Population coding in area V4 during rapid shape detections

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Submitted 23 December 2014; accepted in final form 17 March 2015

Population coding in area V4 during rapid shape detections. J Neurophysiol 113: 3021–3034, 2015. First published March 18, 2015; doi:10.1152/jn.01044.2014.—While previous studies have suggested that neuronal correlations are common in visual cortex over a range of timescales, the effect of correlations on rapid visually based decisions has received little attention. We trained *Macaca mulatta* to saccade to a peripherally presented shape embedded in dynamic noise as soon as the shape appeared. While the monkeys performed the task, we recorded from neuronal populations (5–29 cells) using a microelectrode array implanted in area V4, a visual area thought to be involved in form perception. While modest correlations were present between cells during visual stimulation, their magnitude did not change significantly subsequent to the appearance of a shape. We quantified the reliability and temporal precision with which neuronal populations signaled the appearance of the shape and predicted the animals’ choices using mutual information analyses. To study the impact of correlations, we shuffled the activity from each cell across observations while retaining stimulus-dependent modulations in firing rate. We found that removing correlations by shuffling across trials minimally affected the reliability or timing with which pairs, or larger groups of cells, signaled the presence of a shape. To assess the downstream impact of correlations, we also studied how shuffling affected the ability of V4 populations to predict behavioral choices. Surprisingly, shuffling created a modest increase in the accuracy of such predictions, suggesting that the reliability of downstream neurons is slightly compromised by activity correlations. Our findings are consistent with neuronal correlations having a minimal effect on the reliability and timing of rapid perceptual decisions.

decision making; saccades; reaction time; reliability; synchrony

Many studies have shown that the activity of cortical neurons is correlated on a variety of timescales (Bair et al. 2001; Smith and Kohn 2008; Mitchell et al. 2009; Smith and Sommer 2013). However, while human and other primates visually explore the world, they move their eyes several times a second, strongly constraining the timescales over which correlations may contribute to stimulus representation (Einhäuser et al. 2006). The effect of correlations in the context of rapid vision, when timescales of behavioral relevance are strongly constrained, remains controversial.

Correlations between cells coactivated by a single object might aid in binding disparate representations into a cohesive percept (Milner 1974; von der Malsburg 1981). This may be particularly relevant in rapid vision because, following fixation at a new location, significant synchronization precedes changes in firing rates (Maldonado et al. 2008). However, if visual stimuli are represented by the average firing rates of populations of noisy neurons, correlations may hinder stimulus representation because averaging across correlated neurons cannot compensate for response variability (Britten et al. 1992; Zohary et al. 1994; Mazurek and Shadlen 2002). Such a detrimental effect may be particularly evident in rapid decisions, because downstream neurons are unable to average over long periods of time to ameliorate the effects of transient correlations.

To study the impact of neuronal correlation on rapid visual processing, we trained two monkeys to detect the brief appearance of shape outlines within an otherwise noisy stimulus. While the monkeys performed this task, we recorded from a multielectrode array in area V4, a visual area implicated in tasks involving form perception (Pasupathy and Connor 2001; Pan et al. 2012; Chen et al. 2014). Because of the relatively large number of simultaneously recorded neurons (5–29), we were able to not only examine correlations between pairs of neurons but also how higher order correlations might affect neural signals relevant to rapid shape detection. This is particularly important because correlations may have a greater impact on the encoding of larger populations than is apparent from pairwise correlations (Schneidman et al. 2006; Averbeck and Lee 2006).

We found no evidence of stimulus-dependent synchrony between pairs of neurons when the shape stimulus was present. However, we did observe weak pairwise correlations throughout the period of stimulus presentation, consistent with a broad tendency for neurons to fire together. To assess the impact of these weak correlations on coding, we applied a mutual information (MI) analysis to examine the reliability and precision with which simultaneously recorded neurons signaled shape appearance and predicted the animals’ subsequent actions. To assess the relevance of precise spike timing to information coding, we repeated this analysis with shuffled activity, in which rate modulations were preserved but exact timing was not. We found the ability of these shuffled populations to signal shape appearance was comparable to the ability seen with populations containing physiological correlations. Because our V4 populations were predictive of behavioral choices, we could use a similar technique to evaluate the effect of correlations on downstream structures that mediate the relationship between V4 and the saccade decision. We found that shuffling resulted in a slight increase in the ability to use V4 activity to predict behavior choices. Our results suggest that, in the context of rapid shape detection, the impact of correlations on stimulus representation in area V4 over populations of tens of neurons is negligible but that correlations do have a slight impact on other populations involved in the detection decision.

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www.jn.org 0022-3077/15 Copyright © 2015 the American Physiological Society 3021
MATERIALS AND METHODS

Ethics statement and surgical procedures. All procedures involving animals conformed to guidelines established by the National Institutes of Health and were approved by the Institutional Animal Care and Use Committee of the University of Minnesota. Animals were initially anesthetized with ketamine and anesthesia was maintained with isoflurane throughout all surgical procedures. Analgesics and antibiotics were administered during and following all surgeries to minimize discomfort and prevent infection. To stabilize head position during training and recording sessions, headposts (titanium or PEEK polymer) were chronically implanted under sterile surgical conditions. Once each animal was trained on the shape detection task, a 10 × 10 electrode array (Blackrock Microsystems) was chronically implanted in area V4 on the prelunate sulcus, again under sterile conditions. The data presented here was also used in a study of single unit responses (Weiner and Ghose 2014).

Task. We trained two male monkeys (Maccaca mulatta, ~7 and 13 kg) in a challenging shape detection task. Eye position was monitored by an infrared eye tracker (Arrington Research). Each trial began with the appearance of a fixation dot on a gray background. After a variable period of time (10–1,270 ms), a noise stimulus, consisting of randomly oriented Gabors, was presented at a more peripheral location. The noise stimulus was randomly varied between trials, such that the same series of noise stimulus frames was likely never presented more than once. The animals were required to maintain fixation until an enclosed shape briefly (monkey Z: 83 ms and monkey M: 120 ms) appeared, embedded in the noise. Animals were required to signal their detection of the shape by making an eye movement to the stimulus array within the reaction time window (150–550 ms) to receive a juice reward. The shape was presented at a higher contrast than the noise during initial training, and, as training progressed, the contrast of a surrounding noise stimulus was gradually increased. During recording sessions, elements of the noise and shape stimuli appeared at the same contrast, ensuring that no low-level cue was associated with shape appearance. Approximately 5% of trials were catch trials in which no shape appeared and the animals were required to maintain fixation until the trial ended. All trials ended immediately, without reward, if the animal broke fixation before a shape appeared. Both shape identity and timing of presentation were randomly determined for each trial. Presentation times were drawn from an exponential distribution, with means set at 500 ms for monkey Z and 1,000 ms for monkey J. Because false alarms were frequent, the mean of this distribution ended up slightly shifted towards earlier times (actual mean time to shape appearance was monkey Z: 460 ms and monkey J: 970 ms). The exponential distribution was intended to encourage the animals to maintain a high level of vigilance throughout the trials (Ghose 2006).

Visual stimulation. Visual stimuli were delivered on an LCD monitor (120 Hz). A photodiode affixed to the screen confirmed the timing of stimulus presentation. The noise stimulus consisted of a 7 × 7 array of achromatic Gabors whose orientation varied independently between one of eight different values. This stimulus array was positioned to overlap with the receptive fields of recorded cells; it was centered at an eccentricity of 3.75° (azimuth: 3.75°, elevation: 0.2°) for monkey Z and an eccentricity of 5.5° (azimuth: −2.5°, elevation: −4°) for monkey J. In both animals, the radius of each Gabor element was 0.38°, resulting in receptive fields containing 16–25 elements (Gattass et al. 1988; Motter 2009). The spatial frequency was 2°/cycle, and during recording, all Gabors appeared at 45–50% contrast.

Static noise frames (Fig. 1C, red stimulus) were redrawn randomly at the beginning of each trial but not varied within a trial; in dynamic noise frames (Fig. 1C, grey stimulus), the random pattern varied between successive presentations. These static and dynamic noise frames were interleaved within a trial to prevent the animals from using motion cues to detect shape appearance. When the shape appeared (Fig. 1C, black stimulus), it was embedded within the static noise stimulus. The shapes to be detected were defined by 16–19 Gabor patches spatially aligned and oriented so as to form a contiguous contour. Three different shape stimuli were used. Monkey Z was presented with these shapes at four different orientations (for a total of 12 shape stimuli). Only one orientation of each shape was presented to monkey J. Both animals were trained to report the appearance of any shape.

Behavioral information. To quantify the moment to moment reliability of shape detection, we used a MI analysis (Ghose and Harrison 2009; Harrison et al. 2013; Weiner and Ghose 2014) to quantify the reduction in uncertainty about one task variable given knowledge of another task variable. For the case of behavior, the two relevant variables are the state of the stimulus (noise vs. shape) and the state of eye movement (fixation vs. saccade).

Electrophysiology. Once the animals were trained to perform the task in the absence of any contrast differences between shape and background noise, a 10 × 10 microelectrode array (400-µm spacing, 1-mm length, injected with a 1-mm pneumatic inserter; Blackrock Microsystems) was chronically implanted in visual area V4 on the prelunate gyrus, slightly above the tip of the inferior occipital sulcus. Both the superior temporal and lunate sulci were visible during surgery. Spike times and waveforms were recorded as the animals performed the task and then sorted offline using the Waveclus toolbox (Quiroga et al. 2004).

The results presented here include data from 9 recording sessions with monkey Z and 11 sessions with monkey J. Each of these sessions had at least 375 trials in which the monkey maintained fixation until a saccade was made to the stimulus location or the trial ended. For a unit to be included in the analysis, it had to meet the following criteria: 1) the signal to noise ratio of the waveform had to be at least 2.2; 2) the average firing rate during noise stimulus presentation had to be at least 5 spikes/s; and 3) the units had to be visuallv responsive, defined as having a significantly greater response during the first 50–250 ms of noise stimulus than in the preceding 200 ms, as determined by a Wilcoxon signed-rank test (P < 0.05). Units with fewer than 0.75% of their spikes occurring within an interspike interval of 2 ms were considered to be single units. Only single units were included in the pairwise correlation analyses. Both single- and multiunits were included in the weighted population sum analyses.

Because of the chronic positioning of the microelectrode array, it often seemed that the same units were present during multiple recording sessions. To avoid overrepresenting these units in the pairwise analysis, we considered pairs of electrodes only once. When the same pair of electrodes contained units across multiple days, the pair contributed units to the presented data only from the recording session with the highest number of trials, resulting in the best sampling of pairwise statistics. This resulted in 336 pairs of single units (237 from monkey Z and 99 from monkey J).

Pairwise correlations. The strength of pairwise correlations was characterized by cross-correlograms (CCGs) using standard methods (Bair et al. 2001; Kohn and Smith 2005). The average number of coincident spikes per trial at each time lag was normalized by the product of the geometric mean of the individual units’ firing rates and a triangular function that compensated for reduced observations with increased lag, due to the size of our analysis windows. A shift predictor was computed by offsetting the observations of one cell by one trial relative to the other. This shift predictor was subtracted from all presented CCGs. Because static noise frames were redrawn randomly for each trial and dynamic noise frames were randomly redrawn with each appearance, the stimulus was not identical between trials. Use of the shift predictor could therefore have caused an overprediction of synchrony. If cells shared similar tuning, the appearance of a preferred stimulus within the noise may have caused simultaneous increases in firing between these cells, resulting in the appearance of synchrony. Because the noise in the previous or subsequent trial would have been unlikely to contain this same preferred noise stimulus configuration, as the effect of simultaneous activity increase, evoked by the preferred stimulus, would not have
been present in the shift predictor and therefore would not have been subtracted. However, we found very little pairwise synchrony, suggesting this potential for overprediction is not an issue in our data.

CCGs were initially computed over a 200-ms period of time with a 1-ms resolution, during three different trial-defined periods. “No stimulus” was defined as the 200 ms immediately preceding onset of the noise stimulus, when the animal was fixating a point on a blank grey screen. “Noise stimulus” was the last 200 ms of the noise stimulus, immediately preceding shape onset, and “shape stimulus” included the first 200 ms following shape onset. All trials in which the stimulus appeared at least 300 ms after fixation onset were included in the fixation only condition. For trials to be included in the noise and shape stimulus conditions, a shape had to appear at least 260 ms after noise stimulus onset and the animal had to maintain fixation for at least 200 ms after shape onset. The first 60 ms after noise stimulus onset were always excluded due to the response onset latency of the recorded neurons. Because peaks were noisy and difficult to visualize at a 1-ms resolution, the CCGs were also binned at an 11-ms resolution.

Event-aligned correlations were quantified from CCGs computed over a 40-ms period with a 1-ms resolution. The area under this CCG from lags of \(-25\) to 25 ms was plotted against the time from either stimulus or shape onset. For trials to be included in the stimulus onset-aligned CCGs, there had to be a delay of at least 300 ms between fixation onset and stimulus onset, and at least 200 ms between stimulus onset and shape appearance so that the stimulus-aligned CCGs never included shape responses. For the shape-aligned CCGs, there had to be at least 260 ms between noise stimulus onset and shape appearance, and the animal had to remain fixated for at least 200 ms after shape onset so that the shape-aligned responses never included activity after the saccade.

MI conveyed by pairs of cells. To quantify the strength of the relationship between the activity of pairs of neurons and the state of the stimulus, or “sensory reliability,” we adapted an analysis of MI previously used on the activity of individual cells (Ghose and Harrison 2009; Harrison et al. 2013; Weiner and Ghose 2014). We used a similar analysis to quantify the relationship between pairwise activity and behavioral state, or “choice reliability.” MI measures the reduction in uncertainty in one variable, given knowledge of a second variable. In the context of sensory information, the first variable is a binary representation of the sensory stimulus (noise or shape), while, in the context of choice information, it is a binary representation of eye movement (fixation or saccade). For both contexts, the second variable was neuronal activity. Because the CCG analysis revealed

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Fig. 1. Shape detection task. Animals were trained to detect the appearance of any 1 of 3 shapes, embedded in a noisy stimulus. The shapes in A are shown at a higher contrast than the noise for the purposes of illustration: during recording sessions, noise and shapes appeared at equal contrast. The trial began with the appearance of a fixation point (B1). The animals were required to maintain fixation throughout the presence of a noise stimulus (B2), until a shape briefly appeared (B3, the shape is the same as in A, middle). The animals were required to make a saccade within 150–550 ms of shape onset (B4) to earn a juice reward. If the animals broke fixation early or failed to make a saccade within the reaction time window, the trial ended with no reward. An example correct trial is show in C. Eye position is cyan before the acquisition of fixation, light blue during fixation, and blue subsequent to the saccade. The bar representing the stimulus is red or grey during the noise stimulus to represent the alternation between static and dynamic noise frames, respectively. The black portions of this bar represent when the shape is present, interleaved with the grey dynamic noise. Simultaneously recorded single unit and multiunit spiking activity for this single trial are indicated by green lines.
that the synchrony of pairs of cells is limited to \( \pm 25 \) ms, and we wished to investigate the impact of these correlations on information conveyed about the stimulus, we restricted our pairwise MI analysis to bins of this size. Within this 25-ms bin, neuronal activity was also treated as a binary variable: 0 if the neuron did not fire and 1 if it did. When the joint activity of neurons was considered, this resulted in four possible “words” of neuronal responses (0,0; 0,1; 1,0; 1,1). When single neurons were considered, there were only two possible neuronal responses (0;1). The frequency distribution of these stimuli and neuronal response variables was represented as a contingency table and used to calculate MI via the direct method.

The analysis utilized every trial in which the animal acquired fixation and the noise stimulus appeared and included all data from 60 ms after stimulus onset until the animal made a saccade or the trial ended. To quantify the relationship between activity and stimulus state without making assumptions about the delay from stimulus presentation, we calculated the MI using a range of delays (0–250 ms, in 5-ms increments). We then divided the MI by the size of the bin to convert it into a rate (MIR), resulting in units of bits per second.

Several corrections served to ensure the final quantification of sensory reliability reflected the relationship between the population’s firing and the sensory stimulus or behavior as accurately as possible. Because MI has an inherent positive bias (Treves and Panzeri 1995), we corrected for the information rate that would be expected by chance, if there was no relationship between the stimulus and neuronal response. To calculate this chance value, the contingency tables that were used to compute MI at each delay were all resampled 100 times. This resampling tended to maintain the probability of observing any one variable but destroyed the relationship between stimulus and neuronal activity variables. The 95th highest value was considered to be the significance cutoff at that delay, and if the original value was not greater than the cutoff, it was set to zero. When the original value was found to be significant, we subtracted the average resampled value to account for bias.

As a result of computing MIR over multiple delays, by chance, we would expect information values at 5% of the delays to be false discoveries whose MIR was not actually significant. Because we represented a pair’s reliability as the maximum MIR over all considered delays, we therefore required that the number of delays with significant information exceeded the expected number of false discoveries (0.05 times the total number of delays). Pairs that failed to meet this criteria were considered to have zero sensory reliability.

The final correction served to account for covariances present in our task and has been described previously in detail (Ghose and Harrison 2009; Harrison et al. 2013; Weiner and Ghose 2014). Briefly, because the animals often made a saccade following shape appearance, it was possible that the sensory information we observed was due only to a covariation between neuronal activity and the animal’s subsequent behavior, and a covariation between the animal’s behavior and shape appearance. We therefore also calculated the MI between behavior (saccade or no saccade) and neuronal activity (defined as described above) and between the stimulus and behavior. For each delay, we found the maximum MIR that could be predicted solely on the basis of the relationship between the animal’s behavior and neuronal activity and subtracted it from the sensory MIR. Similarly, we found the maximum predicted choice MIR that could be predicted by covariation and subtracted it from the choice MIR. All measures of sensory and choice reliability presented here have been both bias and covariance corrected.

To determine the extent to which the information conveyed by neurons depended on simultaneous observation and pairwise neuronal correlations, we used the methods described above to calculate two different types of pairwise MI. The “real joint MI” is based on the binary neuronal response “words.” We shuffled the responses of individual cells across observations of “words” for each stimulus condition to examine the impact of pairwise correlations on MI. This shuffling destroyed precise relationships between cells but maintained any stimulus-dependent modulations in firing rate. The MI of the shuffled responses of neuronal pairs is referred to as “shuffled joint MI.”

MI conveyed by larger populations of cells. For the analyses of larger populations of cells, we considered all of the single- and multiunits meeting the criteria above and recorded in a single session to be a “population.” These populations ranged in size from 5 to 29 units (median = 20.5), with monkey Z providing most of the larger populations. The median proportion of single- to multiunits was 0.44. To quantify the strength of the relationship between the activity of neuronal populations and the state of the stimulus (noise or shape), we adapted our analysis of MI to describe the neural activity across larger populations (Ghose and Harrison 2009; Harrison et al. 2013). In larger populations of neurons, we were unable to use the “word” analysis described above due to sampling limitations and the exponential growth of the number of necessary categories. We thus needed a method of quantification to represent the responses of these larger populations with a number of categories suited to our sampling. The discriminant-based analysis used here allowed us to consider the entirety of our sampled population, regardless of the direction of shape or choice modulation in individual cells.

We created population vectors in which each position represented the activity, the number of spikes occurring within the bin of interest, of a single neuron. Parceling trials according to the stimulus state when computing sensory information, or behavioral state when computing choice information, resulted in a group of population vectors observed in the different variable (stimulus or behavior) states (see Fig. 6A). Half of the vectors in each group were used as a training set to determine a discriminant based on the difference between the groups’ average vectors (see Fig. 6B). The value of the discriminant for each cell will be referred to as that cell’s “weight.” For sensory information, cells that increased their firing when a shape is present would have ended up with positive weights, and those that decreased their firing would have had negative weights. Similarly for choice information, cells that increased their firing before saccades were assigned positive weights, while cells that decreased their firing, negative weights. The remaining population vectors were used as a test set.

The test set of population vectors were projected onto the computed weights and these projections were used to discretize the population response into 20 equal-membership categories (see Fig. 6C). These categories represented the neuronal response in the contingency table used to calculate MI. Because this analysis required responses to be divided into a test and training set, MI was always calculated based on 10 different randomly selected test and training sets. Data were presented as the mean of these 10 replications, with error bars representing the SE. Using the Fisher discriminant instead of the difference of the means produced very similar results.

To quantify how the relationship between activity among larger populations and the stimulus (sensory) or the behavior (choice) depended on temporal parameters, we calculated the MI using a range of binwidths (25–250 ms, in 25-ms increments) in combination with the delays used in the pairwise analysis (0–250 ms, in 5-ms increments). Weights and contingency table categories were defined independently for each combination of delay and binwidth. Converting the MI into a rate (MIR, bits/s), allowed for a comparison of reliability across binwidths. This process produced an information surface on which each point represented the reliability of the population at particular combination of delay and binwidth. All points on the surface were corrected for bias and covariance, as discussed in the pairwise analysis. We refer to the maximum corrected MI of the rate of this surface as the population’s sensory or choice information.

To examine the effect of removing interneuronal correlations on the ability of our populations to represent whether a shape was present, we shuffled each cell’s response across observations within a given stimulus condition (noise and shape), as was done in the pairwise analysis. Similarly, to study the role of correlations in the
ability our populations to predict choices, we shuffled across observations within behavior conditions (fixation and saccade). This again maintained the stimulus- or saccade-dependent statistics of individual cells’ activity but destroyed correlations between the activity of different cells. The sensory and choice information of these shuffled populations was then measured in the same manner as the populations with physiological correlations, described above (see Fig. 6D).

RESULTS

To study how populations of neurons may work together to enable rapid perception of objects, we trained two monkeys to detect the brief appearance of shape outlines within a noisy stimulus (Fig. 1). The animals were required to maintain fixation throughout the presentation of the noise stimulus and make a saccade to the location of the stimulus patch when a shape appeared to earn a juice reward. While the animals performed this task, we recorded from populations of neurons in area V4, an area implicated in form processing. To maximize the possibility of population-based encoding, our shapes were approximately two to three times larger than typical receptive field sizes.

Fig. 2. Behavioral performance. Both animals (A; solid lines, monkey Z; dashed lines, monkey J) correctly detected the presence of a shape ~40–50% of the time (A, blue lines). False alarm trials, in which the animal incorrectly reported the presence of a shape before one appeared, were equally prevalent (A, red lines). The animals failed to respond to the presence of a shape ~10–20% of the time (A, black lines), and in ~5% of the trials, the animals remained fixated throughout the duration of a catch trial, when no shape appeared (A, grey lines). The reaction time distributions were similar for both animals (B; purple, monkey Z; orange, monkey J and across shapes (represented by overlapping circles within a reaction time bin). To quantify the strength of the relationship between the presence of a shape and the animals’ behavior, we parsed trials and computed the mutual information (MI) of the 2 variables of interest: the stimulus (noise, red; shape, black) and eye position (fixate, light blue; saccade, blue). The same 2 example trials (trial 1: correct; trial 833: false alarm) have been parsed according to a single combination of delay and binwidth in C. Bin edges were first aligned to shape onset, and then the appropriate delay was established. If a shape was not presented, bins were aligned to fixation onset. Thicker bin edges indicate this point of alignment. Yellow bins indicate how the eye position has been parsed according to the delay from the stimulus and the binwidth. The darkness of the bin (light or dark yellow) indicates whether the stimulus at this delay was a shape or noise and therefore indicates which row of the contingency table (right) should be updated. Whether the animal was fixating or made a saccade within each bin determines which column is updated. When the contingency tables for each pair of variables were summed across all trials, they described the independent, conditional, and joint probabilities for each pair of variables. These probabilities were used to calculate the MI for this particular combination of delay and 24 binwidth. Computing the MI over different combinations of delay and binwidth resulted in an information surface (D).
moment in the trial about whether to saccade or not, trial-based performance does not necessarily reflect his ability to correctly reject noise and detect shapes for trials of extended duration. For example, if after 5 s of noise, the animal made a false alarm decision to saccade, his true performance should reflect not just that false alarm but also all the correct rejections that he made over the 5-s period. When the animals made correct decisions, they did so with temporal precision: most reaction times occurred within a 100-ms window centered around the mean. Most incorrect trials resulted from an early response (i.e.: a false alarm), while the animals failed to detect the appearance of a shape ~10% of the time.

These results suggest that both animals detected shapes with consistent reliability and timing. To directly address both the reliability and temporal precision of behavior performance, we adopted an information theoretic approach in which contingency tables relating behavior (fixation vs. saccade) and the stimulus (noise vs. shape) are constructed on the basis of parcelled trial data. The parcellation process is repeated for a variety of temporal binwidths and behavior-stimulus intervals (delay) to construct an information surface that describes the strength of the correlations between behavior and stimulus (bit/s) as a function of temporal parameters. These behavioral information surfaces have a single peak whose magnitude and position were consistent between animals, thus substantiating the consistency of shape detection performance and timing between the animals.

Pairwise correlations. An influential hypothesis regarding visual shape detection proposes that cells representing the same shape might synchronize their firing while remaining uncorrelated with cells representing other stimuli (Milner 1974; Engel et al. 1991; von der Malsburg 1981). In the present task, this hypothesis suggests that in the presence of the noise stimulus, the activity of single cells should remain largely uncorrelated but that in the presence of the shape, a certain subset of cells would synchronize their firing, rapidly signaling this appearance. Changes in synchrony could conceivably occur even in the absence of changes in the average firing rate of neurons. In our study, if the presentation of a shape increased the degree of synchrony between neurons, then detecting such a change in correlations could be used for shape detection even if overall firing rates changed modestly. To examine this possibility, we looked for changes in synchrony by computing the normalized and shift-corrected CCGs of pairs of single units (n = 336) over 200-ms periods. We separately analyzed activity during three different phases of our behavioral trials: 1) when the animals were fixating but no stimulus was present; 2) during the noise stimulus immediately before shape appearance; and 3) immediately following appearance of the shape (Fig. 3).

When short-timescale correlations were observed between neuronal pairs, they tended to be highest when the animals were fixating but no stimulus was present. However, in many of the pairs of recorded neurons, a clearly defined peak was absent from the CCG during any of the three phases. Figure 3A shows the CCG for a pair of neurons representative of those with more strongly defined peaks. To allow for some jitter in the timing of spikes and improve visualization, we also computed CCGs using a binsize of 11 ms (Fig. 3B). The average CCG across all sampled pairs exhibited the same trend as the example pair: the strongest synchrony was observed in the absence of a stimulus, and synchrony was weaker both when the stimulus contained only noise and when a shape was present. We quantified the synchrony within each window as the area under the CCG, from ±25 ms. There was a significant decrease in synchrony between the no stimulus and noise stimulus conditions (paired t-test, P < 0.001) but no significant change in synchrony between the shape stimulus and shape stimulus conditions (paired t-test, P = 0.34).

While synchrony on the order of ±25 ms was present before stimulus onset, there was no strong tendency for synchrony during stimulus evoked activity. However, both the noise and shape CCGs exhibit a slightly positive baseline, consistent with temporally broad covariance in firing rates. To compare the strength of covariances with those observed by others, we computed the Pearson correlation, or $r_{sc}$, across trials within a stimulus condition using 200-ms windows. The mean $r_{sc}$ for the no stimulus, noise stimulus, and shape stimulus conditions were 0.04, 0.07, and 0.05, respectively. The values are very similar to those previously observed between neurons in V4 when monkeys were attending to a stimulus in the pairs’ receptive fields (Cohen and Maunsell 2009; Mitchell et al. 2009) or when monkeys were passively viewing stimuli (Smith and Sommer 2013).

While calculating CCGs over a 200-ms window revealed no significant changes in synchrony in the noise stimulus and shape stimulus conditions, given the rapid nature of our task, it remained possible that correlations were changing in a meaningful way over shorter timescales. To study the dynamics of changes in neuronal correlations over shorter timescales, we computed CCGs in 40-ms windows, aligned to either noise or shape stimulus onset. We again quantified the synchrony within each window as the area under the CCG, from ±25 ms. This analysis further confirmed that on average synchrony was highest and most prevalent during the fixation period, before any visual stimulation within the receptive fields of the recorded neurons. Following onset of the noise stimulus, as firing rates increased, synchrony rapidly decreased and then stabilized (Fig. 4, left). The average synchrony between pairs of neurons was largely unchanged subsequent to the appearance of a shape (Fig. 4, middle) or before saccades (Fig. 4, right). Thus, while the appearance of a shape or the preparation to saccade does alter the firing rates of neurons, it is not associated with any transient change in synchrony between neurons.

Pairwise reliability. While analyses involving CCGs can indicate the presence or absence of neuronal synchrony, they result from averaging spike coincidences across many trials. In contrast, the rapid shape detection required by our task necessitated accurate encoding of visual information and decoding of neuronal discharge on a moment-to-moment basis. To study how pairs of neurons might provide such coding, we required a method capable of quantifying the reliability and temporal precision of shape and saccade related responses within our pairs of neurons. We used MI analyses to determine how reliably pairs of neurons might convey the presence of a shape and predict an animal’s saccades, over the timescale in which their activity was most prominently correlated (25 ms). MI quantifies the extent to which knowledge of one variable reduces the uncertainty of another variable. For sensory information, one variable was the binary stimulus state (shape or noise) and the other was the neuronal response. Similarly, for choice information, one variable was the binary eye movement.
state (fixation or saccade) and the other was the neuronal response.

To avoid assumptions regarding the delay of informative responses, we calculated the MI at delays from 0 to 250 ms, in steps of 5 ms. At each delay, the MI quantified the extent to which knowing the response of two neurons over 25 ms reduces the uncertainty of whether a shape was present, or the animal’s subsequent behavior, at the given delay. For sensory MI, we parceled trials so that each bin in which a shape did not occur at the given delay were considered “noise responses” and the bin corresponding to the presence of the shape at this delay was considered to be a “shape response.” For choice MI, we parceled according to “fixate responses” and “saccade responses.” In each of these bins, the neuronal activity was also quantified as a binary response. The response was 0 if a cell did not fire within the 25-ms bin under consideration and 1 if the cell did fire.

Considering the joint responses of two cells at a time, we created “words” that took into account the response of each neuron. The possible neuronal responses thus became (0,0; 0,1; 1,0; 1,1), depending on whether neither of the cells, one of the cells, or both of the cells were firing within each bin. For example, in the case of sensory information, if the synchronous firing of two cells indicated the presence of a shape, this would result in a higher incidence of (1,1) observations subsequent to shape appearance than the noise stimulus and would result in an increase in sensory MI. Informative negative correlations would be reflected by stimulus-dependent differences in the (1,0 or 0,1) responses, and meaningful silence would be reflected in stimulus-dependent differences in the (0,0) neuronal response category. Correlations due to shared input, but not dependent on whether or not a shape was present, may result in a higher incidence of both simultaneous activity and silence (1,1; 0,0), reducing the ability to discriminate whether or not a shape was present, based on the pair’s responses.

If correlated responses are helpful or harmful in determining whether a shape was present, shuffling observations should result in an increase or decrease, respectively, in the reliability, or peak MI, with which cells signaled the presence of a shape. To examine the effect of destroying relationships between cells while retaining the stimulus-dependent statistics of individual cells, we shuffled observations across trials within a given condition (shape or noise). The maximum sensory reliability across delays was plotted for each pair in Fig. 5A. Consistent with our results that pairwise correlations were not significantly modulated by the presence of a shape, we found that

Fig. 3. Cross-correlograms (CCGs) during different stimulus conditions. The 1st column includes data from the last 200 ms before stimulus onset, when the animals were fixating a point on a grey screen. The 2nd column includes data from the last 200 ms before shape onset, the 3rd column includes data from the first 200 ms after shape onset, and the 4th column includes data from the last 200 ms before a saccade was initiated. A and B show the same example pair, with coincidences binned by 1 ms in A and 11 ms in B. Despite the fact that this pair was one of the few with a clearly defined CCG peak in any condition, the peak becomes difficult to discriminate in the noise condition and following shape appearance. The average CCG of all pairs (n = 336) is shown in C.
destroying the correlations between cells tended to have no effect on the ability of that pair to signal whether a shape was present. The average difference in maximum MIR conveyed jointly by pairs with real or shuffled correlations within a 25-ms bin was not significantly different than zero (paired $t$-test, $P = 0.52$). This also suggests that other correlations, not specific to the stimulus condition, do not hinder rapid shape detection. Finally, the inclusion of real correlations also failed to alter the delay at which the maximum sensory MIR occurred (paired $t$-test, $P = 0.28$).

We can apply a similar process to measure the effects of pairwise correlations on choice information. In this case, we shuffle observations across trials within the conditions of fixation and saccading. As with sensory information, we found

Fig. 4. Stimulus onset-aligned, shape-aligned, and saccade-aligned firing rates and CCG area. In A, single units were divided into two groups based on whether their firing rate increased (green) or decreased (magenta) following shape appearance. These groups were used only for illustrative purposes and have no bearing on any other analysis. The average firing rates for these 2 groups are plotted, with shaded areas representing SE. B shows the change in the area under the CCG ($\pm 25$ ms) with time. CCGs were computed in 40-ms bins, with the center of the bin indicated on the x-axis.

Fig. 5. Information represented by pairs of neurons. Sensory reliability was quantified by the maximum MI rate (MIR) between the stimulus and the pairs’ activity within a 25-ms bin, across delays of 0–250 ms (A). Choice reliability was quantified by the maximum MIR between the pairs’ activity and behavioral decisions within a 25-ms bin, across delays of 0–250 ms (B). The reliability of activity containing physiological correlations was compared with the reliability when correlations had been removed by shuffling within stimulus (A) or decision (B) conditions. Physiological correlations within the pairs make them no more or less able to signal the presence of shape. Cyan marker corresponds with the example pair from Fig. 3.
that destroying correlations tended to have no effect on the ability of that pair to predict the animals’ choices (Fig. 5B, paired t-test, \( P = 0.64 \)). Similarly, the inclusion of correlations failed to alter the delay at which maximum choice MIR occurred (paired t-test, \( P = 0.23 \)).

**Reliability of larger populations.** Although analyses of pairwise correlations showed that the encoding of V4 neurons may be mostly independent in the context of shape detection, the animals’ behavior likely depended on much larger groups of neurons. Correlations that were difficult to observe when only two cells were studied may have been more prominent or effectual when larger populations are considered (Averbeck and Lee 2006; Schneidman et al. 2006; Moreno-Bote et al. 2014). To understand how larger groups of our sampled V4 neurons may have worked together to support shape detection, we next investigated how the task-related reliability of larger populations of simultaneously recorded V4 cells were affected by response weighting and correlated variability.

To study how neuronal populations might have encoded the presence of a shape on a moment-by-moment basis, we required a method capable of quantifying responses across the sampled populations. Although theoretically the same pairwise methods as described above could be used to measure stimulus- and choice-related differences in the high-dimensional response space describing such larger populations, as a practical manner, adequate sampling of such a high-dimensional space within recording sessions on the order on an hour is challenging. To circumvent this issue, we used a discriminant analysis in which each cell was weighted according to the average difference in its response to the shape and noise conditions for sensory information and to the fixation and saccade conditions for choice information. Because there were indications that correlations between neurons may have extended beyond the short-timescale, prominent areas of the CCGs (Fig. 3, the average CCGs in the noise and shape stimulus conditions tend to remain positive even at long time lags), we examined the reliability of populations of neurons within a variety of binwidths, in addition to the variable delays discussed above (Fig. 6, see MATERIALS AND METHODS for details).

Computing the MI at a variety of delay and binwidth combinations resulted in an information surface that described how the reliability between the population’s response and the stimulus varied with the temporal parameters under consideration. The peak MIR on this surface quantified the highest reliability with which the population could discriminate between the presence of a shape or noise stimulus and will be referred to as “sensory information.” The peak sensory information for our populations tended to be about a third of the peak behavioral information (Fig. 2). This means that our sampled population of cells reflected the presence of a shape approximately a third as reliably as the animals’ behaviors reflected the presence of a shape. The delay and binwidth at which this peak occurred indicated the delay and precision of the population’s most reliable stimulus representation, respectively. To gain an appreciation for the effect of correlations on the largest populations possible, in all of the following analyses of population reliability, populations included all single- and multiunits from a single recording session that met the inclusion criteria discussed in MATERIALS AND METHODS. This data included 9 recording sessions in monkey Z and 11 recording sessions in monkey J, with the number of units in each population ranging from 5 to 29 units (median = 20.5).

Our weighted population sum analysis automatically incorporated physiological correlations in activity across the population of recorded cells, both within and across trials. Higher-order correlations resulting in simultaneous increases in cells with positive weights (determined by their tendency to increase their firing rate when the shape appears) and/or decreases in cells with negative weights (determined by their tendency to decrease their firing rate when the shape appears) would result in a larger value when projected onto the weights. In this case, our weighted analysis of the population should be better able to indicate the presence of a shape when these correlations were taken into account than if they were destroyed. On the other hand, it is often thought that activity correlations within populations of neurons hinder stimulus representation because noise in the representation cannot be removed by averaging across cells ( Britten et al. 1992; Zohary et al. 1994; Mazurek and Shadlen 2002). If this were the case, a population of independent neurons should be better able to signal the presence of a shape than one with physiological correlations.

As in the analysis of the sensory reliability of pairs of neurons, by shuffling spike count observations within neurons, we created synthetic activity distributions in which correlations were destroyed but any rate modulations were preserved. This process was performed separately for shape and noise responses to maintain the response statistics of individual neurons within a given stimulus condition. We then assessed the impact of physiological correlations on shape encoding using the aforementioned weighted population MI analysis. To do this we studied how the peak MI value varied in magnitude (reliability) and position (timing) between the original and shuffled information surfaces. We found the entire information surface was essentially unaltered by shuffling (Fig. 7A). Across our sample, we found no significant changes in reliability, as characterized by the peak MI across the surface, when population responses were shuffled (paired t-test, \( P = 0.74 \); Fig. 7B). Similarly, we found no significant changes in the peak delay (paired t-test, \( P = 0.75 \)) or peak binwidth (paired t-test, \( P = 1 \)) of sensory information (data not shown). Moreover, shuffling also failed to have an effect on information even when only subgroups of the most or least informative neurons within a population were considered. Thus correlated activity in area V4, although modestly present as revealed by cross-correlation analyses, solely reflects changes in rate modulation and precise spike timing has no effect on the ability of V4 populations to signal the appearance of a shape.

Even though there is no evidence that correlations are affecting the representation of behaviorally relevant information in area V4, correlations may have effects in the abilities of other areas and populations to represent and convey shape-relevant information. Without simultaneous recordings in all of the areas and neurons contributing to a decision, it would seem difficult to evaluate such a possibility. However, the finding that the activity from individual neurons in V4 over tens of milliseconds are predictive of behavioral choices Weiner and Ghose (2014) provides a potential avenue for studying such correlations. Because our decision involves eye movements, intermediate structures that receive input from V4 but are more proximately related to eye movement planning and execution, such as area FEF, are likely mediating the relationship between...
V4 activity and saccades. If the reliability of these mediating responses is affected by correlations, then those correlations would in turn affect the reliability of the relationship between V4 responses and choice.

To examine this possibility, we applied a similar shuffling procedures as was applied to sensory information to examine the choice information associated with populations of V4 neurons. Specifically, we created separate synthetic activity distributions for responses preceding fixation and responses preceding saccades in which the overall response statistics of individual neurons was preserved. Similar to our results with sensory information, we found that the shuffling procedure largely preserved choice information surfaces, without dramatic changes in reliability or timing (Fig. 8). However, across our entire sample, we found a statistically significant effect of shuffling with respect the choice reliability, as indicated by the maximal information rate across the surface. We found ($P = 0.009$, paired $t$-test) that choice reliability was slightly higher (mean increase of 13%) when V4 responses were shuffled, consistent with the notion that correlations are limiting the reliability of signals in other areas that are contributing to saccadic decisions.

**DISCUSSION**

We found that during rapid shape detection, the impact of neuronal correlations was negligible in V4. Pairwise synchrony decreased in response to the onset of the noise stimulus and failed to increase subsequent to shape appearance. Removing the precise timing relationships between pairs of neurons by shuffling across observations neither improved nor diminished their ability to signal the presence of a shape or predict behavioral choices. When considering larger multineuronal populations, the information content associated with shuffled observations of population discharge were also similar to those from populations with physiological correlations both in magnitude and timing.
An attractive hypothesis for many researchers, known as binding-by-synchrony, is that precise correlations between neurons with disparate receptive fields could serve as a code for linking the activity of these neurons into a single percept. According to this hypothesis, the same two cells should synchronize their firing when representing the same shape and desynchronize their firing when representing parts of different shapes (Singer 1999; von der Malsburg 1981). Early influential studies (Engel et al. 1991; Kreiter and Singer 1996) suggested a role for synchrony in the representation of a single percept by comparing synchrony between conditions with a single moving bar and those with two moving bars. However, it is not clear how prevalent these observations were or if this type of stimulus was an appropriate test of the binding hypothesis (Shadlen and Movshon 1999). Additionally, a later study by Golledge et al. (2003), using very similar stimuli, showed that stimulus was an appropriate test of the binding hypothesis (Shadlen and Movshon 1999). Moreover, a later study by Golledge et al. (2003), using very similar stimuli, showed that stimulus was an appropriate test of the binding hypothesis (Shadlen and Movshon 1999).

However, several of these negative results were found in early visual areas, while the mechanisms of grouping or binding may only be observed in higher cortical areas (Uhlhaas et al. 2009). For example, work by Hirabayashi and Miyashita (2005) suggested that in the inferotemporal cortex, correlations over short timescales may help to signal the presence of meaningful, global stimuli. A failure to find binding-dependent correlations could also be due to the large temporal windows (hundreds of milliseconds) often used in these analyses, which may fail to detect brief periods of meaningful synchronization (Uhlhaas et al. 2009). Because populations of neurons in area V4 have been proposed to represent complex objects through their joint firing (Pasupathy and Connor 2002), lesions to area V4 can result in binding deficits (Merigan 2000), and synchronous activity may be particularly advantageous in the context of rapid vision (Maldonado et al. 2008), we reasoned that the activity of neurons in area V4, while animals were performing
a difficult task requiring rapid identification of global stimuli, would provide more conclusive evidence to support or reject the binding-by-synchrony hypothesis.

We found that precise correlations in area V4 did not signal the appearance of shape within a noise stimulus. Consistent with previous literature (de Oliveira et al. 1997; Smith and Sommer 2013), our CCG analyses found that short timescale pairwise correlations were highest during the fixation period, when no stimulus was present. The fact that short timescale correlations present during the noise stimulus were virtually unchanged following shape appearance provides strong evidence that synchronous firing in area V4 could not be used as a binding signal. A recent study in areas V1 and V4 (Supplemental Fig. S4 in Chen et al. 2014) with a similar stimulus configuration, which did not require a rapid behavioral report of global stimulus detection, also failed to find a relationship between an increase in synchrony and global form representation.

To examine how these pairwise statistics affected the moment-to-moment reliability of shape representation, we analyzed the MI within bins of 25 ms between the activity of pairs of neurons and the appearance of a shape. We tested the importance of precise spike timing relationships by comparing the MI when population activity contained physiological correlations with the MI of a synthetic data set, obtained by shuffling actual observations across trials. We found that such precise timing relationships were neither helpful nor harmful to stimulus information rates.

While our pairwise analysis indicated that it was not necessary to take correlations into account to determine whether a shape appeared, it remained possible that within larger populations, these correlations would become functionally relevant (Schneidman et al. 2006; Averbeck and Lee 2006). We therefore modified our pairwise analysis for use with larger populations, quantifying the population response as a weighted sum of the sampled neuronal activity, with weights determined by shape responsiveness. There is evidence that both perceptual learning (Ghose et al. 2002; Law and Gold 2008; Gold et al. 2010) and attention (Masse et al. 2012) result in perceptual improvements by such a selective weighting mechanism. We also used this method to consider population responses in larger binwidths, where correlations are often presumed to be harmful and may have hindered shape representation (Mazurek and Shadlen 2002; Zohary et al. 1994).

To investigate the potential role of correlations in larger populations, we again compared the stimulus information available in a population with physiological correlations to the stimulus information of the same population under conditions of activity independence. We found that over the timescales in which neurons are informative about this task, destroying correlations between cells in our sampled populations neither improved nor diminished the reliability of the population. This does not mean that correlations play no role in sensory representation. Certain aspects of the correlation structure could be improving the representation while others are adding noise, but the net effect is that our sampled populations are approximately as informative as independent populations of cells (Latham and Nirenberg 2005). Recent studies have suggested that a main role of attention in area V4 is to reduce interneuronal correlations (Cohen and Maunsell 2009; Mitchell et al. 2009), suggesting that covariances in firing rate are a major obstacle that must be overcome by the nervous system. The distribution and brevity of shape appearance in our task were designed to encourage a high level of attention to the stimulus throughout trials. It is therefore possible that the challenging nature of our task encouraged a level of vigilance that suppressed correlations and that for less demanding tasks, including those without substantial temporal constraints, correlations might play a different role.

While previous studies have examined the potential for correlations to affect the encoding of visual stimuli by neurons, these studies, as we have, have adopted an “ideal observer” approach in which an optimal linear discriminant is used to decode neuronal activity. However, this approach may not accurately characterize the actual decoding of sensory neuronal signals by neurons more proximally involved in saccade planning and initiation during task performance. To address this issue we can examine the relationship between the studied neuronal activity, namely in area V4 in our case, and the actual behavioral choice.

Previous work in our laboratory has established that the activity of individual V4 neurons over timescales of tens of milliseconds is predictive of the animals’ choice to saccade in a shape detection task Weiner and Ghose (2014). In some cells the delay between activity and eventual saccade is consistent with a feedforward contribution to the actual decision, in other cells that delay is considerably shorter, and more consistent with a presaccadic feedback signal Moore and Chang (2009). Consistent with this diversity in choice delays from individual cells, we find a similar diversity of presaccadic when populations of V4 neurons are considered (Fig. 8), with one animal having population delays more consistent with saccadic feedback and the other having delays more consistent with feedforward contributions to the saccade. However, in both of these situations, because V4 cannot directly trigger a saccade, the strength of the relationship between V4 activity and choices is dependent on the reliability of responses in areas, such as the frontal eye field, more proximally related to saccade generation. For example, if such presaccadic responses were highly sensitive to correlated patterns of discharge, then the relationship between V4 population activity and behavioral choices should be weaker when those correlations are removed by our shuffling techniques. Paradoxically, we find just the reverse: a slight increase in choice information in our shuffled controls. One possible explanation is that, in contrast to our findings of V4 encoding performance, correlations are compromising the ability of downstream neurons to accurately encode shape appearance using V4 activity. This compromised stimulus encoding would then lead to a weaker relationship between choices and V4 activity.

Our study was motivated by the limited time windows associated with most foveation decisions and an interest in measuring both stimulus reflective, and behaviorally predictive, activity within V4. Our results show that for such rapid decisions, there is evidence neither that precise synchrony provided useful information nor that longer timescale correlations decreased information. Our results represent a significant extension of previously reported effects of correlation of stimulus encoding because we limit our analyses to behaviorally relevant timescales and go beyond pairwise statistics by analyzing the reliability of larger populations of neurons. However, our population samples, especially when compared with
the number of cells likely activated by the stimulus, are still relatively small. It is therefore possible that correlations that have only modest effects on information coding and transmission for relatively small populations (<30 in our study) have considerably larger effects when hundreds or thousands of neurons are considered Moreno-Bote et al. (2014). Given the development of large scale recording and imaging technologies, the effects of correlations on encoding and decoding within such large populations might soon be measurable using analytical techniques such as those described within this study.

Our study shows that small populations over tens of milliseconds can provide stimulus information that is comparable with behavioral performance and that the same sets of neurons over the same small time scales reflect behavioral choices. For such population, a rapid decoding that preferentially weights informative neurons according to firing rate statistics can achieve the same performance whether or not physiological correlations are present. This is consistent with theoretical work of Abbott and Dayan (1999) and more recent empirical studies (Nirenberg et al. 2001; Berens et al. 2012; Adibi et al. 2014). While we feel that the simplicity of our weighted population sum analysis is a strength, it is possible that a more complicated decoding mechanism (Pillow et al. 2008; Graf et al. 2011) may be theoretically useful for other types of tasks. Even if this were true, however, it is far from clear how the high-dimensional signals associated with characterizing the precise timing across neuronal populations could be reliably and quickly decoded by downstream neurons to form percepts and guide actions. By contrast, our studies of the effects of correlations on choice information in area V4, suggest that correlations slightly compromise the reliability of responses in downstream neurons associated with saccade initiation. Given the lack of correlation effects in our sample of V4 neurons, this finding emphasizes the importance of studying correlations across the entire set of neurons responsible for decision making when evaluating models of populating coding and behavior.

ACKNOWLEDGMENTS

We thank Pantea Moghimi, Elisabeth Moore, Tom Nelson, and Scott Warren for comments on the manuscript.

GRANTS

This work was supported by National Institutes of Health Grants R01-EY-014989, P30-NS-5057091, and P30-NS-076408, the Alfred P. Sloan Foundation, and University of Minnesota Graduate School and Frieda Martha Kunze Fellowships.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: K.F.W. and G.M.G. conception and design of research; K.F.W. performed experiments; K.F.W. and G.M.G. analyzed data; K.F.W. and G.M.G. interpreted results of experiments; K.F.W. prepared figures; K.F.W. drafted manuscript; K.F.W. and G.M.G. edited and revised manuscript; K.F.W. and G.M.G. approved final version of manuscript.

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