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Temporal Precision of Neuronal Information in a Rapid Perceptual Judgment

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a rapid perceptual judgment. *J Neurophysiol* 101: 1480–1493, 2009. First
published December 24, 2008; doi:10.1152/jn.90980.2008. In many sit-
uations, such as pedestrians crossing a busy street or prey evading
predators, rapid decisions based on limited perceptual information are
critical for survival. The brevity of these perceptual judgments con-
strains how neuronal signals are integrated or pooled over time
because the underlying sequence of processes, from sensation to
perceptual evaluation to motor planning and execution, all occur
within several hundred milliseconds. Because most previous physio-
logical studies of these processes have relied on tasks requiring
considerably longer temporal integration, the neuronal basis of such
rapid decisions remains largely unexplored. In this study, we examine
the temporal precision of neuronal activity associated with a rapid
perceptual judgment. We find that the activity of individual neurons
over tens of milliseconds can reliably convey information about
sensory events and was well correlated with the animals' judgments.
There was a strong correlation between sensory reliability and the
correlation with behavioral choice, suggesting that rapid decisions
were preferentially based on the most reliable sensory signals. We
also find that a simple model in which the responses of a small number
of individual neurons (<5) are summed can completely explain
behavioral performance. These results suggest that neuronal circuits
are sufficiently precise to allow for cognitive decisions to be based on
small numbers of action potentials from highly reliable neurons.

INTRODUCTION

Our actions and perceptions can occur both quickly and
reliably, yet neuronal discharge is commonly considered noisy
and imprecise. These observations are often reconciled by
assuming that temporal integration or some form of neuronal
pooling reduces the influence of neuronal noise. However,
current models, even those trying to explain automatic and
precise movements such as smooth pursuit (Osborne et al.
2004), rely on temporal integrations of 100 ms or more, despite
the likelihood that briefer epochs of perceptual information
must be used in critical situations. For example, most models
that account for both the performance and timing of reaction
time tasks are based on the sequential sampling of signals
accumulated over a population of sensory neurons (Palmer
et al. 2005; Ratcliff and Smith 2004; Smith 1995). In these
models, sensory information pooled across a populations of
neurons is assumed to be noisy at any instant, and reliability is
increased by accumulating over time. Behavioral responses are
initiated when this accumulated signal reaches a criterion
(Ratcliff 2001).

Although several electrophysiological studies have provided
support for such a model (Mazurek et al. 2003), two lines of
evidence suggest it may not generalize to all perceptually based
decisions. First, most studies examining visually based judg-
ments have used one specific kind of stimulus: a field of
randomly appearing dots in which a certain percentage of the
dots are constrained to move in a particular direction. Such
stimuli contain a variety of local and global motion signals
(Burr and Santoro 2001) because of dot density variations in
both space and time (Barlow and Tripathy 1997). For both
detection and discrimination tasks using such stimuli, response
times are much longer (≤1 s) than those observed in tasks
using simpler stimuli (Luce 1986). Long reaction times might
arise if there were substantial neural noise or imprecision
among neurons participating in the decision (Mazurek and
Shadlen 2002). However, when identical sequences of random
dots are presented, the discharge of neurons in the middle-
temporal area (MT) is precise on a scale of milliseconds (Bair
and Koch 1996). The discrepancy between this precision and
the large means and variances of reaction times for low-
coherence random dot stimuli suggest that decisions based on
such stimuli may be limited by noise in the stimulus rather than
by neuronal noise. If this is the case, the precision of sensory
signals used in a decision, and therefore potentially the entire
algorithm for arriving at a decision, may be highly stimulus
dependent. This is particularly relevant for the case of motion-
based decisions: if reaction times for coherent motion were on
the order of a second, even simple activities such as crossing a
street would be impossible (Zeki 1991).

Evidence from our laboratory using a coherent motion de-
tection task (Ghose 2006) suggests that the processes underly-
ing perceptual decisions that are completed within a few
hundred milliseconds may indeed be fundamentally different
(Ludwig et al. 2005). In our study, the distribution of reaction
times was inconsistent with a uniform accumulation of sensory
information over time, which is a fundamental assumption of
sequential sampling models (Ghose 2006). The study showed
that subjects engaged in the detection of a predictable motion
stimulus do not acquire stimulus information uniformly or
randomly, but instead base their decisions on an optimized and
task-appropriate filtering of that information in both space and
time.

The physiological basis of rapid decisions—ones that re-
quire sampling information over tens of milliseconds—has not
been previously explored, even though the neural machinery
that underlies such decisions may be typical of the nervous
system. In particular, the reliability of neuronal signals and
behavioral performance has not been evaluated or compared
under such strict time constraints. To reasonably ascribe neural
activity to such behavior, simultaneous measures of neuronal
and behavioral temporal precision, and not just reliability, are

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required. For example, a neuronal response that is reliable only when averaged over long epochs of time cannot play a critical role in a rapid behaviors. Similarly, a temporally precise response that occurs with high latency cannot play a role. Finally, a short latency signal that is highly unreliable is unable to account for a reliable behavioral response. A further complication is that, even if sensory responses of individual neurons are sufficiently precise and reliable to explain behavior, it is unclear whether such precision on the cellular level can actually be used by the animal (deCharms and Zador 2000). For example, neurons at a subsequent stage of processing might receive convergent input from a large population of sensory neurons, making the activity fluctuations of any individual neuron inaccessible and therefore irrelevant to the decision process.

To examine how rapid decisions requiring the precise sampling and evaluation of sensory signals might be achieved, we recorded from neurons within the cerebral cortex likely to be involved in the detection of a briefly presented visual stimulus. Based on previous studies that found activity in specific extrastriate areas to be correlated with both sensory information and behavioral choices in motion discrimination judgments (Britten et al. 1996), we recorded from single neurons in area MT of monkeys while they performed a challenging motion detection task. We used a novel method based on information theory to simultaneously quantify the time course and precision of behavioral and neuronal reliability. Using this method, we found that individual neurons could provide sensory information over periods as brief as tens of milliseconds that was sufficiently reliability to explain behavioral performance. Although this precision in the encoding of motion information is consistent with previous observations, we observed that the correlation between MT activity and behavior was much more temporally precise than has been previous assumed. In further contrast to previous results, we find that activity of individual neurons in MT was strongly correlated with behavioral choice and that those neurons with the most reliable sensory information were also the most linked to behavioral choice. Because discharge from individual neurons over time scales on the order of typical interspike intervals is correlated with both sensory events and behavioral choices, these results suggest that rapid decisions depend on a small number of action potentials from the most reliable neurons.

METHODS

Visual stimuli

Stimuli were arrays (spanning 5–7°) of small 100% contrast achromatic patches (31 Gabors, 1 cyc/° SF, sigma = 0.4°) containing luminance-modulated sine waves of identical orientation (Ghose 2006) (Fig. 1B). Although the phase of each sine wave varied independently, the Gaussian envelopes of the Gabors were fixed. Stimuli were presented on a CRT placed 57 cm in front of the animals, and patches were updated on every frame refresh (120 Hz, *monkey P*; 160 Hz, *monkey B*). Motion noise was produced by randomly and independently stepping the phase within each patch ($\pm 90°$ at 120 Hz, $\pm 72°$ at 160 Hz), and coherent motion was introduced by briefly (60–83 ms) enforcing a consistent phase change across all patches (motion pulse). Local temporal frequency and velocity was therefore constant (30 and 32°/s). For all neurons within the same animal, identical random sequences were used to generate the motion noise for each recording neuron. These random sequences described the relative motion of the 31 Gabors for 2^{18} frames. Progress through the random sequence was interrupted on all trials except successful catch trials by either an eye movement or the introduction of a motion pulse. The sequence position at which a pulse or eye movement occurred within each trial was recorded and used as the random sequence starting point for motion noise in the following trial. Thus the actual sequence describing motion noise was unique for each trial of a given cell, with the exception of a small percentage of trials (2%) in which the sequence was sampled from its beginning. The recording session was concluded when the entire random sequence had been presented. Two arrays were placed at symmetric locations with respect to the vertical meridian. Motion pulses occurred according to a specific spatio-temporal schedule between these patches (Ghose 2006); only the stimulus located at the receptive field of the neuron under study, and saccades to this location, are considered here. The timing of motion pulse presentation within each trial was randomized, so that there was no tendency for pulses to occur at specific times within the overall random noise sequence.

Task design

Two monkeys (*Macaca mulatta*) performed a motion detection task. All surgeries were done under asceptic conditions and full anesthesia in accordance with the animal care guidelines of the University of Minnesota and the National Institutes of Health. Head position was stabilized by a chronic titanium head post implant secured with orthopedic screws. Eye position was monitored by scleral eye coil recorded at 200 Hz. Trials started with the presentation of a small centrally located dot (0.1°). Animals were required to fixate on this dot within a window (width, 1.25°) until a coherent motion pulse was presented. When a motion pulse was presented, the animals were required to saccade to the location of the Gabor array. Such saccades were detected by centering a target eye position window on the Gabor array. Motion noise started 250–500 ms after fixation. The appearance of the motion pulse with regard to the start of the noise was exponentially distributed to preclude temporal anticipation (mean: 2,000 ms, *monkey P*; 900 ms, *monkey B*) (Luce 1986). To further ensure vigilance throughout the trial, no pulse was presented in 4% of trials, and the animals were rewarded if they maintained fixation throughout the entire trial. The duration of these catch trials was consistent with the exponential distribution of pulse presentation times (T; Fig. 1C). The brevity of the motion pulse combined with the statistics of its appearance ensured that successful task performance required the constant evaluation of sensory information as the basis for a potential behavioral response. If animals saccaded to the location of the Gabor array between 150 and 550 ms after the onset of the motion pulse, they were rewarded with juice (C; Fig. 1C). Alternatively, if the animals made an eye movement to the stimulus when no motion pulse was presented, saccaded to an inappropriate location, or broke fixation in any other way, the trial was immediately terminated without reward (W; Fig. 1C). Failure to respond within 550 ms resulted in the termination of the trial without reward (F; Fig. 1C). Because the reaction time window was only 400 ms and the timing of the pulse could not be readily anticipated, chance performance in this task is close to zero (~1.5% correct).

Motion stimuli were retinally stabilized to reduce the influence of small fixational eye movements on neuronal activity (Bair and O'Keefe 1998; Gur and Snodderly1997) and behavioral performance. Eye position was continually calibrated throughout experimental sessions by randomly alternating between four fixation points separated by 1° around the center of the screen. Stabilization was accomplished by shifting the entire Gabor array, but not the fixation point, according to the most recent eye position sample after calibration. Behavioral control, visual stimulation, and data acquisition were computer controlled using customized software (http://www.ghoselab.cmrr.umn.edu/software.html). We recorded well-isolated single neurons using standard extracellular recording techniques and digitized the occur-
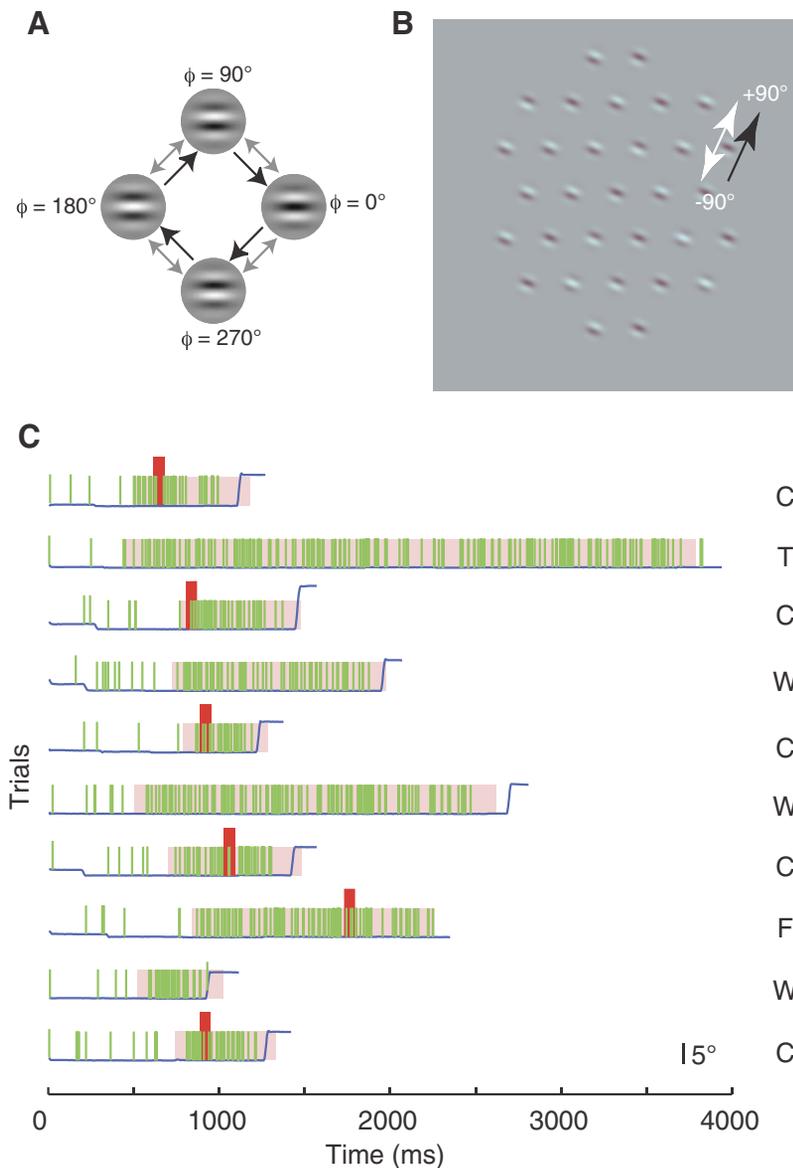
FIG. 1. Motion stimulus and sample data. *A*: monkeys detected coherent motion associated with a consistent phase shift direction (black arrows) in Gabor patches. Brief coherent motion was embedded in motion noise produced by random phase shifts of the Gabors (gray arrows). *B*: a hexagonal array filled the receptive field of the neuron under study, and the orientation of the Gabors were adjusted to be aligned with the preferred direction of motion for the cell. During motion noise, each Gabor shifted independently (white arrow); during the pulse, each shifted in a consistent direction (black arrow). *B* and *C*: the motion pulses (red), eye movements (blue), and action potentials (green) of 10 consecutive trials from an example cell. Pink rectangles indicate duration of motion noise. The beginning of each trial is defined by the animal's initial fixation on a small dot. Letters to right of traces indicate behavioral classification: C (correct), T (catch), W (false alarms), and F (failed). Performance (excluding trials with fixation breaks) for *monkey P* was 60% C, 10% F, and 30%W; for *monkey B*, 50% C, 18% F, and 32% W.

rence of action potentials and CRT frame updates (1 kHz, *monkey P*; 10 kHz, *monkey B*). Area MT was identified physiologically by the presence of audible low-frequency (<100 Hz) local field potential responses to the motion noise stimulus, a high proportion of direction selective responses, and receptive field mapping. For each neuron's receptive field, mapping was done by shifting the position of the entire array while the monkey performed the task. Direction selectivity was assessed by recording responses to relatively long (167 ms) motion pulses of eight different directions while the monkey performed the motion pulse detection task. On the basis of these tuning runs, a specific stimulus location and direction was chosen for extended recording.

Data analysis

Each trial was parceled into equally sized temporal windows (4, 8, 16, 32, 64, 128, and 256 ms), and the onset of the motion pulses, the initiation of saccades to the stimulus, and the number of action potentials within each bin were used to increment contingency tables between these events (Fig. 2). Both the visual stimulus and the behavioral response were treated as point processes, so that the onset of a motion pulse or saccade anywhere within a bin incremented the

corresponding location within the table. Neuronal activity was characterized according to the number of spikes within a bin. Contingency tables between any two variables at a particular resolution were computed with a temporal resolution of 4 ms. For example, contingency tables between motion pulse occurrences and saccade initiation at a resolution of 64 ms were separately computed for pulse-saccade intervals of 0–63, 4–67, and 8–71 ms, etc., for a total of 64 different delays.

For behavioral information, the contingency table for each combination of resolution and delay was 2 (pulse and no-pulse) × 2 (saccade and no-saccade). For neuronal information, the contingency tables were 2 × *N*, where *N* was the maximum number of spikes observed within a single bin. These contingency tables were used to estimate conditional probabilities whose discriminability was quantified according to information theory. The uncertainty of a particular variable that assumes discrete values is quantified by entropy *H*

$$H = -\sum_i p_i \log(p_i) \qquad (1)$$

where p_i is the probability of observing value *i*. This analysis makes no assumptions concerning the underlying probability distribution of the variable.
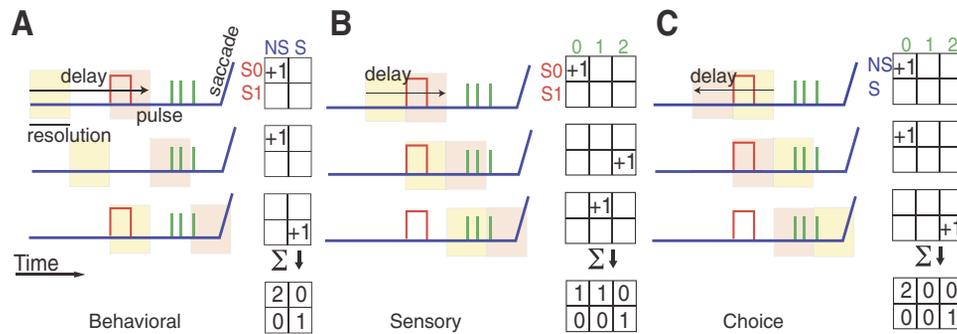
FIG. 2. Three types of mutual information were computed: behavioral, existing between stimulus and behavior response (*A*); sensory, existing between stimulus and spike train (*B*); and choice, existing between spike train and behavioral response (*C*). Events within trials were binned according to a time window, and contingency tables incremented according to delay. Here the process is shown for a single resolution and delay. For behavioral and sensory information measures, the presence (S1) or absence (S0) of motion pulse onset in the yellow windows is correlated with either the presence (*S*) or absence (NS) of saccade onset (*A*) or with a certain number of spikes in the pink windows (*B*). For choice information, the presence (*S*) or absence (NS) of a saccade in the yellow window is correlated with the number of spikes that occur in the pink window (*C*). The combination of events in a particular yellow-pink pairing determines what is incremented in the 2 × 2 or 2 × *N* contingency table, where *N* represents the maximum number of spikes that occurred in a given resolution. The process is repeated for all possible pairings within all trials. The contingency tables, which are specific to a particular resolution and delay, were used to estimate conditional probabilities for mutual information analysis.

To quantify mutual information between two variables, entropies of the two variables considered separately and considered together were computed. For example, to quantify the mutual information between the stimulus (*s*) and behavioral response (*b*), we first compute the entropy of stimulus $H(s)$ using the probabilities that motion pulse onset or motion noise was present, the entropy of behavioral response $H(b)$ by the probabilities of saccade onset or fixation, and the entropy of the whole system $H(s,b)$, by the two-dimensional (2-D) probability distribution of stimulus and response. Mutual information I between two variables defines how much uncertainty is reduced by simultaneous observation of the variables

$$I_{s,m} = H(s) + H(b) - H(s,b) \quad (2)$$

Thus in the previous example of mutual information between stimulus and eye movements at a resolution of 64 ms, mutual information values are derived for each of the 64 interval ranges. CIs and bias correction for all information rates were computed on the basis of sample size (Roulston 1999).

Mutual information surfaces between variables were constructed by varying the resolution at which events were tallied and the temporal interval between the variables (Supplementary Fig. S2).[1] To facilitate comparison across different temporal resolutions, information values were converted to an information rate by dividing by the resolution used to construct the contingency table. For each neuron, two mutual information surfaces were computed based on the correlations between neuronal activity and the stimulus (pulse or no-pulse) and between neuronal activity and behavior (saccade or no-saccade). Behavioral mutual information for each animal was acquired by compiling a contingency table using all recorded neurons between the stimulus (pulse or no-pulse) and behavior (saccade or no-saccade). Because information rates over these surfaces are largely separable with respect to delay and resolution, we extracted two 1-D curves of information versus delay and information versus resolution from each sheet that included the point of maximal reliability. Latency was defined by the center of the delay bin at which the peak was found. For example, if the peak reliability is found at a delay 100 ms at and a resolution of 64 ms, latency is defined by the center of the 100- to 163-ms bin, or 132 ms. Information rate as a function of temporal resolution was constructed by selecting information rates at this latency across the different temporal resolutions. Temporal precision was defined by an average of the temporal resolutions weighted by the information rates on this curve.

Because mutual information simply reflects correlations as measured by conditional probabilities, it does not provide insight about the causes of the correlations. Of particular concern for our study is the possibility that the statistical relationship, for example, between neuronal activity (*n*) and behavioral response (*b*), can be completely explained by the relationship between activity (*n*) and stimulus (*s*) and the relationship between stimulus (*s*) and behavioral response (*b*). For example, a "bottom-up" factor such as stimulus variability may cause variations in both neuronal and behavioral responses that cause the neuronal and behavioral responses to covary. To evaluate this possibility, we therefore computed the 2-D contingency table between activity and behavior expected according to the covariance of these variables with the stimulus, where all probabilities depend on the temporal interval between the observations. For example, if $p[n = i|s = j](t_1)$ describes the probability of observing *i* spikes at an interval t_1 after stimulus *j*, and $p[b = k|s = j](t_2)$ is the probability of observing the behavior *k* at an interval t_2 after the stimulus *j*, the probability of observing *i* spikes at an interval $t_2 - t_1$ before the behavioral response *k* solely caused by chance because of these relationships to stimulus *j* is the product of these two probabilities

$$p[n = i, b = k|s = j](t_2 - t_1) =$$
$$p[n = i|s = j](t_1)p[b = k|s = j](t_2) \quad (3)$$

and the total probability of observing *i* spikes before the behavioral response *k*, taking into account all possible stimuli is

$$p[n = i, b = k](t_2 - t_1) =$$
$$\sum_j p[n = i|s = j](t_1)p[b = k|s = j](t_2)p(s = j) \quad (4)$$

Note that for any given interval between activity and saccade, there is a range of intervals between activity and stimulus (t_1) that may be responsible. We therefore compute the mutual information from the chance derived contingency tables for each possible t_1 and choose the maximal value as an estimate of the highest mutual information that could be expected according to chance.

RESULTS

We trained two monkeys to detect the sudden and unpredictable appearance of a brief (60–83 ms) coherent motion signal, which we term a "motion pulse," preceded by up to 6 s of motion noise. (Fig. 1). Animals indicated their detection of

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[1] The online version of this article contains supplemental data.

this motion pulse by immediately making an eye movement to the location of the stimulus array. The task was challenging for both animals because of the brevity and unpredictable occurrence of the pulse; unlike a two alternative forced choice task design in which guessing results in 50% correct trials, chance performance in this reaction time limited detection task is close to zero. Performance varied little according to trial length with ~50% correct for both animals (trials less than mean duration: correct, 62%; false alarm, 28%; failure, 10% in *monkey P*; correct, 54%; false alarm, 30%; failure, 16% in *monkey B*; trials more than mean duration: correct, 53%; false alarm, 27%; failure, 20% in *monkey P*; correct, 48%; false alarm, 21%; failure, 31% in *monkey B*).

We recorded action potentials from isolated single neurons during the behavioral trials. We followed two procedures to maximize the chances that the neuron under study contributed to the animals' perceptual judgments. First, the animal was required to respond rapidly (within 550 ms of the motion pulse), thus minimizing the time between sensation and perceptual judgment and increasing the chances that low latency stimulus signals would affect behavioral choice (Seidemann et al. 1998). Second, the stimulus was centered on the receptive field of the neuron under study and configured according to the neuron's preferred direction of motion and receptive field size. These were the only optimizations done: for all neurons from the same animal, stimulation was identical with respect to the exact sequence of random motion as well as spatial and temporal frequency content. All neurons encountered in area MT were visually responsive to either the motion noise or

motion pulse stimulus. Here we present data from 62 cells (33, *monkey P*; 29, *monkey B*) for which >100 trials were recorded. We include neurons irrespective of the magnitude or reliability of their responses to the coherent motion pulse.

Both individual neurons and the neuronal population were influenced by sensory events and were predictive of the animals' choices (Fig. 3). Most neurons responded to the presentation of the motion pulse with a sharp low-latency increase in firing rate; on average, firing rate increased by a factor of 1.6 over the rates evoked by the motion noise. A broader and more gradual increase in firing rate preceded saccades to the stimulus. Notably, neuronal responses depended on both the stimulus and the animals' decision: stimulus-triggered responses varied according to the behavior that followed (correct detections vs. failures), and the choice-triggered activity varied according to the stimulus (correct detections vs. false alarms). The correlation of neuronal activity with both sensory input and behavioral outputs suggests the possible participation of these neurons in the animals' decision making (Romo et al. 2004; Shadlen and Newsome 2001). However, the interpretation of these averaged responses is limited in several respects. First, because these activity profiles were constructed by averaging over hundreds of stimulus presentations and saccades in the case of single neurons (Fig. 3A) and many thousands of events for the neuronal population (Fig. 3, B and C), they do not address whether the correlations between neuronal activity and the sensory and behavioral events are sufficiently reliable to explain behavioral performance on a trial-by-trial basis (Parker and Newsome 1998). Second, these analyses correlate
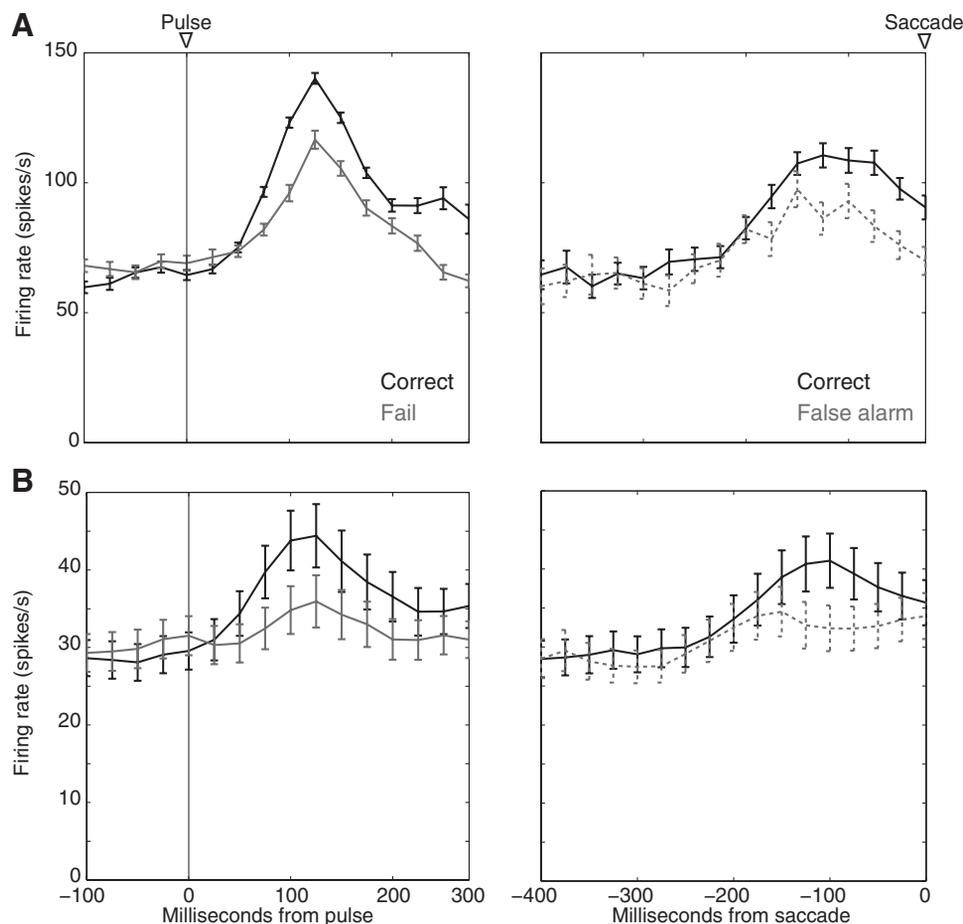

FIG. 3. Motion pulse-triggered and saccade-triggered neuronal responses. Spike trains were convolved with a 25-ms-width Gaussian; error bars are SE. Sensorimotor interactions were visible in an example neuron (*A*) consisting of 451 trials and the population of visually responsive neurons in the 2 monkeys (*B*; 62 cells). Population averages were constructing by averaging the responses from individual cells; error bars in *B* therefore reflect variability in firing rate across the neuronal population. Firing rate consistently increased shortly after the motion pulse (*left*), and the increase was correlated with behavior: peak firing rates were higher for correct detections (green) than for failures (red). An increase in activity preceded saccades (*right*), and the increase was correlated with the stimulus: peak firing rates were higher for correct detections (green) than for false alarms (purple).

averaged neuronal activity with task events known to the experimenter, but fail to take into account the biological problem faced by the animal: how accurately can neuronal activity on a moment-by-moment basis be used to identify the introduction of a behaviorally relevant signal or to initiate the requisite behavioral response (Rieke et al. 1997)? Third, the averages do not provide information on temporal precision and the time scales over which discharge is most reliably associated with sensory events or behavioral actions.

Behavioral and neuronal reliability

It is particularly important to consider these issues for behaviors in which timing is strongly constrained by short reaction times. We therefore require a metric that allows us to evaluate and compare the reliability of both neuronal activity and behavior over multiple time scales. Because conventional signal detection measures of discriminability such as receiver operator characteristic (ROC) analysis (Britten et al. 1992) are based on single sampling periods, they do not directly permit such a comparison. We therefore used information theory to compute the mutual information rate (bits/s) between behavioral response (saccade vs. fixation) and stimulus (coherent motion vs. noise) over a range of delays and temporal resolutions (Rogers et al. 2001) (Fig. 2A). With respect to behavior, this analysis incorporates the traditional measures of reaction time, which only examines the dynamics of correct choices, and performance, which only compares the number of correct choices with the number of failures and false alarms. It also incorporates correct rejections, in that the animals must maintain fixation during the entire period before pulse presentation for every trial. Finally, because it is based on changes in uncertainty, information theory is able to accommodate any biases in behavioral statistics caused by strategies or task designs. Our results show that both animals (*monkey P*, Fig. 4, A–C; *monkey B*, Fig. 4, D–F) made rapid decisions on the basis of information acquired over brief epochs of time: the corre-

lation between behavior and stimulus decreases when epochs of the order of hundreds of milliseconds are considered (Fig. 4, B and E). Behavioral information was maximal at a delay of 241 ms for *monkey P* (Fig. 4, A and C) and 281 ms for *monkey B* (Fig. 4, D and F), consistent with their mean reaction times (239 ms, *monkey P*; 282 ms, *monkey B*; Supplementary Fig. S1). Both animals had similar reliability (0.623 ± 0.004 bits/s, *monkey P*; 0.365 ± 0.007 bits/s, *monkey B*). Remarkably, the animals' responses indicated that they had significant sensory information even at a temporal resolution of milliseconds: half-maximal information spanned resolutions from 32 to 128 ms in both animals. To characterize the temporal precision of behavioral response into a single number, we computed an average of the computed resolutions weighted by information rate. By this analysis, both animals' responses had a precision of ~100 ms (81 ms, *monkey P*; 104 ms, *monkey B*). These results are consistent with a behavioral reverse correlation and reaction time analysis indicating that the animals based their decisions on stimulus filtering that was matched to the spatial and temporal extent of the coherent motion pulse (Ghose 2006).

To examine whether neurons in our sample could play a role in such rapid judgments, we quantified neuronal reliability in a manner directly analogous to the behavioral analysis (Fig. 2B). Mutual information between neuronal activity (spike counts) and stimulus (coherent motion vs. noise) irrespective of behavioral response was computed across all resolutions and delays (Supplementary Fig. S2). We term this mutual information measure sensory information. Similarly, we define choice information as the mutual information between neuronal activity and behavioral response (saccade vs. fixation) irrespective of stimulus (Fig. 2C). Because the position of spikes within a bin was not considered, the analysis measures the reliability of spike rate changes at a given temporal resolution with respect to sensory events or behavioral choices. Interpreting these reliability measures is potentially problematic because of the possibility that purely sensory responses temporally overlap with activity that is strictly associated with motor preparation
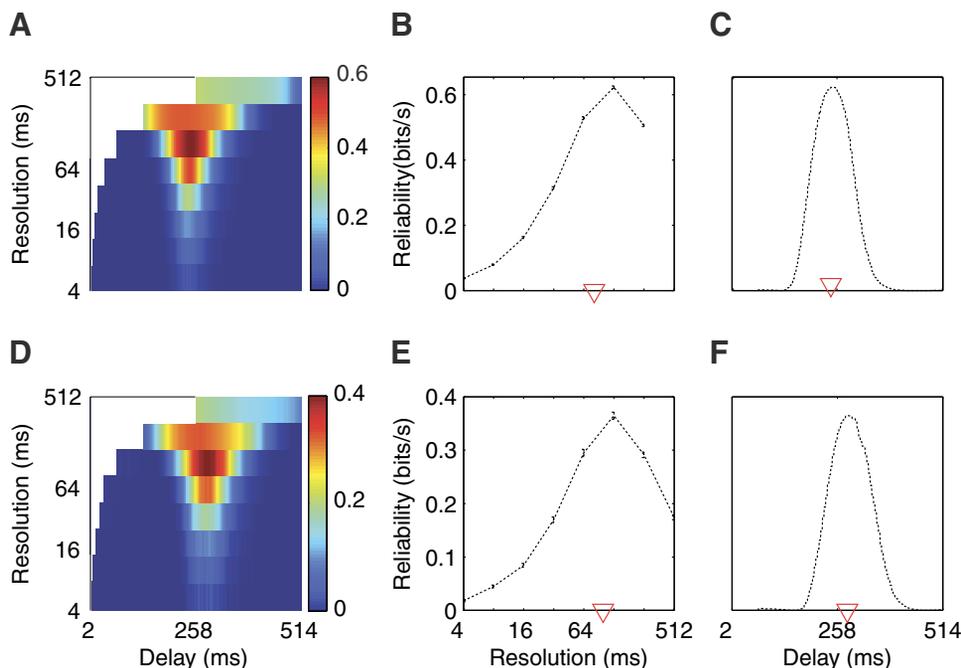

FIG. 4. Behavioral reliability, precision, and latency. Information rates averaged over all behavioral sessions for the 2 monkeys as a function of delay (linear scale) and resolution (log scale) (A–C, *monkey P*; D–F, *monkey B*). Because the delay resolution is defined by the temporal resolution, the width (delay, x-axis) of unique data points broadens with larger binwidths (resolution, y-axis). Dependence of information rate on resolution (B and E) and delay (C and F) is evaluated around the peak information point in the 2-dimensional plots (A and D). Behavioral latency is characterized by the center of the peak (red triangles, 241 ms, C; 281 ms, F). Information rate as a function of resolution (B and E) is obtained by selecting data at this peak delay (C and F). Temporal precision (red triangles, B and E) is computed by an average of the sampled resolutions weighted according to information rate. In both animals, this precision (81 ms, B; 104 ms, C) is slightly larger than the duration of the motion pulse, consistent with the notion that the animals used sensory information over an epoch of time appropriate for the behaviorally relevant stimulus.

(or vice versa) (DiCarlo and Maunsell 2005). The extent to which neuronal correlations with behavior can be explained by common neuronal and behavioral covariation with the stimulus has only been examined over time scales of hundreds of milliseconds or seconds by previous studies of perceptual decisions (Britten et al. 1993; Cook and Maunsell 2002). For example, imagine a highly stereotyped instinctive behavioral response, such as an eye blink to a puff of air. The activity of a purely sensory neuron would be well correlated with behavior simply by virtue of the consistent relationship between stimulus and behavioral response. In our behavioral data, because of the presence of failed and false alarm detections, the relationship between stimulus and behavior is less consistent, as is expected with a challenging perceptual judgment. However, even in such a situation, bottom-up modulations, such as those associated with attention, anticipation, stimulus variations, or eye movements, might simultaneously affect both physiological and behavioral responses to give rise to neuronal responses significantly correlated with behavioral choice by virtue of covariation.

To address this possibility, we examined the extent to which covariation between two variables, such as activity and the behavioral response, could be solely explained by the covariation of the variables with a third variable, such as the stimulus. The conditional probabilities between stimulus and behavioral response and between neuronal activity and the stimulus were used to estimate the probabilities between neuronal activity and behavioral response that could arise solely by chance. The mutual information derived from this chance estimate was subtracted from the mutual information directly computed from the contingency tables to yield a corrected information rate for each temporal resolution and delay. Any remaining information therefore indicates correlations that cannot be accounted for solely by covariances between other variables. A similar correction was applied to the sensory information by

taking into account the correlations between discharge and behavioral choice and stimulus and behavioral choice. These corrections were validated using synthetic datasets in which neuronal activity was solely correlated with the stimulus or solely correlated with the behavioral response (Supplementary Fig. S3).

Figure 5 shows corrected (black) and uncorrected (gray) information rates as a function of delay and resolution for the same example cell shown in Fig. 3A. For almost all values of delay and resolution, the covariance correction was negligible in this neuron: visible differences between the corrected and uncorrected information rates are only visible for choice information at the largest temporal resolution of 256 ms (Fig. 5E). Consistent with many of the sample neurons (Fig. 8A), neuronal activity predicted behavioral choice (Fig. 5, D–F; 0.22 ± 0.02 bit/s) almost as reliably as the nature of the preceding stimulus (Fig. 5, A–C; 0.41 ± 0.03 bit/s). Because of the corrections applied to account for covariance, this correlation to behavioral choice cannot solely be explained by covariation between sensory and behavioral responses. In contrast to results obtained with more steady-state stimulation (Kara et al. 2000), this neuron shows that reliability can actually decrease when larger epochs of time (>64 ms) are considered (Fig. 5, B and E), just as was observed for resolutions >128 ms in behavior (Fig. 4, B and E). Thus contrary to traditional assumptions, longer periods of temporal integration can actually reduce the reliability of task-relevant information. Given the average firing rates of this neuron (Fig. 3A), the presence of both sensory and choice information at a resolution on the order of interspike intervals implies that the presence or absence of individual action potentials (<6) was correlated with both the stimulus and the monkey's actions.

Although in this neuron, covariances could not explain the mutual information between neuronal response and behavioral choice, in many neurons, covariances made large contribu-
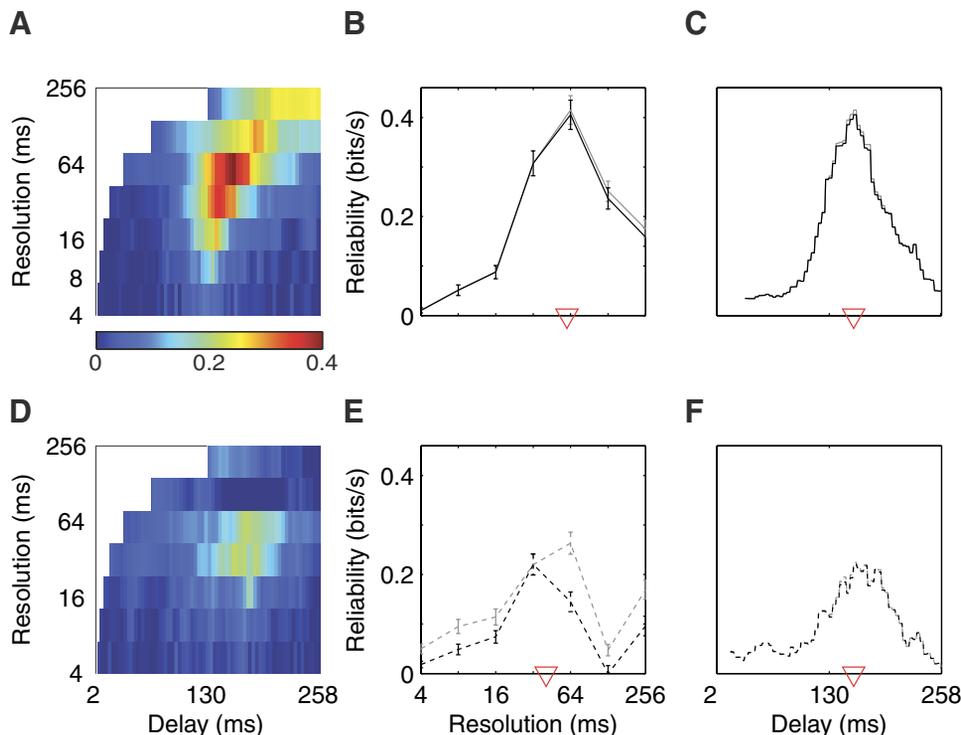

FIG. 5. Sensory (solid) and choice (dashed) information for the neuron of Fig. 3A. The neuron's discharge over time windows on the order of its average interspike interval (~17 ms) was informative about the both the stimulus (A) and the monkey's choices (B). Corrected information rates (black), which take into account covariances, are indistinguishable from uncorrected rates (gray) except at the largest resolution of 256 ms for choice information (E). Sensory and choice information in this neuron were comparable in reliability (0.41 and 0.22 bits/s), precision (47 and 34 ms), and latency (157 and 157 ms).

tions. This is shown in Fig. 6 for a neuron with similar precision and delays to the neuron shown in Fig. 5. Unlike the previous example, however, covariance corrections for this neuron have a large effect on information rates. This is especially true for the mutual information between neuronal response and behavioral choice, for which more than one half of the uncorrected information (Fig. 6*E,* gray) can be explained by the covariance of neuronal and behavioral choice with the stimulus. For all the following figures and results, only information rates after covariance correction are reported. Because covariations might also be occurring over the course of trials in a consistent manner, for all neurons in which information remained after covariance correction, we applied the covariation correction algorithm to data from the same epochs within each trial to verify the existence of nonzero information rates throughout the trial.

In these example neurons, the precision of correlations to stimulus and behavioral choice were very similar (Fig. 5, *B* vs. *E*). To illustrate the epochs over which sensory and choice information was present over our entire sample population, we plotted each neuron's covariance corrected reliability as a function of delay at 16-ms resolution and sorted the neurons according to the latency at which their information was maximal (Fig. 7, *A* and *B*). Information rate across delay was normalized according to the peak rate for each neuron. Sensory information was more consistent with regard to latency than choice information: most neurons exhibited peak sensory information at latencies between 100 and 150 ms (Fig. 7*A*), whereas a broad range of choice latencies was observed (Fig. 7*B*), consistent with the temporal distribution of premotor cortical signals associated with smooth pursuit (Schoppik et al. 2008). However, for both sensory and choice information, reliable information was remarkably transient: the width of nonzero information was seldom >48 ms across the sample population.

Stimulus and choice information in single neurons

To characterize the resolutions over which neurons provided information about the stimulus and behavioral choices, we analyzed how peak covariance corrected information rate over our neuronal population varied with precision (Fig. 7*C*). This analysis shows that the most reliable physiological signals of stimulus and behavioral choice have precisions that are centered between 32 and 64 ms. Thus circuitry in the brain is sufficiently precise to allow behavior to reflect information at the same temporal resolution (tens of milliseconds) as it emerges from the retina (Chichilnisky and Kalmar 2003). Moreover, the distributions of sensory and choice precisions are not significantly different (2-sample Kolmogorov-Smirnov). Because the distributions of sensory and choice precision are so similar, we conclude that temporal precision was largely maintained throughout the neuronal pathways between these neurons and the motor output associated with this task. There is also a significant correlation (0.29, $P = 0.02$) between sensory and choice precisions among neurons. This suggests that decisions are nearly optimal with regard to temporal integration: the temporal resolution at which neurons most reliably encode stimulus information is similar to the resolution over which they are sampled to give rise to behavior, and the neurons with the most precise sensory information also tend to be sampled the most precisely.

To test whether the cells that were most informative about the stimulus were also the most predictive about the behavioral response, we compared sensory and choice reliability on a cell by cell basis (Fig. 8). We used two metrics of reliability: a single threshold based measure of the discriminability of spike count distributions (ROC) and the covariance-corrected information rate analysis of those same distributions. For each neuron, we chose the spike count contingency tables (Fig. 2) associated with the peak information rate. For example, if peak sensory information was found at a resolution of 64 ms and a
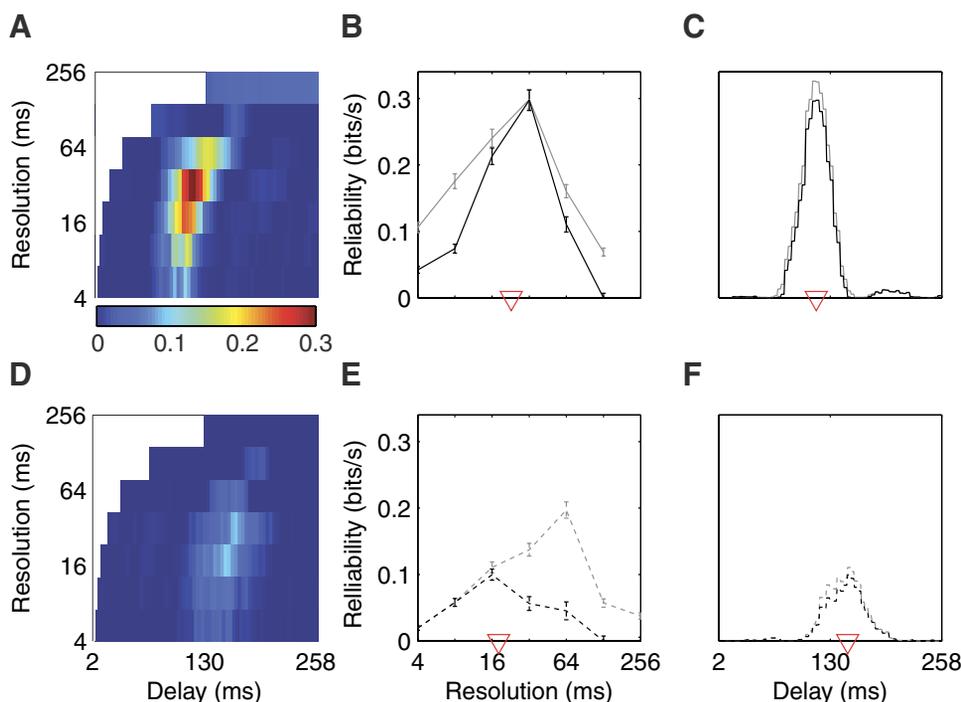
FIG. 6. Sensory (solid) and choice (dashed) information for another neuron. Format is the same as Fig. 5. Neuronal precisions (25 and 16 ms) and delays (117 and 149 ms) for both sensory and choice information are similar to those shown in Fig. 5. However, unlike the neuron of the previous figure, covariances are potentially responsible for a significant portion of the observed correlations between neuronal response and choice at resolutions from 32 to 256 ms. Information rates corrected by covariance (black) are significantly lower, especially for choice information, than uncorrected information rates (gray). After correction, neuronal responses are significantly more informative about the stimulus (0.30 bits/s) than the animal's choices (0.10 bits/).

A Sensory

0   128   256
Delay (ms)

B Choice

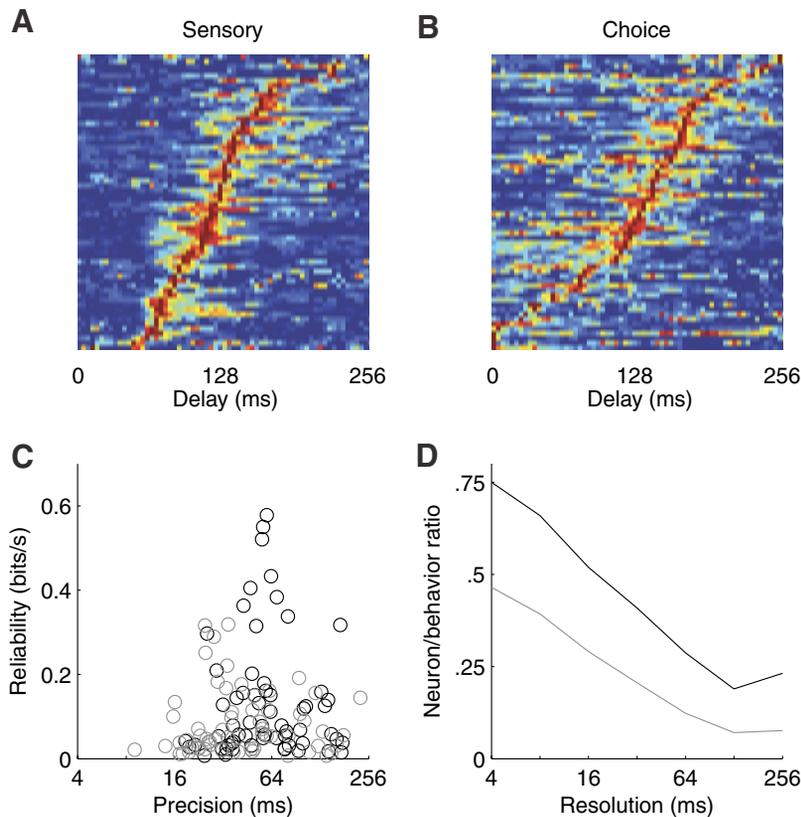0   128   256
Delay (ms)

C

D

FIG. 7. Temporal parameters of stimulus and choice information across the neuronal population (33 cells, *monkey B*; 29 cells, *monkey P*). All information rates have been covariance corrected. Surfaces indicate the distribution of normalized information curves across our sampled population with each neuron contributing a single row. Each neuron's sensory (*A*) and choice (*B*) reliability as a function of delay at a resolution of 16 ms was used to define a normalized curve. Curves were sorted according to the delay position of the peak. Although there were latency variations within our population sample, the narrowness of the red and yellow points describing peak information shows that most neurons were informative over brief periods of time (typically <32 ms). The most precise signals of both stimulus and behavioral choice typically had precisions between 32 and 64 ms (*C*). The ratio of neuronal sensory information to behavioral information varies according to temporal resolution in both animals (*monkey P*, gray line; *monkey B*, black line) (*D*). At the finest resolutions (4–16 ms), sensory reliability of individual neurons is comparable with behavioral reliability.

delay of 128 ms, the spike count distributions as a function of stimulus at that resolution and delay were compared. Because the same spike count distributions were used for the information rate and ROC analyses, the measures are significantly correlated (sensory: $r = 0.72$, $P \ll 0.001$; choice: $r = 0.61$, $P \ll 0.001$). However, there are several important issues

A
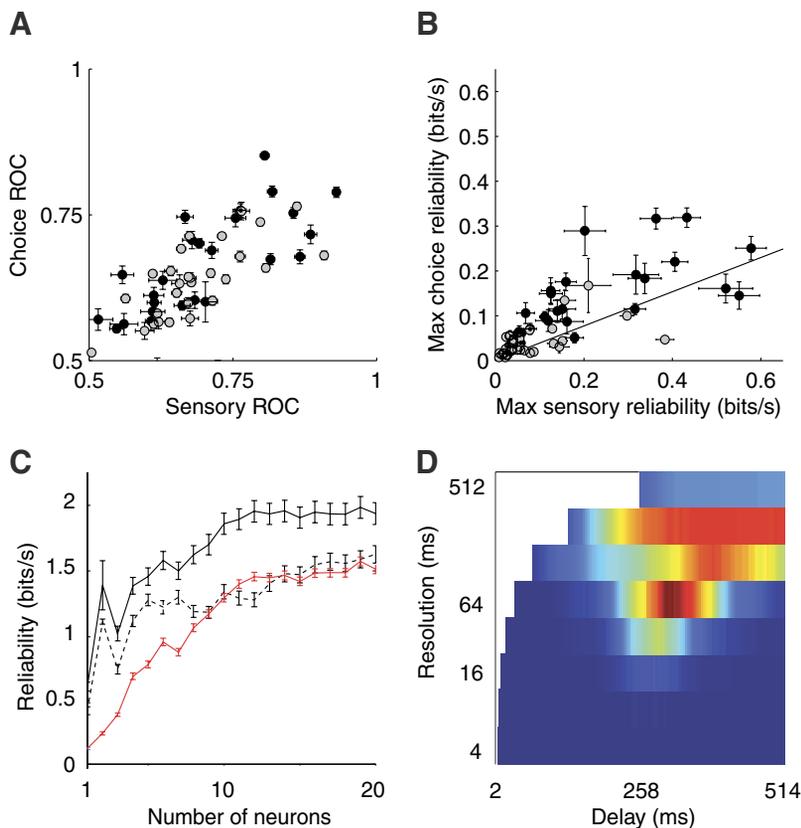

B

C

D

FIG. 8. Reliability of signals across the neuronal population and for a simple neuronal pooling model. Error bars indicate SE. Sensory and choice reliability was significantly above chance according to ROC (*A*) and covariance-corrected information rate (*B*) analysis for most neurons (black dots, *monkey P*; gray dots, *monkey B*; 8 outliers omitted in *A*). For each neuron, the analyses were based on the same contingency table, as defined by the resolution and delay at which the information rate was maximal (Supplemental Fig. S2). Sensory and choice reliability were well correlated in both measures ($r = 0.59$, *A*; $r = 0.83$, *B*), indicating that the most reliable sensory signals were also the most predictive of behavioral choice. The regression line in *B* indicates that a linear model in which a neuron's influence on behavior is directly proportional to its stimulus reliability provides a good explanation of our data. To test a simple pooling model, the 20 most informative neurons from *B*, with regard to the stimulus content (solid), behavioral choice (dashed), and predicted behavioral performance (red), were considered (*C*). In this model, the inputs from independent neurons are linearly summed before readout. Both sensory (solid) and choice (dashed) information increase with small numbers of neurons. Predicted reliability if behavior was solely based on the pool (red) also saturates quickly with neuronal pool size, and a pool size of between 4 and 6 neurons is able to completely explain observed behavioral reliability (Fig. 4). The dependence of this predicted behavioral reliability on resolution and delay for 5 neurons closely mimics the dependence seen in our observations (Fig. 4, *A* and *D*).

regarding precision and reliability that cannot be readily addressed with ROC analysis but can be with information theory. First, information theory allows for a comparison across different temporal resolutions because it quantifies reliability in terms of rate, as opposed to a resolution dependent probability. Although ROC analysis can be applied using a variety of sampling intervals, it is not clear how to compare the results from different samplings. For example, it is not clear how to compare a ROC value of 0.54 with 16-ms sampling to a ROC value of 0.52 with 8-ms sampling. Similarly, it is difficult to compare neuronal and behavioral reliability with ROC analysis. Although the ratio of neuronal and behavioral information rates can be used to infer the number of independent neurons sufficient to explain behavior, no such algorithm can be readily applied to ROC measurements. As described previously, information rate, unlike ROC analysis, provides a means to correct for the covariances present in any task in which sensory and choice related signals potentially overlap (Fig. 6). Finally, information theory is readily extensible to higher dimensions and numbers of states, unlike ROC, which is restricted to comparisons between pairs of distributions.

According to ROC analysis (Fig. 8*A*), most neurons' activity was significantly correlated with both the presence of a motion pulse (mean = 0.67) and the execution of a saccade (mean = 0.64). This is larger than the values typically reported in motion discrimination tasks (Britten et al. 1996) (~0.54) and similar to the value reported for a perceptually bistable motion stimulus (Dodd et al. 2001) (0.67). Similarly, most covariance corrected information rates (Fig. 8*B*) were significantly positive (sensory mean = 0.13 and choice mean = 0.08) and, on average, choice information rates were 0.79 as large as sensory information rates. The common occurrence of activity correlated with behavioral choice is consistent with the example neuron shown in Fig. 5 but is in contrast to previous studies of MT neurons (Cook and Maunsell 2002; Majaj et al. 2007; Mazurek et al. 2003), which have found modest choice-related signals and large modulations with sensory variations in random dot motion tasks. Finally, according to both the ROC (*r* = 0.59, *P* ≪ 0.001) and information rate (*r* = 0.77, *P* ≪ 0.001) analyses, neurons that conveyed the most information about the stimulus also tended to be the most predictive of behavioral choice. The high correlation seen between information rates shows that a linear regression model, in which behavioral choice reliability is proportional to sensory reliability, provides a good model of our data (choice = 0.38 ± 0.04 × sensory + 0.001 ± 0.0002 bit/s; Fig. 8*B*).

Our data suggest that the most informative neurons could largely explain behavioral reliability in this task, unlike previous studies that, by virtue of the relatively weak relationship between discharge and behavioral choice (e.g., low values of choice probability), have required the pooling of signals from hundreds or thousands of cortical neurons to explain behavioral performance (Britten et al. 1996; Mazurek et al. 2003). Because our stimulus is likely to evoke activity in a similarly broad population of neurons, we wished to examine how information might change as greater numbers of neurons are considered using a simple pooling model that has been invoked in previous studies of motion discrimination (Britten et al. 1996; Mazurek et al. 2003). In this model, behavioral choices are based on the decoding of activity summed across a range of sensory neurons. To implement this model, we constructed synthetic contingency tables in which the spike counts from subpopulations within our sample were combined in a resolution- and delay-specific manner. Because we compute reliability across all resolutions and delays, we can test whether the model is able to predict the entire dependency of behavioral reliability on resolution and delay observed in our data (Fig. 4). Neurons whose firing increased the most reliably after pulse presentation were included in these subpopulations. This table describes the input statistics of a hypothetical neuron at a subsequent stage of processing that receives equal input from independent MT neurons. These contingency tables were used to evaluate sensory mutual information as a function of temporal resolution and delay (Fig. 2), and a peak information value was extracted. The method was therefore exactly analogous to the procedure applied to individual neurons. Because the most reliable neurons were able to explain behavioral reliability, we examined how this peak information in the hypothetical neuron was affected by the inclusion of progressively less reliable input neurons. We examined three reliability measures: sensory (solid) and choice (dashed) information of the hypothetical neuron and the covariance of these two measures (Fig. 8*C*, red). The latter covariance allows us to assess what behavioral performance would be if the relationship between stimulus and behavioral response were solely defined by the activity correlations of the hypothetical neuron. This covariance measure therefore incorporates both encoding and decoding reliability to predict behavior. We find that all three measures of reliability increase rapidly with small numbers of neurons and saturate with a pool size of about five neurons. The covariance calculation shows that this small number of neurons is completely capable of explaining behavioral reliability (0.3–0.45 bit/s; Fig. 4). Moreover, the information surfaces produced by this covariance calculation mimic not only the peak information rate seen in behavioral data but also its location in terms of delay and resolution (Fig. 8*D* vs. 4, *A* and *D*). For this model, variations in neuronal latencies (delays in sensory information) among the neuronal sample have a modest effect: when latency variations are eliminated, maximum reliability saturates at higher value, but a small number of neurons (<5) is still capable of explaining behavioral reliability.

DISCUSSION

In this study, we examined the behavioral and physiological precision and timing associated with the detection of a briefly presented motion stimulus. We found that animals sample perceptual information over epochs of time on the order of tens of milliseconds and that the discharge of individual neurons in MT is maximally informative about the occurrence of coherent motion over the same time scales. Moreover, activity over the same time scales in individual neurons is also well correlated with behavioral choice. The reliable correlation of brief epochs of neuronal activity from single neurons to both sensory information and behavioral choices suggests that temporally precise decisions do not require extensive pooling of neuronal signals over neurons and time.

The observed correlations of neuronal activity with sensory events and behavioral choices may reflect global modulations in sensory attention or motor intention but not actual participation in the decision making process (Krug 2004). Several

observations suggest otherwise. First, these correlations cannot be explained by simple covariation because of our covariance correction procedure. Second, for cells participating in the decision process, the sum of the intervals between maximal sensory information and maximal choice information should correspond with the delays over which behavioral information is high. No such constraint exists for cells that convey sensory information that is behaviorally irrelevant or choice information that is unrelated to sensation. In our sample, the sum of the delays for maximal neuronal stimulus and maximal choice information (Fig. 7, *A* and *B*; resolution = 16 ms) was within 100 ms of the latency of maximal behavioral information (Fig. 4, *C* and *F*) for 57 of 62 recording sessions. Third, a purely motor corollary should have increased information for activity immediately preceding the saccade. Although a few cells within our population display such premotor information (as might be expected from saccadic suppression; Burr et al. 1999), for most cells, choice information was negligible immediately before the saccade and peaked from 100 to 300 ms before the saccade (Fig. 7B). This interval is consistent with motor delays predicted in a previous reaction time study of motion detection (Cook and Maunsell 2002). Fourth, the strong correlation between sensory and choice reliability suggests that the best sensory signals were the most predictive of the animals' choices (Fig. 8, *A* and *B*), consistent with these signals' participation in the decision process.

Our information rates are considerably lower than have been reported by analyses that solely take into account the diversity of neuronal responses to dynamic stimulation (Buracas et al. 1998; Reinagel and Reid 2002). In this regard, it is important to realize that a mutual information rate between any two variables necessarily depends on the manner in which the variables are classified. In particular, we have classified both eye velocity and the stimulus into two states and neuronal activity according to spike count. With such a classification, the highest possible information that an animal or neuron could convey about the stimulus or eye velocity is 1 bit for every temporal window (or rates of 2 bit/s for a window of 500 ms, 10 bits/s for 100 ms). However, an infinite variety of classifications could be applied to our variables of observation. For example, our stimulus could be parametrized according to the individual phase transitions of each Gabor element (31×2 values per frame), the actual phase values of each Gabor (31×4 values per frame), or, in the extreme case, the actual luminance values of each pixel used to construct the stimulus. Neuronal discharge in our experiments unquestionably carried more information about the stimulus than simply the presence or absence of coherent motion: reverse correlation of neuronal responses to motion noise sequences revealed directional selectivities that are specific to particular spatial patches. Our parameterization of both the stimulus, in terms of the occurrence of the motion pulse, and behavioral response, in terms of the beginning of an appropriate saccade, was dictated by the behavioral design: we required the animal to signal as quickly as possible the occurrence of the motion pulse with an appropriate saccade. Therefore the behaviorally relevant information metric should examine the statistical relationship between pulse and saccade onsets. Similarly, our neuronal information metric reflects spike count in relation to pulse and saccade onsets. This is notably different from previous applications of information theory to neuronal discharge which have focused on how accurately

neuronal discharge could represent the complete time course of stimulus variation. In contrast, we constructed an analysis based on the potential of neuronal activity to encode task-relevant stimulus information and to reflect task-relevant behavior. Our choice of stimulus description was not a principled choice based on the response selectivities of the neuron under study and therefore our information rate grossly underestimates the potential encoding capabilities of MT neurons. Rather, our stimulus description was dictated by behavioral relevance so as to enable a direct comparison between neuronal and behavioral reliability by describing a conservative and consistent lower bound for behavioral and neuronal information rates.

It is worth considering the potential influence of several specific factors that could affect both behavioral and neuronal responses and are not accounted for in our variable classifications. As already mentioned, we simplified our description of the stimulus to a single dimension with two states. However, within the noise sequence, brief epochs have a majority of Gabors traveling in the relevant direction and therefore influence both neuronal discharge and behavioral responses, as assessed by reverse correlation methods. The strongest effect such variations could cause would be a change in the contingency table equivalent to small number of motion pulse stimulus bins being incorrectly classified as noise. By changing the designation of some bins from noise to pulse, stimulus-related differences in behavioral response probability, and therefore the mutual information between stimulus and behavioral response, would necessarily increase. In this sense, to the extent that we simplified the description of the stimulus to a two-state variable, we underestimated both behavioral and physiological information rates. Similar arguments apply to eye movements which we simplified to a two-state variable as well. Microsaccades might have occurred that were related to variations in the noise and could affected discharge, but incorporating such instances can only increase the mutual information between stimulus and behavior response and MT activity and behavioral response. The only possible result of a factor that has been ignored in our analysis is therefore either no change or an increase in mutual information rates. Finally, with regard to neuronal activity, we assumed the simplest possible quantification of spike count within a bin and ignored the possibility that particular temporal patterns of spikes within a bin are informative. Therefore all information rates in this study should be considered as a lower bound based on minimal assumptions regarding our variables of observation.

These factors could also have an effect on our covariance calculations. For example, the presence of presaccadic activity in neurons and saccades in the animal even when no pulse was presented (Fig. 3) may be caused by the random occurrence of brief strong motion signals within the noise sequence. Reverse correlation methods showed that such noise fluctuations can evoke both discharge and behavioral responses. To account for such possibilities, we reanalyzed our data according to a four-state classification for both the stimulus and eye velocity. For the stimulus, motion noise within a bin was classed into one of three states according to the large global motion signal present between adjacent frames. This global motion signal was computed by summing across all Gabors within the array, with movement in the preferred direction encoded as +1 and movement in the opposite direction as −1. The fourth state in the stimulus was, as in the previous two state analysis, assigned

to motion pulse onsets. For eye velocity, maximal eye velocity within a bin was classed into one of three states to allow for a separate treatment of microsaccades from periods of relatively steady fixation, and the fourth state was reserved for saccades to the stimulus target. These modifications resulted in very modest changes in information rate and the computed covariance correction compared with the results in the original two-state classification of stimulus and behavior.

Over our population, the average neuronal sensory information rate (0.11 bit/s) was comparable with the animals' behavioral information rates (Fig. 4). This is consistent with previous studies of neuronal and behavioral sensitivity using weak motion stimuli and analyzing neuronal and behavioral responses over much larger time scales (on the order of seconds) (Britten and Newsome 1998; Prince et al. 2000; Tolhurst et al. 1983; Uka and DeAngelis 2003). In both animals of our study, the discharge over tens of milliseconds from small numbers (2–3) of independent neurons is sufficient to explain behavioral performance. However, our data showed that the ability of individual neurons to explain behavior depends on the temporal resolution under consideration: neurons in our sample were the most capable of explaining behavioral performance at the finest time scales (Fig. 7D). This suggests the possibility that, for large time scales on the order of hundreds of milliseconds, neurons outside of MT might preferentially contribute to the perceptual judgment. In particular, individual neurons in other cortical areas, such as medial superior temporal (MST) (Celebrini and Newsome 1994), lateral intraparietal (LIP) (Huk and Shadlen 2005), ventral intraparietal (VIP) (Cook and Maunsell 2002), and dorsolateral prefrontal (Kim and Shadlen 1999), with substantially longer sensory integration windows, might be more capable of explaining performance over longer time scales. If perceptual decisions are preferentially based on those neurons with the most appropriate temporal filtering for the stimulus, this also might explain why the choice correlations in our sample are significantly larger than would be expected from previous studies, which have used stimuli requiring extensive temporal integration.

Pooling of neuronal signals

The distribution of sensory and choice precisions and delays, the mean strength of choice information, and the correlation of choice information and sensory information on a cell-by-cell basis are all suggestive of limited pooling over both neurons and time. Previous models have suggested that coarse motion discrimination or detection decisions are based on the accumulated activity from a broad population of MT neurons (>100) integrated over hundreds of milliseconds (Cook and Maunsell 2002; Huk and Shadlen 2005; Mazurek et al. 2003; Shadlen et al. 1996). These numbers were required in previous studies because the relationship of individual neurons to choice was low and uncorrelated with neuronal sensitivity. In contrast, the high choice correlations and consistent relationship between sensory and choice reliability in our data suggest that perceptual judgments may be based on the activity of individual neurons over tens of milliseconds. In particular, the regression model (Fig. 8B) of the relationship between sensory and choice reliability suggests that those neurons with no information concerning the stimulus were not sampled at all by the animal (*y*-intercept ∼ 0).

A realistic physiological model must be able to replicate not only the peak reliability seen in behavior (Fig. 4), but also how that reliability depends of delay and resolution. For example, if a neuron or neuronal pool provides reliable sensory information on a timescale of 64 ms, but reliable choice information only on a scale of 128 ms, it cannot subserve reliable behavior on the timescale of 64 ms. Previous models and experiments have not addressed this critical issue. In this regard, the pooling analysis shown in Fig. 8 is particularly valuable. It shows that small number of neurons are not only able to predict peak behavioral reliability but also how behavioral reliability varies over time and temporal resolution. Moreover, unlike previous examinations of potential neuronal pool sizes (Cook and Maunsell 2002; Shadlen et al. 1996), this model does not make any assumptions regarding pooling noise or filtering: both encoding and decoding are completely derived from experimental observations and, for a given set of neurons, there are no free parameters.

Our task design may be responsible for this more limited pooling. Our task is a motion detection (essentially discrimination of signal from noise), whereas previous studies have relied on direction discrimination. The requisite pooling and integration of motion signals may be different, just as there are likely differences between coarse and fine motion discrimination (Purushothaman and Bradley 2005). Another difference between our design and previous ones is that, although the appearance of our stimulus (the motion pulse) was uncertain, the nature of the pulse in terms of its coherence and direction could be readily anticipated by the animals because it was held constant for the 30- to 60-min periods during which we recorded from individual neurons. Although psychophysical analysis showed that the animals were preferentially sampling a particular direction of motion (Ghose 2006), the effect on such strategies on neuronal reliability remains to be established and is currently a subject of investigation in our laboratory.

Stimulus differences may also be responsible for the limited spatial and temporal pooling suggested by our data. Our stimulus was composed of high contrast patches that might be better matched to the selectivities of particular individual neurons than the flickering random dot stimulation used in previous studies (Barlow and Tripathy 1997). Furthermore, whereas the strength of motion signals in the random dot stimuli used in previous studies was weak and relatively constant over time, our stimulus contained transient periods of highly coherent motion capable of evoking reliable discharge (Buracas et al. 1998). Both of these stimulus differences suggest that, in our paradigm, individual MT neurons may be far more capable of providing task relevant information over short epochs of time and that the neuronal pooling underlying decision making may be highly dependent on the nature of the stimulus. For example, if a stimulus evokes no reliable signal in any particular cell at any particular time, such as might be the case with low coherence random dot stimulation, detection decisions might necessarily rely on considerable integration (Gold and Shadlen 2003; Watamaniuk and Sekuler 1992). Moreover, if decisions are based on the most appropriate neurons (Olshausen and Field 2004) and if neurons in different areas have different receptive field properties, the designation of an area as "sensory" or "sensory-motor" is in large part stimulus dependent. In this scheme, the labeling of area MT as a largely "sensory" area by numerous studies might simply

reflect the use of motion stimuli, unlike those in this study, that require extensive temporal integration.

The strong correlation between sensory and choice reliability (Fig. 8B) as well as the ability of small number of neurons to explain behavioral reliability (Fig. 8, C and D) suggests that detection could be preferentially based on the most reliable signals (Purushothaman and Bradley 2005). However, another possibility is that there are significant correlations between the activity of different neurons that can be used to infer stimulus information (Romo et al. 2003). Although correlated activity between MT neurons responding to random dot motion seems to be stimulus independent over a variety of time scales (Bair et al. 2001), it is unclear whether neuronal responses to stimuli such as ours, which include brief epochs of coherent motion, show the same properties. For example, it is possible that neuronal latencies are consistent enough (Figs. 3A and 7A) for a brief coherent signal to produce highly correlated activity within a narrow time window (Thorpe et al. 2001). However, even if such correlation exists, it might only exist at a temporal resolution too coarse to be involved in the perceptual judgment (Panzeri et al. 1999). Resolving this issue will therefore require further experiments in which multiple neurons are simultaneously recorded during the task.

Our data allow us to examine how perceptual judgments may be optimized with respect to temporal properties of particular neurons: decisions based on these neurons should rely on activity over a time scale in which stimulus information is maximal. In such a situation, the temporal resolution of sensory information and choice information in participant neurons should be similar. Figure 7 confirms this relationship and shows the epochs and time scales that are the most informative about the stimulus are also the most predictive of behavioral choice. Combined with the correlations shown in Fig. 8, our data suggest that cognitive decisions may be highly optimized with regard to both space and time in that they can be based on the most informative epochs of activity from the most informative neurons. One question that remains to be resolved is whether this precision is an inherent property of the activity evoked by our stimulus, or whether, as suggested by psychophysical evidence (Ghose 2006), it develops as a consequence of training. Independent of its origins, the correlation of brief epochs of activity with both sensory events and behavioral actions implies a remarkable level of neuronal precision in which decisions can be based on a small number of action potentials from a small number of neurons.

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