulse timings to “fall out” out of the parameters used to fit the no-pulse trials.

Note that for each model, two parameters were adjusted to fit the data. For the DDM these were the threshold $T$ and the noise $\Theta$, while for the UGM they were the $\mu$ and $\sigma$ parameters used to determine the urgency slope. These pairs are functionally related: $T$ and $\mu$ influence the means of RT distributions, while $\Theta$ and $\sigma$ influence their variability. While the settings of the DDM parameters were determined through an exhaustive search for the least mean squared error fit to data from all trials, the UGM parameters were only adjusted to fit the no-pulse trials, and the effects of pulses expected to follow simply from the assumption of a short time constant. The models were used to simulate 5,000 trials for each trial type in each task condition, and the results analyzed in the same way as the behavioral data.

Results

Effects of sessions

The first step of our analyses was to determine whether our manipulation of decision policy succeeded in slowing subjects down in the interleaved condition. We did this by comparing RTs for identical no-pulse CMD trials across the two conditions. Mean RTs (± s.e.m.) of individual subjects are shown in Figure 3a for constant-evidence, 3% motion coherence trials without pulses in both the “blocked” (x-axis) and “interleaved” (y-axis) conditions. All individual data points lay above the unity slope line, indicating that the mean RTs for identical CMD trials were slower when these were interleaved among VMD trials than when blocked together ($p=3.3\times10^{-41}$, K-S test), thereby corroborating the efficacy of our decision policy manipulation. Similarly, cumulative RT distributions for no-pulse CMD trials for the 9 subjects who completed the greatest number of experimental sessions (Figures 3b & 3c) show both a clear rightward displacement along the x-axis, indicating later RTs in the interleaved condition.

The main effect on overall mean RT was found for nearly all of our subjects (42/44 subjects, $p<0.05$ for each, K-S test) in spite of the otherwise large inter-subject variability in overall speed. Thus while some subjects tended to be considerably faster than others, all of them individually slowed down during the interleaved sessions. Crucially, this behavior emerged despite the fact that no explicit instructions were ever provided to the subjects regarding the timing of their decisions. The strength and consistency of this result across all of our subjects thus strongly supports the effectiveness of our contextual manipulation on subjects’ decision policies. Moreover, because these differences obtain in no-pulse CMD trials that were otherwise identical, the most parsimonious interpretation of this effect implicates a slowed decision policy for the interleaved sessions relative to the blocked sessions. Within the
framework of the DDM, this corresponds to increasing the decision bound during interleaved sessions, or in the framework of the UGM, to decreasing the slope of the urgency signal (Figure 1).

**Effects of pulses on reaction times**

Next, we analyzed the effects of pulses in each task context to distinguish between the specific predictions of each model under conditions of changing evidence (Figure 1). Similar to the above, this analysis also focused exclusively on CMD trials (both with- and without pulses) which were identical in both session types.

As can be seen in Figure 3a, collectively our subjects varied greatly in terms of average RTs within both task conditions. Such inter-subject variability prohibited a general comparison of across subject means, as pooling together data from subjects with such different RT distributions could weaken any latent significant effects within each subject. Additionally, normalizing by RT would obscure the time course of the impact of evidence on the developing decision. Thus, we instead pooled subjects into subgroups on the basis of the similarity of their mean RTs. Two such subgroups are indicated in Figure 3a. The “fast subgroup” was defined so as to capture fast responders while including most of the subjects for whom we had 10+ sessions’ worth of data, while the “slow subgroup” aimed to capture a similar range of slower responders.

The pooled RT distributions for all CMD trials appear in figures 4a and 4b. For the “fast” subgroup, the 100ms and 200ms pulses significantly sped up response time in the “blocked” condition (K-S test $p=6.7x10^{-16}$ and $p=1.8x10^{-9}$, respectively), while pulses at 400ms had no significant effect ($p=0.21$, K-S test). For the interleaved sessions, however, the 100ms pulses lost their efficacy ($p=0.052$, K-S test), while the 400ms pulses became effective ($p=2.1x10^{-5}$, K-S test). The 200ms pulses remained effective in the interleaved condition ($p=0.002$, K-S test). This is consistent with the predictions shown in Figure 1c,d.

Results for a second, “slow” subgroup appear in figure 4b. For these subjects, the mean response times were long even during the “blocked” condition, and none of the pulses had a significant effect on decision timing, although there is an apparent trend for faster decisions with later pulses (Fig. 4b, top). Response times for the “interleaved” condition are even later, and also not affected by any of the pulses, (Fig. 4b, bottom). Note, however, that this subgroup consists only of subjects who completed 3 sessions each (see figure 3a) and therefore comprises substantially fewer trials than the “fast” subgroup, which may therefore account for the failure of this trend to reach statistical significance.

While here we have shown only two subject groups, other arbitrary groupings of subjects along similar lines (data not shown) yield effects which are qualitatively similar to those discussed above. Similar results were also obtained on the level of individual subjects. Figure 5a shows the cumulative RT distributions from blocked and interleaved sessions for one representative subject (JM; $n_{sessions}=20$; $n_{trials}=12,900$). Like 42/44 subjects, JM’s median RTs for all CMD trial types were significantly shorter during the blocked condition than during the interleaved condition (727ms vs 1057ms, $p=1.53x10^{-80}$, K-S test). Furthermore, in the blocked condition, the 100ms and 200ms pulses (blue and red traces) significantly sped up JM’s response times ($p=6.98x10^{-12}$ and $2.42x10^{-6}$, respectively; K-S test), while pulses at 400ms (green trace) were not significantly effective ($p=0.21$, K-S test). When JM was completing an interleaved session, however, pulses at 400ms now significantly sped up RTs (K-S test $p=0.03$), while the RT distributions for trials with early pulses (100ms & 200ms) were no longer statistically distinguishable from no-pulse trials (K-S test $p=0.75$ and 0.98, respectively).
A similar – though not identical – pattern obtained for other subjects as well. For example, for subject VC (n_sessions=16, n_trials=9,957; data summary shown in figure 5b) only the 200ms pulse had a significant effect in the blocked condition (K-S test p=0.016 in the blocked condition, p=0.27 in the interleaved condition), whereas only the 400ms pulse was effective in the interleaved condition (K-S test p=0.38 in the blocked condition, p=0.001 in the interleaved condition). For subject SC (n_sessions=16), the first two pulses were effective in the blocked condition, whereas only the last two were effective in interleaved sessions. Overall, of the 9 subjects who performed more than 10 sessions, six (JM, EC, VC, SC, EG, TM) showed patterns in their data that are qualitatively consistent with the results described above, insofar as the most effective pulse was earlier in the blocked than in the interleaved condition (although this only reached significance in 4/6 cases). Of the remaining subjects, two (FK and CS) showed no effects of pulses at all – these were our two slowest subjects, while one (LH) showed similar effects in both blocks – this subject was fast in both blocks (Figure 3a). This too is consistent with the UGM, which predicts that the relative difference between a subject’s overall mean RT and the timing of relevant changes in sensory evidence determines the extent to which these changes influence the timing of the decision. Because the pulse timings we selected occurred relatively early in a trial, the differences between the effects of these pulses on response time between the two session types are most pronounced for subjects whose mean RTs are relatively short. A clear demonstration of this comes from the fact that one subject’s RTs were extremely slow (Figure 3b, outlying red line), and did not appear to be influenced by any pulses in either condition – as if they have leaked away.

The relationship between the median RT of an individual subject and the efficacy of pulses at different times is summarized in figure 6, where the fastest eight of our subjects with >10 experimental sessions are plotted together to illustrate how the effect of a given pulse on RT depends on the RT itself. In the blocked condition – where RTs are faster for any given subject – the 100ms pulse (blue) has the strongest effect, followed by the 200ms pulse (red), with the 400ms pulse (green) having little or no effect. However, for the slowest subjects (TM, FK) even the effects of 100ms and 200ms pulses are reduced. In contrast, the patterns of effects are inverted in the interleaved condition, where median RTs are longer. Here, most of the subjects are most strongly influenced by the 400ms pulse (green), while some relatively faster subjects are also influenced by the 200ms pulse (red). While there is variability in the data, and many points do not reach significance, there is a clear tendency for early pulses (blue) to be stronger than late ones (green) in the blocked condition, while the opposite is true in the interleaved condition. Furthermore, there is a “window” of reaction times in which the pulses influence behavior, and that window shifts as subjects slow down their decision policy. The 100ms pulse is most effective on RTs between 650-750ms (blocked sessions), while the 400ms pulse is most effective (in interleaved sessions) approximately 300ms later, as expected.

Analyses of performance accuracy

For the fast subgroup of subjects, accuracy in the no-pulse CMD trials was 83.0% (9939/11969) during the blocked condition and 86.4% (1703/1972) during the interleaved condition, and this difference was significant (binomial test, p<0.01). Within the blocked condition, pulses at 100ms produced a slight and significant increase in accuracy (2633/2997, 87.9%), as did pulses at 200ms (2587/3002, 86.2%), but the increase in accuracy in 400ms pulse trials (2548/3007, 84.7%) was not significant (binomial test, p>0.05). Within the interleaved condition, none of the pulses had a significant effect on accuracy (100ms: 926/1120, 82.7%; 200ms: 908/1034, 87.8%; 400ms: 996/1132, 88.0%). These trends can be captured by
both the DDM and UGM (data not shown), and therefore do not help to distinguish between the models.

Figure 7 shows that the accuracy of decisions decreases as reaction times increase, for all conditions, both for individual subjects (subject JM shown) as well as for both the “fast” and “slow” subject subgroups. This may at first appear paradoxical, since longer viewing of a motion stimulus should allow one to better filter-out noise and thus better estimate the underlying signal. An increasing accuracy with time is often reported in tasks in which observation time is externally controlled (Ratcliff & Rouder, 1998; 2000; Ratcliff & Smith, 2004). However, in our task the subjects are allowed to respond at any time, which means that the distribution of trials within each RT bin can be distorted by the distribution of trials in earlier bins. In such conditions, a decreasing performance for longer RTs can be easily explained if we suppose that a subject’s attention can vary between trials. If a subject happens to be more attentive on a given trial then he/she will both respond more quickly and be more accurate than if he/she is less attentive. Thus, the short RT trials will be biased toward those in which attention was high, while the long RT trials will be biased toward those in which attention was lower. As a result, accuracy will tend to decrease for longer RT bins, and in theory this should hold for both models.

Modeling results

As shown in Figure 8, both models correctly simulated the tendency for accuracy rates to decrease over time. This tendency simply results from variations in the “attentional gain” parameter \( \alpha \), included in both models, which effectively varies the signal-to-noise ratio from trial to trial. This causes differences in the distribution of otherwise identical trials in different RT bins, as described above. We added this parameter because the results shown in Figure 7 may otherwise be taken as direct evidence for a dropping bound, and thus favor the UGM (which effectively implements a decreasing bound by including a growing evidence-independent urgency signal). However, that conclusion would not be accurate; both the UGM and the DDM can explain this phenomenon, so it cannot be used to distinguish between the models. The true distinction between the model prediction lies in analyses of the effects of pulses on RT distributions (see Figure 1), to which we turn next. Importantly, all of the simulations described below have been performed both with- and without the attentional gain parameter, yielding qualitatively identical results.

Figure 9 shows the RT distributions produced by an urgency-gating model with a filter time constant of 167ms (see Methods), and urgency signal parameters that were condition-dependent: for the “fast” subgroup, the slope of the urgency signals were drawn from a log-normal distribution with \( \mu=-0.50 \) and \( \sigma=0.65 \) for modeling the blocked condition, and \( \mu=-1.65 \) and \( \sigma=0.7 \) for modeling the interleaved sessions. These parameters were chosen so that the RT distributions produced by the model for no-pulse trials fit those of the fast subgroup (Fig. 4a, black). Next, the various pulses were added to the simulated input signal and their effects on response time determined by the same analyses performed on the real data.

As expected, the output of a model parameterized according to the data obtained from the “fast” subgroup resulted in the 100 and 200ms pulses being effective during the blocked condition (Fig. 9a, top, K-S test \( p=7.2\times10^{-22}, p=3.7\times10^4 \), respectively), while the 400ms pulse was not \( (p=0.31, \ K-S \ test) \). In contrast, during the interleaved condition, the 200ms and 400ms were effective (Fig. 9a, bottom, K-S test \( p=3.7\times10^{-6}, p=3.2\times10^{-6} \), respectively) while the 100ms pulse was not \( (p=0.07, \ K-S \ test) \), as expected (Fig. 1d).
Data from the “slow” subgroup were modeled in a similar way (Fig. 9b), with urgency parameters $\mu=-.41$, $\sigma=.30$ for the blocked condition and $\mu=-.50$, $\sigma=.17$ for the interleaved condition. With these parameters, the UGM predicted that 400ms pulses will have an effect in both conditions (blocked, $p=0.04$; interleaved, $p=0.01$, K-S test). While such a trend can be seen in the “slow” subgroup data from the blocked condition (Fig. 4b, top), it did not reach significance, perhaps because this subgroup contained only a few sessions of data for each subject.

Figure 10a shows simulations of the DDM with parameters adjusted to fit the “fast” subgroup. For the blocked condition, the best fit was provided by $T=550$ and $\Theta=16$, and these parameters simulated the major features of the data quite well – correctly producing an effect of 100ms and 200ms pulses (K-S test $p=9.6\times10^{-39}$, $p=2.2\times10^{-12}$, respectively) but not late pulses ($p=0.07$, K-S test). For the interleaved condition, the best fitting parameter settings were $T=1550$ and $\Theta=35$, and they correctly predicted a significant effect of 200ms and 400ms pulses (K-S test $p=1.9\times10^{-9}$, $p=5.5\times10^{-4}$, respectively). However, the DDM also predicted that the 100ms pulses had a significant effect ($p=4.4\times10^{-11}$, K-S test), as is clear by examining the cumulative RT distributions. This prediction follows directly from the assumption of perfect integration, which is inherent in the DDM and which does not depend on parameter settings. For the same reason, the DDM predicts that for the “slow” subgroup of subjects, all pulses always have significant effects in both blocked and interleaved conditions (Fig. 10b, $p<10^{-4}$ for all pulses, K-S test).

The best fitting parameters for the slow subgroup were $T=1100$ and $\Theta=25$ for the blocked condition and $T=2500$ and $\Theta=40$ for the interleaved.

Delays in the onset of integration

Because the motion signal during VMD trials can often reach conspicuously high values, but nonetheless cannot grow much in strength until several steps into the trial, it could be argued that during the interleaved sessions our subjects had simply learned to delay the onset of evidence integration for the first few hundred milliseconds so as to avoid having to discern weak early motion in favor of what could be assumed to be an easier discrimination later on. If this was true, it would cause them to show no effects of the earliest pulse timings (e.g. the 100 and 200ms pulses) in the interleaved CMD trials, because these pulses would have already ended before the subjects began integrating evidence. Correspondingly, if the onset of integration was delayed by 200-300ms, the 400ms pulse would effectively become a 100ms pulse, which would explain why such pulses suddenly became effective in the VMD sessions. This would not only explain the shifts in pulse efficacies obtained in the VMD condition, but also the slower RT distributions for all VMD trials in general, providing an explanation for the data that would still be consistent with the DDM.

To test this conjecture, we added two more parameters to the DDM to allow a pre-integration delay with a mean and standard deviation. For modeling the blocked sessions, we set both of these to zero because the DDM could fit that data without any pre-integration delay. For modeling the interleaved session, we searched for the best-fitting setting of threshold and pre-integration mean (with standard deviation set to 100ms). With $T=1250$ and pre-integration delay of $150\pm100$ms, the DDM correctly simulated our finding that 100ms pulses lost efficacy in the interleaved session, simply because most of them were ignored by the model.

However, for obvious reasons such a model could not produce decision times that are shorter than the pre-integration delay. Only 0.7% of its decision times were made before 200ms, and only 9.1% before
This contrasts with the data, in which we observed that 11.6% of decision times in no-pulse trials were shorter than 200ms and 27.6% were shorter than 400ms. Importantly, these early decisions were not merely random; they were correct 78.9% and 78.2% of the time, respectively, indicating that the early information was not in fact being ignored by our subjects.

In summary, the DDM could either be parametrized to capture the patterns of pulse efficacy in the interleaved trials, or to produce early decisions comparable to those observed in the data, but we found no setting of parameters that could allow it to reproduce both of these findings. Nevertheless, it is possible that advocates of the DDM may find other ways to modify that model to explain our results. To that end our data is available upon request.

Discussion

The main result of our study is that when subjects slow down their decision policy, the effect of early pulses becomes weaker while the effect of later pulses grows (Figs. 4, 5, 6). Although the specific pattern of pulse efficacy varied across subjects, the earliest pulse timings consistently lost their efficacy as subjects slowed down. This result is important because it cannot be reproduced by any model involving perfect integration of the motion signal (Figure 10). In particular, the DDM predicts that early pulses will always be at least as effective as late pulses in reducing RTs, because a perfect integrator retains all input until decision time regardless of the threshold setting. In order to explain our results, a strong leak would have to be added to the DDM, effectively turning it into a low-pass filter with a relatively short time constant. Our previous analyses of behavioral and neural data in changing evidence tasks suggest that the time constant is between 100-250ms (Cisek et al. 2009; Thura et al. 2012; Thura & Cisek, 2014).

There may be many reasons why subjects slow down during the interleaved sessions. Above, we proposed that they do so because in the VMD trials higher motion strengths are reached later in time, and thus many individual trials tend to get easier with longer viewing. It is also possible that subjects slow down because sometimes the net direction of motion might change just after they make their decision, reducing their overall confidence. While such reversals occurred in less than 3% of trials, the very possibility of reversals might motivate subjects to be more conservative. There may still be other reasons. Regardless of why subjects slow down, different models suggest different mechanisms for how they do so. The DDM assumes that there is a change in the threshold while the UGM assumes that there is a change in urgency. Other mechanisms may also be proposed, such as a reduction in the strength of recurrent feedback in attractor-type models (e.g. Wang, 2002). What is important to emphasize, however, is that our present results and their interpretations are not dependent upon any of these issues. Regardless of why subjects slow down and regardless even of how they do so, it is the fact that they slow down that is most pertinent to the question of the time constant. If slowing down causes early pulses to lose their efficacy, then the time constant must be short.

The possibility of a “two-model” solution

One possible objection to the above interpretation, however, is that our subjects may have employed radically different strategies during each of our two session types. For example, perhaps they used a DDM in our blocked sessions (and in previous studies) and a UGM in our interleaved sessions. Because none of the trials presented in the blocked sessions ever exceeded 3% baseline motion coherence, all trials in the blocked condition can be considered fairly difficult, which may therefore have motivated our subjects to integrate motion evidence with a long time constant. By contrast, VMD trials presented...
during the interleaved sessions could often reach much larger values of coherence, and may therefore
have motivated subjects not to integrate motion evidence across time, but rather to simply wait for the
motion signal to become highly conspicuous before deciding.

However, there are a number of reasons to doubt this account. First, in both sessions subjects were
always given the same instruction: to respond as soon as they were able to detect any motion signal at
all. This is the same instruction typically given to subjects in a large variety of studies using the random-
dot task in conditions similar to our blocked sessions. Thus, the only feature of the task which may have
motivated subjects to change their strategy in interleaved sessions is the reinforcement provided
regarding correct or incorrect choices. If our subjects’ default strategy was to use a perfect integration,
the only reason they would switch to an alternative, short-time-constant strategy would be if they were
penalized often enough for choosing the direction indicated by the total net motion, but which was
contraindicated by the current motion at the time of their decision. Such cases – if they occurred often
enough to be noticeable – might motivate subjects to begin to discard past evidence, and to instead
weight recent evidence more heavily.

To examine this possibility, we compared overall accuracy rates that would ensue from a post-hoc
reclassification of “correct” and “incorrect” choices according to the total cumulative motion evidence,
as opposed to our original classification based on the sign of the motion evidence at the estimated time
of decision. This revealed that out of all VMD trials completed by our subjects, only 9% would have been
incorrectly reinforced according to a cumulative-motion-evidence criterion, and that this discrepancy
falls to only 3% when considering VMD trials in which the motion signal ever reached or exceeded 15%
coherence, i.e. the trials which would have conspicuously stood out to the subjects. Consequently, it
seems unlikely that the reinforcement provided to our subjects was significant enough to be responsible
for the changes in decision strategy we observed across the session types.

Furthermore, the logic of this proposal can be reversed. In natural behavior, sensory evidence does
change, and changes often. To react quickly to such changes, leaky integration is much more effective
than perfect integration, which first needs to “undo” previously accumulated evidence before moving
toward the new decision bound. Thus, reinforcement in the real world would seem to favor mechanisms
with short time constants (as long as the time constant is long enough to filter out noise) to be the
default strategy. This then raises the question of why humans would ever change their strategy and use
perfect integration, even when performing a standard constant motion discrimination task. In such
tasks, the motion does not change so the reinforcement obtained by a perfect integrator would be no
different than that obtained by a leaky model.

Finally, while a two-model solution is plausible, it lacks parsimony. It proposes two different models for
explaining two different kinds of data, and necessitates additional mechanisms for arbitrating between
them. From a modeling perspective, it is certainly possible that such a hybrid, “switching” model could
produce better quantitative fits to our data; however, by the same token, such a model would
necessarily include a larger total number of parameters than either model by itself. Any measure of
goodness-of-fit to any given data set would be penalized by the additional parameters of the switching
mechanism as well as those of the “unused” model, and therefore rank low according to traditional
model-comparison measures (e.g. AIC/BIC criteria, etc.). In contrast, the UGM can explain all of the data
with just a single parameter change – a modification of urgency – that is motivated by optimization of
reward rates. In a recent paper (Thura & Cisek, 2014), we directly demonstrated that neural activity in
dorsal premotor and primary motor cortex combines both urgency and evidence-related components,
and that the latter is processed with a short time constant. While this used a different species and a
different task, we propose that the conclusions generalize to a broad range of tasks and species. Indeed,
although we acknowledge that perfect integration is commonly assumed when interpreting data, we are
not aware of data that conclusively proves that assumption to be correct.

**Narrowing down the value of the time constant**

The present results could, in principle, be explained by the leaky competing accumulator (LCA) model
(Usher & McClelland 2001; Tsetsos *et al.* 2012; Ossmy *et al.* 2013), as long as the leak parameter is set
high enough to produce a short time constant. With such a high leak, however, the evidence signal in
the LCA model will equilibrate long before it reaches any appreciable bound, and until that point the
temporal shape of the build-up will be a saturating exponential, not the linear build-up usually observed
in neural data (*c.f.* Roitman & Shadlen 2002). Consequently, something else is needed to explain the
prolonged linear time-course of neural activity growth and long decision times. We and others have
proposed that this growth is at least partially caused by an urgency signal that pushes neural activity
toward the threshold even in the absence of new evidence, effectively implementing a decreasing
accuracy bound (Ditterich 2006; Churchland 2008; Cisek *et al.* 2009; Thura *et al.* 2012). In fact, the UGM
is equivalent to the LCA model with a high leak parameter and an urgency signal. Such a model can
explain not only the present data but also the lack of biasing effects observed by Thura *et al.* (2012),
suggesting that the effects observed in that study are not task-dependent but rather indicative of a
general strategy of low-pass filtering a noisy stimulus signal.

A recent analysis using the LCA (Ossmy *et al.* 2013) suggested that time constants can change between
conditions with different distributions of signal durations. Across subjects, the best-fitting time constant
values varied from 29ms to 1995ms (mean 78ms and 493ms) in the two conditions (see their table S2).
However, because the LCA assumes a fixed bound, it forces the use of a long time constant for
explaining any late decisions. We believe that if that assumption was relaxed, and the bound was
allowed to decrease through the use of a context-dependent urgency signal, then long decisions could
be explained even if the time constant was always short.

While a precise estimate of the time constant is difficult to make without direct neural data, the present
results are nonetheless useful for providing bounds on the possible values that it may take. In particular,
while results similar to Figure 9 could be generated with a 200ms time constant, a 250ms time constant
consistently predicts a significant effect of the 100ms pulse even in the interleaved sessions, in contrast
to our data. In principle, one could use a model fitting optimization procedure to try to find the best-
fitting time constant, but in our view that would not be fruitful in practice. The reason is that once the
time constant is set below 250ms, small variations of it can be traded off against changes in inter-trial
variability parameters (e.g. the $\sigma$ parameter of the UGM) producing similar goodness of fit. Our
approach is not to try to estimate these parameters precisely, but rather to eliminate sections of the
parameter space. The results of the present study as well as previous ones (Cisek *et al.*, 2009; Thura *et al.*
2012; Thura & Cisek, 2014), allow us to eliminate models with long time constants (>250ms), including
perfect integrators such as the DDM.

**Alternative (non-integration-based) models**

It is possible that during the interleaved sessions, subjects neither integrate the motion signal nor
combine it with a growing urgency, but simply wait until a large coherent motion appears randomly
during a trial. However, we consider it unlikely that this strategy – akin to a threshold detection process – was used in our task. Because our subjects could not predict ahead of time what the range of motion coherence would be on a given trial, there was no way for them to set any particular decision threshold. For example, simply waiting until the motion coherence exceeded 15% would have failed to produce any decision at all on ~40% of VMD trials, whereas the number of ‘time out’ trials we actually observed was less than 1%. Indeed, any threshold much higher than 3% would have failed to produce any decisions on the no-pulse CMD trials. Conversely, setting the threshold lower would have produced many more errors than what we observed. Thus, while a detection strategy is plausible and may be used in some situations, it seems unlikely to explain our data.

The UGM suggests that low-pass filtered evidence is brought to threshold through combination with an independent urgency signal that controls the decision timing policy. After a pulse, activity related to evidence increases briefly but then quickly returns to the baseline “no-pulse” level. Thus, a motion pulse reduces the RT on a given trial only if the decision is made before the effect of the pulse has leaked away (see figure 1c,d). The UGM thus predicts that the efficacy of a given motion pulse will depend on its timing with respect to the decision time. By extension, any systematic change in average decision times will change which pulse timings reduce RTs. This is precisely what we observed. Moreover, this not only explains the general trends we found, but also many of the differences obtained across subjects, with different individuals susceptible to a different set of motion pulses based on the average timing of their decisions in a given context (Figure 6).

An alternative way to implement a build-up of neural activity is through recurrent feedback between the populations representing the different options, as in the model of Wang (2002). While such models differ from the DDM in many important ways, their recurrent feedback effectively implements a long time-constant of integration. Indeed, simulations by Wang (2002) show that reduction in the strength of the recurrent connections causes the system to lose its slow build-up of neural activity, and equilibrate within 200-300ms after stimulus presentation. If the recurrent connections are strong enough to produce continued build-up, then they effectively implement temporal integration with almost no leak. Consequently, we conjecture that such models, like the DDM, would also predict a persistent effect of the 100ms pulses even in the interleaved condition, in contrast to our data. However, variations of attractor models in which the interaction function governing the recurrent connections becomes steeper over time (see Standage et al. 2011) can produce dynamics that approximate a leaky integrator with urgency, and consequently are in principle able to reproduce our findings (Marcos et al. 2012 SFN poster). Indeed, such models were the original inspiration for our experiment, though their detailed implementation is beyond the scope of the present paper.

Noise

Integrator models deal with noise by adding together successive samples on the assumption that the noise components will cancel each other out over time, leaving an estimate of the underlying signal. On the surface, the UGM may appear susceptible to noise because it privileges recent information. However, because the UGM includes a low-pass filter, it is just as effective as an integrator at dealing with noise. Indeed, for stimulus components above the filter cutoff frequency, a low-pass filter and an integrator are approximately equivalent. The time constant of the filter jointly determines both the frequency of input fluctuations which will be screened out as noise as well as the amount of time required for the decision variable to respond to a genuine change in the underlying signal. This issue is relevant for two recent papers that attempted to argue against the UGM. Winkel et al. (2014) showed
that early motion signals influence response times and took this as evidence against the UGM. However, in their implementation of the UGM they did not include the low-pass filter. If a low-pass filter is added to the model, it can easily reproduce that data (Carland, Thura, & Cisek, 2015). Indeed, as shown here (Fig. 9), a low pass filter with a short time constant is capable of simulating the effects of early motion signals, even on reaction time distributions whose means are approximately 1000ms. Churchland et al. (2012) suggested that the UGM cannot explain correlations in neural activity, but those authors also did not include the low-pass filter. If the UGM is implemented fully, including the low-pass filter, then analyses of high-frequency correlations cannot distinguish between it and an integrator model, because a low-pass filter and an integrator are equivalent with respect to reducing the gain of high frequency components in their input.

The definition of “evidence” and its ramifications for modeling the decision process

Important to the present discussion is the question of what constitutes evidence in a given task. The DDM is often seen as equivalent to the sequential probability ratio test (SPRT), a statistical test that optimizes sampling time to attain a given level of accuracy (Wald, 1945). However, the equivalence between the DDM and SPRT holds only under the assumption that each sensory sample is statistically independent from preceding ones (Bogacz et al. 2006; Thura et al. 2012; Huang & Rao, 2013). In any constant-evidence task, repeatedly sampling the stimulus means that each additional sample is increasingly redundant, providing less and less information. Ideally, the decision process should be governed primarily by novel information. Thura et al. (2012) suggested that for simple tasks, this may be approximated by a low-pass filter, which quickly adjusts the current estimate of evidence while ignoring fluctuations whose frequency is above the range at which the signal of interest is likely to change. This mechanism not only ensures that redundant information is ignored, but also enables faster transitions between options under conditions in which evidence can change. A perfect integrator would be slow to reflect such changes, as it would have to first “undo” the previously-integrated sum for the initial choice before it could begin to accumulate evidence in favor of the new choice. In contrast, an urgency-gating model could respond to the new choice after only a brief delay determined by its time-constant.

In light of the above, we can consider some of the specific tasks that have been described in the literature. In some tasks subjects are being given new sensory information over time – this includes the “weather prediction” task (Yang & Shadlen, 2007; Kira et al. 2015), the “tokens” task (Cisek et al. 2009; Thura & Cisek, 2014; Thura et al. 2014), the VMD task (Thura et al. 2012), and the “click-counting” task of Brody and colleagues (Brunton, Botvinick & Brody 2014; Hanks et al. 2015). In such conditions, information from each new piece of information is novel and should indeed be accumulated, as supported by both behavioral and neural data. In contrast, in some tasks the stimulus is completely static – this includes “brightness discrimination” (Ratcliff 2002; Ratcliff et al. 2007), “dot separation” (Ratcliff, Cherian & Seagraves, 2003), and “color discrimination” tasks (Coallier & Kalaska, 2014). In such conditions, each sample of the visual stimulus is identical to previous samples and provides no new information, so it should not be integrated. The random-dot motion discrimination task (Britten et al. 1992) as well as noisy image categorization tasks (e.g. Tremel & Wheeler, 2015) are a variant of the latter category – they are tasks in which the underlying signal is static and all that changes between sequential samples is noise. In such conditions, each sequential sample provides some novel information but with diminishing returns, because once the noise has been filtered out there is no more new information to be obtained. Thus, in such tasks, an accurate estimate of evidence should stop growing quickly and therefore could not be responsible for the prolonged build-up of neural activity.
Perfect integration models such as the DDM have a long history and have become well-accepted because they capture a great deal of data within a simple and intuitively appealing framework. However, the intuition of accumulating sensory samples must be supplemented by considering the evidence actually provided by those samples, which are increasingly redundant in most tasks. Strictly speaking, only novel evidence should be accumulated. Furthermore, in nearly all previous experiments the sensory information provided to subjects was constant over the course of each trial. In such conditions it is difficult to distinguish between different parameter settings, and even sophisticated comparisons of model fits (Hawkins, Forstmann, Wagenmakers, Ratcliff & Brown 2015) do not yield consistent conclusions across tasks, subjects, or modeling assumptions. In contrast, tasks in which evidence changes during each trial cause different models to make clearly divergent predictions that are empirically distinguishable. Our previous analyses of behavioral and neural data in such tasks strongly favored the urgency-gating model (Cisek et al. 2009; Thura et al. 2012; Thura & Cisek, 2014), but those results could have been task-dependent.

Here, we used the same random-dot motion discrimination task that has been used many times to support the DDM. However, we designed our experiment to directly test situations in which the two models make empirically distinguishable predictions. We did this by both blocking trials into two distinct contexts which implicitly motivate either faster or slower responses, and by presenting in each context some identical trials with brief motion pulses. The finding that early pulses become less effective as subjects slow down their decisions (Figures 4, 5, 6) cannot be explained with any version of a perfect integrator (Figure 10), regardless of parameter settings, and points to the necessity of including a strong leak term. The consequence of the leak term, however, is that with constant-evidence the system will equilibrate quickly and therefore cannot explain long RTs or the prolonged linear build-up of neural activity. This suggests the necessity of including an urgency signal. Neural data supporting the presence of an urgency signal at the individual cell level have been found during constant-evidence tasks (Churchland et al. 2008; Hanks et al. 2014) as well as during changing-evidence tasks (Thura & Cisek, 2014; Kira Yang Shadlen 2015; Gluth et al. 2012). We conjecture that an urgency signal is a general mechanism for controlling speed-accuracy tradeoffs in decision-making and movement control (Thura, Cos, Trung & Cisek 2014) and that it is responsible for much of the neural activity build-up observed during decision-making.
Figure captions

Figure 1: Schematic of predicted effects of motion pulses assuming the drift-diffusion (DDM) versus the urgency-gating (UGM) models. A. Here, following the DDM, we assume a perfect integrator of motion signals with a fixed bound that is set to a low value, to emphasize speed in a “fast” task context. As a result, early motion pulses (red line) will result in significantly shorter reaction times (RT) distributions than in no-pulse trials (black dotted line), but late motion pulses (blue) will have no effect because they occur after the decision bound has already been reached. Schematic reaction time distributions are shown on the x-axis. B. In a “slow” task context, the bound is set to a higher value, and as a result both early and late pulses cause a reduction of RTs as compared to no-pulse trials. C. Here, following the UGM, we assume that the motion signal is low-pass filtered and combined with a growing urgency that is steep, to emphasize speed in the “fast” task context. As in A, early pulses have an effect but late pulses occur too late to reduce the RT. D. In the “slow” task context, the urgency is shallower, and so late pulses now significantly reduce the RT. However, in contrast to panel B above, early pulses no longer reduce RTs because their effect has leaked away by the time the threshold is crossed.

Figure 2: Experimental setup and the variable motion discrimination (VMD) trials. A. Overhead view of the experimental display. Subjects discriminated the direction of movement of a random dot motion display contained within a central circle (the border of which was not drawn on-screen) by moving a handheld stylus (solid black circle) from a start target (small circle) to one of two equidistant peripheral targets, each separated by 180° and oriented with respect to the elbow’s natural direction of motion. B. Example trajectories of the time-course of motion evidence in VMD trials. After being initialized at 0% at the beginning of each trial, the motion signal is adjusted in increments of 3% motion coherence towards one of the two targets (with equal probability) every 200ms. Note that when the motion signal already favors a target, a step “toward” the opposing target corresponds to a weakening of the strength of the motion signal.

Figure 3: Reaction times in no-pulse trials in the blocked and interleaved conditions. A. Mean RTs of individual subjects in no-pulse trials during the blocked (x-axis) versus the interleaved (y-axis) conditions. Crosses show the standard error of the mean, and colored points indicate subjects who performed 10 or more experimental sessions each. All but two subjects (shown in light grey) showed a significant difference between conditions (p<.05, KS-test). The dotted rectangles show subjects that were grouped together for the pooled analyses shown in figure 4. B. Cumulative RT distributions in no-pulse trials during the blocked condition, for the 9 subjects who performed >10 sessions (same colors as in 5a); vertical lines indicate medians. C. Cumulative RT distributions and medians of the same subjects in no-pulse trials during the interleaved condition. In all cases, RTs for such trials are significantly shorter in the blocked condition than in the interleaved condition (all no-pulse trials pooled by session type, p=8.84x10^{-43}, K-S test).

Figure 4: Comparison of reaction time effects of pulses in constant motion discrimination (CMD) trials. A. Cumulative RT distributions for no-pulse (black), 100ms pulse (blue), 200ms pulse (red), and 400ms pulse (green) for the “fast” subgroup of subjects indicated in Figure 3. Insets show the corresponding median RTs (with 95% confidence intervals) and asterisks indicate significant differences (large asterisks indicate statistical comparisons against no-pulse trials, small asterisks show comparisons between pulse trials). B. Cumulative RT distributions for the “slow” subgroup of subjects. Same format as A.
Figure 5: Comparison of reaction time effects of pulses in constant motion discrimination (CMD) trials; individual subjects. A. Cumulative RT distributions of subject JM during the blocked condition (top) and during the interleaved condition (bottom). Same format as in figures 4a & 4b. JM’s mean estimated non-decision time across all sessions was 451ms. B. Median RT data for all subjects presented in figures 3b & 3c. Individual subjects identified by initials, and correspond to the data shown in figures 3b & 3c. Numbers in parentheses next to subject initials indicate the total number of experimental sessions completed by each subject.

Figure 6: Summary of the effects of pulses on median RTs of eight individual subjects for whom we collected >10 sessions of data. A. Data from the blocked condition. Each point compares an individual subject’s median RT in no-pulse trials (x-axis) against the median RT of that same subject during 100ms (blue), 200ms (red) and 400ms (green) pulse trials (y-axis). The no-pulse trials (black) define the unity slope line, and colored points below that line indicate an effect of the given pulse. Filled circles indicate significance (K-S test, p<0.05). B. Data from the interleaved condition, same format.

Figure 7: Accuracy as a function of time. Trials were grouped into 300ms bins on the basis of reaction time, and for each bin the accuracy was plotted separately for no-pulse trials (black) as well as trials with pulses at 100ms (blue), 200ms (red), and 400ms (green). The top row shows the results from blocked sessions and the bottom row for interleaved sessions. A. Data for subject JM. B. Data for the fast subgroup. C. Data for the slow subgroup.

Figure 8: Simulations of accuracy as a function of time, in the same format as Figure 7. A. Simulations of the UGM fitted for the fast subgroup in the blocked (top) and interleaved (bottom) sessions. B. Simulations of the DDM fitted for the fast subgroup in the blocked (top) and interleaved (bottom) sessions.

Figure 9: Simulated cumulative reaction times generated by the urgency gating model, same format as Figure 4. A. Simulations of the fast subgroup in the blocked (top) and interleaved (bottom) sessions. B. Simulations of the slow subgroup.

Figure 10: Simulated cumulative reaction times generated by the drift-diffusion model, same format as Figure 4. A. Simulations of the fast subgroup in the blocked (top) and interleaved (bottom) sessions. B. Simulations of the slow subgroup.
References


Fig. #1: the divergent predictions of the two models

A

Drift-diffusion

Fast context

Distributions of decision times (DT)

B

Drift-diffusion

Slow context

C

Urgency-gating

Fast context

D

Urgency-gating

Slow context
Fig. #2: the experimental task
Fig. #3: data from multiple subjects

![Graph A](image)

**A**

Mean RT (no-pulse trials, interleaved condition) vs. mean RT (no-pulse trials, blocked condition).

**B**

Proportion of trials vs. blocked RTs (ms) for multiple subjects.

**C**

Proportion of trials vs. interleaved RTs (ms) for multiple subjects.
Fig. #4: Pooled RT data
Fig. #5: Individual Subject RT data

A. Subject ‘JM’ (n = 20)

B. LH [13], FK [12], EC [10], SC [16], CS [15], EG [24], VC [10], TM [13]
Fig. #6: time-course of pulse effect on across-subject RT

- Unfilled circles = p > .05
- Filled circles = p < .05

**Blocked condition**

**Interleaved condition**
Fig. #7: Accuracy rates over time
Fig. #8: Model simulations of accuracy rates
Fig. #9: UGM simulations of RT data

A  UGM - fast group

B  UGM – slow group
Fig. #10: DDM simulations of RT data

A  DDM - fast group

B  DDM - slow group

Proportion of trials (%) vs. blocked RTs (ms)

Proportion of trials (%) vs. interleaved RTs (ms)

\* = p < .01
\** = p < .001