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Activity in LIP, But not V4, Matches Performance When Attention is Spread

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Abstract

The enhancement of neuronal responses in many visual areas while animals perform spatial attention tasks has widely been thought to be the neural correlate of visual attention, but it is unclear whether the presence or absence of this modulation contributes to our striking inability to notice changes in change blindness examples. We asked whether neuronal responses in visual area V4 and the lateral intraparietal area (LIP) in posterior parietal cortex could explain the limited ability of subjects to attend multiple items in a display. We trained animals to perform a change detection task in which they had to compare 2 arrays of stimuli separated briefly in time and found that each animal's performance decreased as function of set-size. Neuronal discriminability in V4 was consistent across set-sizes, but decreased for higher set-sizes in LIP. The introduction of a reward bias produced attentional enhancement in V4, but this could not explain the vast improvement in performance, whereas the enhancement in LIP responses could. We suggest that behavioral set-size effects and the marked improvement in performance with focused attention may not be related to response enhancement in V4 but, instead, may occur in or on the way to LIP.

Key words: attention, change detection, orientation, parietal cortex

Introduction

Visual attention is of fundamental importance to us in everyday life. This can be illustrated using a number of psychological tools, such as change and inattentional blindness tasks (Simons and Levin 1997; O'Regan et al. 1999; Simons and Chabris 1999; Kim and Blake 2005). In the lab, this limited ability to attend to the entire visual world can be seen best in tasks in which performance decreases as a function of set-size (Treisman and Gelade 1980). Focused visual attention has also been shown to increase visual sensitivity (Yeshurun and Carrasco 1998; Cameron et al. 2002) and decrease reaction times (Posner 1980; Posner and Cohen 1984). These effects tend to be moderately small and seem quite different from the striking inability to notice changes in a visual scene when one does not know where to attend, such as in change blindness.

For over 30 years, it has been known that the responses of neurons in many visual areas are enhanced when animals attend to a particular location (Moran and Desimone 1985; Treue and Maunsell 1996; Reynolds et al. 2000). While these effects can be quite striking when 2 stimuli are in a single receptive field, they are much smaller when attention is allocated to single objects inside or outside of the receptive field: conditions more akin to those studied in change blindness. Indeed, the attentional modulation seen when attention is focused inside or outside the receptive field could explain the benefits of visual sensitivity (Reynolds and Chelazzi 2004; Luo

and Maunsell 2015), but it is unclear whether these relatively small modulations are the correlates of attention that allows us to notice changes in change blindness (Rensink et al. 1997). To test whether they are, we recorded the responses of neurons in visual area V4 while animals performed a change detection task under conditions of distributed attention and when attention was biased to a single location. Our expectation was that under spread attention, performance of the task would be affected by set-size, as in change blindness, but if the change occurs at the biased location, then performance should be enhanced. We additionally examined the responses of neurons in the lateral intraparietal area (LIP), a part of the oculomotor network thought to be involved in the allocation of attention (Gottlieb et al. 2009; Bisley and Goldberg 2010). We did so because recent work has suggested that activity in this network, which includes the frontal eye field (FEF) and superior colliculus (SC), may be related to the limited capacity for memory (Buschman et al. 2011) and deficits in this network can limit the ability to utilize visual information for behavior (Wardak et al. 2004, 2006; Balan and Gottlieb 2009; Lovejoy and Krauzlis 2010) while leaving attentional modulation in visual areas intact (Zenon and Krauzlis 2012).

Materials and Methods

Subjects

We collected data from 3 male adult macaque monkeys (monkeys A, D, and G, *Macaca mulatta*), weighing 8–14 kg. Surgical procedures have been described previously (Mirpour et al. 2009; Arcizet et al. 2015). Briefly, head posts, scleral search coils, and recording cylinders were surgically implanted under general anesthesia. Animals were initially anesthetized with ketamine and dexdomitor and were maintained with isofluorane. Surgery was conducted using aseptic techniques and analgesics were provided during postoperative recovery. All experiments were approved by the Chancellor's Animal Research Committee at UCLA as complying with the guidelines established in the Public Health Service Guide for the Care and Use of Laboratory Animals.

Change Detection Task

The animals were seated in a primate chair (Crist instruments) with their heads fixed and placed in front of a computer monitor (Samsung SyncMaster 1100DF CRT running at 100 Hz) 57 cm away in a dimly lit room. The temporal precision of stimulus onset was set by the output of the video card driving the CRT—this was confirmed by the use of a photoprobe on the corner of the monitor during early sessions. Eye position was monitored using scleral coils (Riverbend Instruments) and recorded at 1 kHz. Stimulus presentation and data acquisition were controlled using VEX and REX (Hays et al. 1982).

Monkeys started a typical trial by fixating a central white spot for 900–1300 ms, which was presented on a gray background (Fig. 1). Then, an array of 1, 2, 4, or 8 oriented bars (light gray; 50% or 25% contrast) was flashed for 500 ms (array 1). Arrays were set so that one bar was positioned within the neuron's response field (V4 or LIP) and was randomly oriented to either the neuron's preferred or nonpreferred orientation; the other bars were evenly spread around an imaginary circle, centered at the fixation point. If in the 4 or 8-stimulus condition a neighboring bar ended up being close to the edge of or in the receptive field, the condition was not recorded. The animal was required to keep fixation on the central spot during this presentation. After the array was extinguished, there was a gap of 100–300 ms during which nothing but the fixation point remained on the screen, then the bars reappeared for 1000 ms (array 2). The gap duration remained the same within a session, with the vast majority of the 165 sessions having a gap of 100 ms (n = 118) or 150 ms (n = 22). On some trials (50% for set size 1 and 66% for all other set sizes), one bar rotated 90° before reappearing and the monkey was rewarded by a few drops of diluted apple juice for making a saccade toward that bar (change trial, Fig. 1). Although the fixation point remained on, the animals had been trained that they could make an eye movement to a stimulus at any time during array 2. In the remaining trials, no rotation occurred and the monkey was rewarded for maintaining fixation of the central spot (no change trial, Fig. 1). The inclusion of the gap masked the apparent motion on change trials and greatly affected the animals' abilities to detect the change, much like the gap in a typical change blindness example. Change and no change trials were interleaved pseudorandomly within a block and the probability of each bar rotating on change trials was equal. The task was designed to mimic behavior in change-blindness examples, with a change that is obvious when the location is attended. It is not a classic working memory task: it is thought to be driven by iconic memory, as evidenced by the fact that a cue appearing up to 200 ms after array 1 offset can improve performance in the task (Becker et al. 2000).

In blocks with only 1 bar present, the animals usually performed 20–40 trials per block and performance was relatively stable within the block. These blocks were randomly interleaved among blocks with 2, 4 or 8 bars, each of which had considerably more trials (approximately 2 times, 4 times, and 8 times the number of trials, respectively). We refer to them as S1 (set-size of 1), S2 (set-size of 2), S4 (set-size 4), and S8 (set-size 8). Note that the probability of receiving a reward was equal or greater if the animal maintained fixation than if it made a saccade to one of the bars, accordingly each animal appeared to retain the default behavior of maintaining fixation when unsure (Arcizet et al. 2015).

Within some sessions, we also included another condition to bias the animals' attention to a particular location. In the high-reward block (S4h), we used a set-size of 4 items, but one location had a higher reward associated with it. Specifically, if the animal made a correct saccade to that location, he would receive 2.5 times his standard reward. The task remained the same, so there was an equal probability that each bar could rotate and a 33% chance that no bar would rotate. Although the location of the high reward was not explicitly indicated, we used a red fixation point to let the animal know that one location had the extra reward. The high-reward block was usually run late in the session and the data from any blocks run after it were excluded from analyses because we found that the animals often maintained their bias toward that location.

Recording and Data Analysis

We recorded extracellular single unit activity from either LIP or V4 using glass-coated tungsten electrodes with impedances of 0.8–1.2 MΩ (Alpha Omega). Their position was controlled with a stepping motor microdrive (NAN). The electrical signal was amplified, filtered and single unit activity was recorded online using Plexon (Plexon Inc., Dallas, TX). Spikes were accurately sorted offline using the Plexon SortClient software. Neurons were considered to be in V4 according to their anatomical location, confirmed with MRI scans and neurons were considered

to be in LIP according to their location in the intraparietal sulcus and whether they, or any of their neighbors at the tip of the electrode, had visual, memory or motor responses in the memory guided delayed saccade task (Barash et al. 1991).

After isolating a neuron in V4, we mapped the position and the size of the receptive field by hand and then with an automated mapping task. In this task, the animals started by fixating a point for 700–1000 ms, after which 12 small spots flashed for 100 ms each in pseudorandomly picked locations on a 9° × 9° grid centered on the hand-mapped receptive field. We used the responses from this task to identify the limits of the V4 receptive field, by roughly fitting the data with a 2D Gaussian. We recorded the responses of 188 V4 neurons (70 from animal A and 118 from animal D).

After isolating a neuron in LIP, we mapped the position and the size of the response field by hand and then with an automated memory guided saccade task with 9 or 25 different target positions across a 3 × 3 or 5 × 5 grid extending over the edge of the hand-mapped response field (for details, see Mirpour et al. 2010). We recorded the responses of 185 (26 from animal A, 97 from animal D, and 62 from animal G) neurons from LIP. The responses during the interstimulus interval from some of these neurons have been published previously (Arcizet et al. 2015). The response field eccentricities in both areas ranged from 5° to 16°. We felt it was necessary to use the same general stimulus configurations for both areas so that we could match each area's contribution to the behavior in the same task.

After mapping the location and the size of the response field, we examined the neuron's responses to 8 orientations to identify the preferred orientation of the neuron. The animals kept fixation of a central spot for 600–1400 ms, after which a bar appeared in the response field for 250 ms. The animals had to keep fixating the central spot during this presentation to be rewarded. The bar could be in 1 of 8 orientations starting from 0° (horizontal), stepping by 22.5° steps to 157.5° and we changed the size of the bar according the eccentricity of the response field (2° at 5° eccentricity to 4° at 15° eccentricity). We identified the preferred orientation by fitting the data with a Gaussian function and used the preferred and orthogonal orientations in the change detection task. For neurons in which there appeared to be no clear tuning, as was common in LIP, we defined the orientation that produced the greatest response as the preferred orientation. The animals' performances in the change detection task were not biased by the orientations.

Behavioral Performance

To analyze the performance in the change detection task, we broke the behavioral data into 2 unambiguous categories. A correct eye movement toward a bar that had rotated was defined as a hit, while maintaining fixation of the central spot when no rotation occurred was defined as a correct rejection (CR). To estimate signal detection theory measures d-prime and criterion, we used a latent variable formulation previously developed and used to model behavior in multialternative detection and change detection (m-ADC) tasks with unequal sensitivities (Sridharan et al. 2014, 2017), termed the m-ADC model. The m-ADC model relates the conditional probability of each type of response for each stimulus event to the perceptual sensitivity (d-prime) and choice criterion at each location. The model defines a multivariate decision variable for each location which represents the sensory evidence at that location. As in conventional signal detection theory, this variable at baseline (i.e., a no change event) has a different mean and unit variance Gaussian distribution, called the "noise" distribution. Factors that alter the selective gating of sensory evidence (choice bias) do not change the distribution or mean of the perceptual sensitivity although they change the decision of the animal. The m-ADC model algorithm employs maximum likelihood and Bayesian methods to estimate sensitivities and criteria from the behavioral response probabilities (Sridharan et al. 2014, 2017).

Neuronal Responses

Mean neuronal activity is illustrated using spike density functions (Richmond et al. 1987), which were created by convolving spike trains with a Gaussian kernel with a sigma of 6 ms, and responses are calculated using the number of spikes within a particular window. Spike trains were not truncated by any events (such as saccade onset). When mean responses or the results of statistical analyses are plotted as a function of time, the point is plotted at the middle time point of the analysis window. For all analyses, except where noted, we include all completed trials and neurons are only included if we have at least 5 trials in each condition being compared.

To see how well activity in each area could differentiate between change trials and no-change trials we used 2 approaches. In both cases, we used change trials in which the change occurred in the receptive field and trials in which the nonpreferred orientation was presented in array 1, so that the change trials had the preferred orientation stimulus in the receptive field and the no-change trials had the nonpreferred orientation stimulus in the receptive field for array 2. The first analysis utilized signal detection theory (Green and Swets 1966; Britten et al. 1992) to see how well the population response could discriminate between 2 different trial types (change and no-change trials). Using a receiver operating characteristic (ROC) analysis, we examined the responses in 100 ms bins, stepped every 5 ms for each set-size to compare the responses in the 2 different trial types. The area under the ROC curve (auROC) indicates how well an ideal observer could differentiate between the responses distributions for 2 conditions using the activity from the neurons in that window. We used a permutation analysis to identify when the auROC values for a single set-size became significantly different from 0.5 ($P < 0.05$, 1000 shuffles) and running ANOVAs at each time point to see whether the mean auROC values were different across set-sizes. A value of 0.5 indicates the chance level, that is, the neuronal population could not differentiate between 2 conditions (change and no-change trials); values greater than 0.5 indicate that the neuronal population responded more on change trials than on no-change trials.

The second analysis utilized a contrast function to illustrate how different the mean response on change trials was to no-change trials at the single neuron level. We defined the difference index as the mean response on change trials minus the mean response on no-change trials divided by the sum. We present the mean (±SEM) difference indices from the population of neurons for 100 ms windows stepped every 5 ms.

It is important to realize that the use of all trials, rather than just correct trials, in the ROC and difference index analyses means that we are averaging across different proportions of trials with and without saccades. This is because the proportion of hits decreases as set-size increases. As such, the use of all trials may bias our metrics around the time of the saccade. We have previously shown that the activity in LIP during the interstimulus interval biases the animals' performance (Arcizet et al. 2015). When the interstimulus interval activity was high, the animals were more likely to make a hit or false alarm and

when the interstimulus interval activity was low then the animals were more likely to miss a change or make a CR. Because of this bias, metrics such as the difference index or auROC do not start at 0 or 0.5, respectively, when using only correct trials. For this study, we wanted to include the full set of data to see how these metrics changed from baseline levels. Importantly, we do not rely on these metrics alone to make any of our points: we additionally show the responses of only correct trials to show that the principle results remain.

Results

Performance on the Change Detection Task

We recorded the behavioral performance and the neuronal responses in V4 and LIP of 3 animals while they performed a change detection task (Fig. 1). The LIP and V4 recording sessions were not done simultaneously so behavioral performance was analyzed separately, however the behavioral results were similar (Fig. 2). We recorded the behavioral performance in 103 V4 sessions for 2 animals (55 for monkey A and 48 for monkey D) and 62 LIP sessions for 3 animals (8 for monkey A, 29 for monkey D, and 25 for monkey G). Figure 2A, B shows the overall percentage of hits on change trials as a function of the set-size for V4 sessions and LIP sessions, respectively. For sessions in both areas, the percentage of hits for each animal decreased as the set-size increased ($P < 0.001$, linear regressions for each animal in each area) showing that the change detection task is attentionally demanding. The percentage of CRs (Fig. 2C, D) stayed somewhat similar across set-sizes, with some animals showing small, but significant negative correlations. Monkey A showed a significant negative correlation between CR and set-size in V4 ($P = 2.53 \times 10^{-5}$, $n = 55$) and LIP ($P = 0.030$, $n = 8$), monkey D showed a weak, but significant correlation in V4 ($P = 0.020$, $n = 48$), but not in LIP ($P = 0.90$, $n = 29$) and monkey G showed a significant correlation in LIP ($P = 1.96 \times 10^{-8}$, $n = 25$).

Based on the reaction times, all 3 animals seemed to trade off accuracy for speed (Fig. 2E, F). We used an ANOVA on inverted reaction times for each animal to see if there was a significant effect of set-size on response. Animal A showed a significant effect of set-size ($F[3134] = 7.77$; $P = 8.00 \times 10^{-5}$ in V4 and $F[3,19] = 11.42$; $P = 0.0002$ in LIP); animal D showed a significant effect in V4 ($F[3123] = 2.79$; $P = 0.043$), but not in LIP ($F[3,76] = 2.30$; $P = 0.085$); and animal G's reaction times were not significantly different ($F[3,71] = 1.0$; $P = 0.40$). Post hoc analyses (HSD) in all significant cases showed that reaction times in the S1 condition were slower than in the S2 and S4 conditions, but there were no significant differences among S2, S4, and S8 in any animal. Given the similar performance as a function of set-size, these results suggest that each animal employed a similar strategy to perform the task: when more than one bar was present, they responded as quickly as possible and maintained fixation when unsure about whether a bar rotated.

Neuronal Response as a Function of Set-Size

We recorded the activity of 188 V4 neurons (70 from monkey A and 118 from monkey D) and 185 LIP neurons (26 from monkey A, 97 from monkey D, and 62 from monkey G). Neuronal responses from the 3 animals were qualitatively similar and, as the animals used similar strategies to perform the task, we have pooled the neuronal data for simplicity.

We start by asking whether there is neuronal evidence that the animals were covertly shifting their attention among locations. We predict that if the animals attended one location at a time in a serial fashion, whether it be for short or long periods of time, the average response in V4 would have an apparent, but small, set-size effect: the animal would attend 1 of 2 locations more often than 1 of 4 locations or 1 of 8 locations. Thus, the relative time in which the stimulus in the receptive field has an attentional enhancement would be greater for smaller set-sizes than for larger set-sizes. For example, if there are only 2 items, then the animal will attend the item in the receptive field approximately half the time and the mean response will be halfway between the "attend in" response and the "attend out" response. But when there are 8 items, the animal will attend the item in the receptive field approximately one-eighth of the time and the mean response will be one-eighth of the way between the "attend in" response and the "attend out" response. Thus, when looking at the entire response profile, the mean response should decrease as a function of set-size but the range would only be within the "attend in" and "attend out" levels seen with focused attention.

We found that the neuronal responses of V4 neurons did not vary as a function of set-size even though the responses of LIP neurons did (Fig. 3). For this analysis, we have pooled the

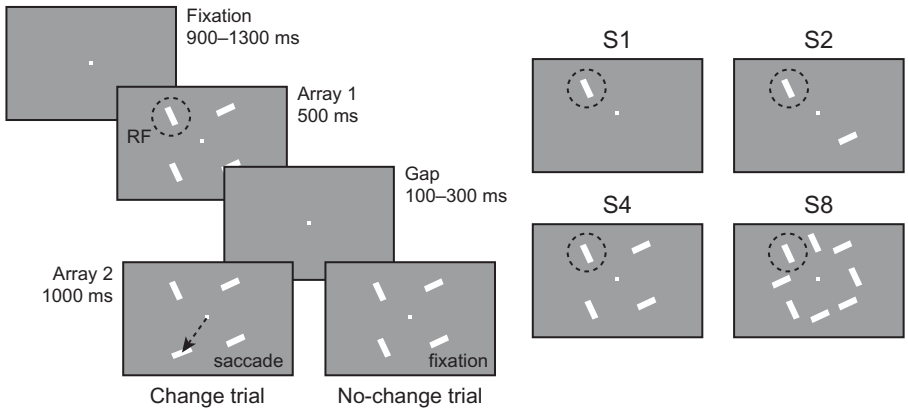

Figure 1. Change detection task. After fixating a central spot, 1, 2, 4, or 8 oriented bars were flashed in a circular array around the fixation point, with one bar placed in the center of the receptive field (RF) of the neuron symbolized by a dashed circle. The animals had to keep fixation during the presentation of this array (array 1). After a gap of 100–300 ms, the oriented bars reappeared (array 2) but one of the bars could have changed orientation by rotating 90° (change trial), in which case the animals had 1 s to make an eye movement to the rotated bar to be rewarded (saccade indicated by a dashed arrow). If no rotation occurred, the animals had to keep fixation to be rewarded (No change trial). The right panels show the arrangement of the different set-sizes: 1 bar (S1), 2 bars (S2), 4 bars (S4), and 8 bars (S8).

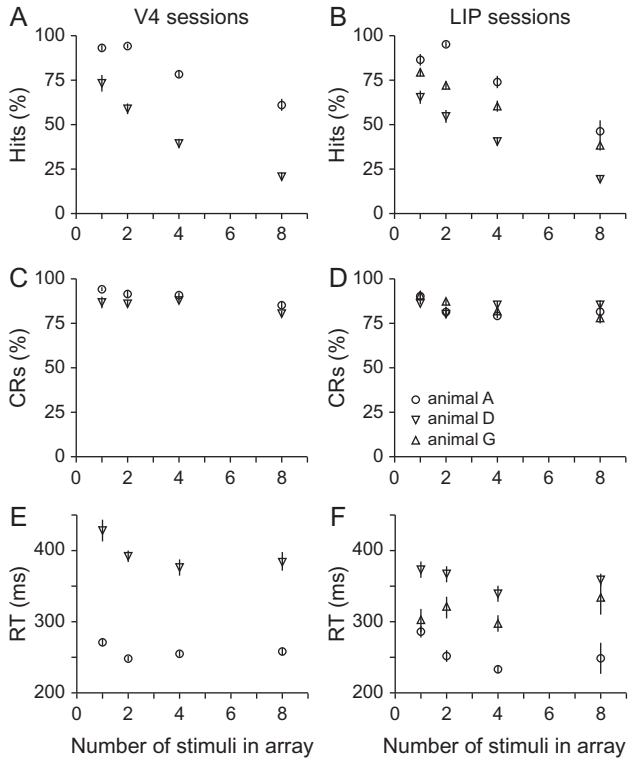

Figure 2. Behavioral performance in the change detection task. (*A*, *B*) Mean percentage of correct change trials (hits) is plotted as a function of set-size (number of stimuli in the array) for the individual animals during the V4 sessions (*A*) and the LIP sessions (*B*). (*C*, *D*) Mean percentage of correct no-change trials (correct rejections: CR) is plotted as a function of set-size for the V4 sessions (*C*) and the LIP sessions (*D*). (*E*, *F*) Mean reaction times for the individual animals during the V4 sessions (*E*) and the LIP sessions (*F*). All error bars represent SEM. Different symbols indicate each animal's performance.

responses to the preferred and the nonpreferred stimuli, however, we get qualitatively similar results when we examine only the preferred or only the nonpreferred stimuli (Fig. S1). Figure 3*A*, *B* shows the responses of example V4 and LIP neurons, respectively, to the 4 different set-sizes (S1, S2, S4, and S8). The V4 neuron shows similar patterns of activity for all set-sizes after the presentation of both arrays 1 and 2 (Fig. 3*A*). In this neuron, the responses during array 2 and the visual transient response during array 1 are similar across set-sizes. While there appears to be some differences among the set-sizes about 200–400 ms after the onset of array 1, the responses do not appear to be ordered by set-size: the traces for the S1 and S8 conditions overlie completely. The LIP neuron shows a very different pattern of activity (Fig. 3*B*). Consistent with previous studies (Balan et al. 2008; Churchland et al. 2008; Mirpour and Bisley 2012), the LIP neuron responded most vigorously for the single bar (S1) and with a monotonic decrease according to set-size. In the S4 and S8 conditions, the mean responses during arrays 1 and 2 were lower than the response before array 1 onset, suggesting that some form of inhibition may play a role in reducing the firing rates as the set-size increases. These 2 neurons were typical of the populations from which they were taken (Supplementary Fig. S2).

The mean responses of the population of the V4 (Fig. 3*C*) and LIP (Fig. 3*D*) neurons from which we recorded activity to all 4 set-sizes showed similar patterns of responses. In LIP, the mean population response varied with set-size, but in V4, the mean population response did not show any difference among the set-sizes. To quantify whether the responses for different set-sizes were significantly different within the V4 and LIP populations, we performed a running one-way ANOVA with set-size as the independent factor on the raw data using 100-ms sliding windows with 1-ms steps. Using this analysis, we find only 2 sporadic occurrences of significance in the V4 population ($F[3,35] > 4.40$, $P < 0.01$, ANOVA, main effect of set-size, black

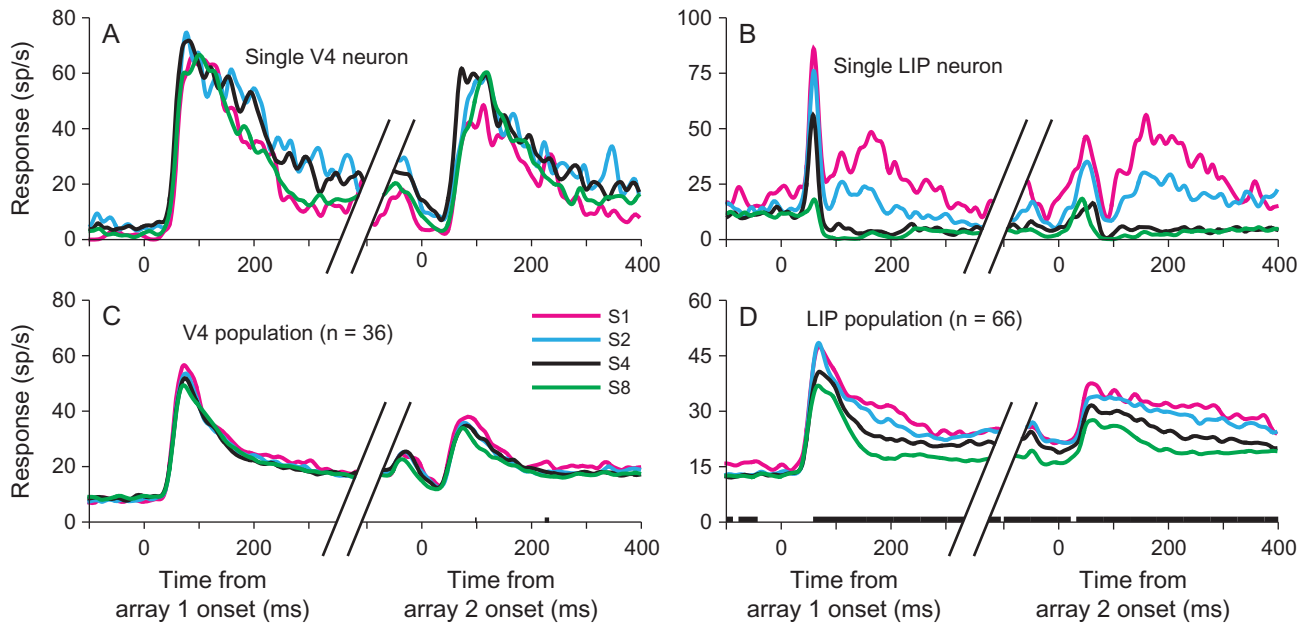

Figure 3. V4 and LIP neuronal responses to set-size during the change detection task. (*A*, *B*) Examples responses from single cells in V4 (*A*) and LIP (*B*) from all completed trials are plotted as a function of time from both array 1 and 2 onsets for different set-sizes indicated by the different colors. (*C*, *D*) mean population responses for the subset of neurons tested with all 4 set-sizes for V4 (*C*) and LIP (*D*). Horizontal dark bars on the *x*-axis indicate significant bins in which there was a significant main effect of set-size ($P < 0.01$, ANOVA using 100 ms bins every 1 ms; $F[3,35]$ for V4 and $F[3, 65]$ for LIP).

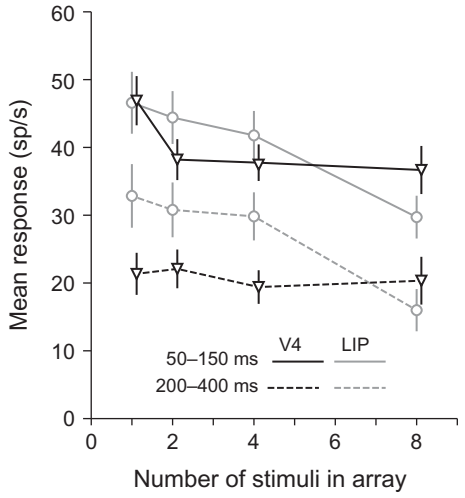

Figure 4. Mean responses of the V4 (black triangles) and LIP (gray circles) populations as a function of set-size during 2 distinct temporal periods after array 1 onset. Each point represents the mean (± SEM) response of the averaged responses for all neurons tested with that particular set-size (n = 93, 137, 173, and 82 in V4, and n = 126, 145, 157, and 106 in LIP, for S1, S2, S4, and S8, respectively). Solid lines represent responses 50–150 ms after array 1 onset, while dashed lines represent mean responses 200–400 ms after array 1 onset.

lines above the x-axis in Fig. 3C), around 100 and 220 ms after array onset. Whereas in LIP, we find almost continuous significance ($F[3,65] > 4.10$, $P < 0.01$, ANOVA; Fig. 3D). Importantly, the mean responses in LIP were ordered by set-size.

Thus far, we have focused our analyses on the subset of neurons from which we recorded all 4 set-size conditions. We now examine the average responses of all V4 and LIP neurons (Fig. 4). We calculated the mean responses for each neuron over 2 temporal periods: 50–150 ms after array 1 onset (early) and 200–400 ms after array 1 onset (late). Because different numbers of neurons were collected in each condition and because no single condition was run in all sessions, we present the mean ± SEM of the raw responses rather than normalized responses. The data were analyzed using a two-way ANOVA examining how the responses of neurons in a given area were affected by set-size and epoch. In both areas, the neuronal responses were significantly affected by epoch ($F[3,1,3] > 47$, P«0.0001). This can be seen in the data as greater responses during the early period (solid lines, Fig. 4) than during the late period (dashed lines). In LIP, we found a significant main effect of set-size ($F[3,1,3] = 6.55$, $P = 0.0002$), but no significant interaction between set-size and epoch ($F[3,1,3] = 0.28$, $P = 0.84$). This can be seen as the 2 gray lines descend in parallel as a function of set-size. The mean firing rates during the early epoch in V4 appeared to be higher for the S1 condition but dropped and stayed uniform for S2, S4, and S8. However we found neither a main effect of set-size ($F[3,1,3] = 1.7$, $P = 0.17$) nor a significant interaction ($F[3,1,3] = 1.3$, $P = 0.27$). Independent t-tests comparing the V4 responses in the early epoch across set-sizes showed borderline significance ($T[226] = 1.93$, $P = 0.055$, S1 vs. S2; $T[264] = 2.12$, $P = 0.035$, S1 vs. S4; $T[173] = 2.09$, $P = 0.038$, S1 vs. S8), none of which passed a standard Bonferroni correction ($P = 0.0167$). Moreover, V4 responses in the late period were uniform, with no comparisons coming close to significance ($Ps > 0.61$). Given the number of V4 neurons in each condition (93, 137, 173, and 82 for S1, S2, S4, and S8, respectively) and the lack of significance in the ANOVA, we conclude that there are no clear response differences among the different set-sizes in V4. Thus, we conclude that the animals were not covertly shifting their attention among locations.

Despite the lack of significance, the apparent response difference in the S1 condition during the early period in V4 and the differences in reaction times between S1 and the other set-sizes suggests that the animals could be treating trials with a set-size of 1 differently. As such, we focus on only interpreting the results from the S2, S4, and S8 conditions, however, we will plot the S1 data for comparison.

Discriminating Change From No-Change Responses as a Function of Set-Size

We have shown that during a change detection task, increasing the set-size of potential targets substantially affects the behavioral performance and that activity in LIP exhibits a decrement in mean response as the set-size increases, whereas V4 does not. However, finding that the response varied as a function of set-size does not necessarily signify that the neurons are unable to process the information equally well. For example, it could be that different sized receptive fields and larger suppressive surrounds in LIP produce a change in response gain, but the relative responses for each behavioral outcome remain the same, which would suggest that the set-size effects may have no behavioral relevance. To test whether the number of items in the array might affect performance, we examined the capacity of the V4 and LIP neuronal responses to discriminate between change and no-change trials in order to make the correct decision: either to make a saccade toward the target or to maintain fixation during a no-change trial.

As we have shown previously in LIP (Arcizet et al. 2015) and MT (Bisley et al. 2004), the responses in both V4 and LIP were greater on change trials than on no-change trials (Fig. 5A, B). To test this statistically, we ran three-way ANOVAs on the averaged population responses during a 150-ms period in each area (150–300 ms after array 2 onset, shaded area), with set-size, orientation and whether the stimulus in the receptive field had changed or not as main factors. In V4 we found a significant main effect of orientation ($F[3,1,1] = 20.1$, $P = 7.8 \times 10^{-6}$) and of whether a change had occurred ($F[3,1,1] = 22.6$, $P = 2.1 \times 10^{-6}$), but no effect of set-size ($F[3,1,1] = 1.34$, $P = 0.26$) or any interactions ($Ps > 0.31$). In LIP we found a significant main effect of set-size ($F[3,1,1] = 15.3$, $P = 7.0 \times 10^{-10}$) and of whether a change had occurred ($F[3,1,1] = 30.5$, $P = 3.7 \times 10^{-8}$), but no effect of stimulus orientation ($F[3,1,1] = 1.43$, $P = 0.23$) or any interactions ($Ps > 0.38$). Note that the lack of significance for stimulus orientation in LIP illustrates how little orientation selectivity was present: we defined the preferred orientation using passive fixation, yet the tuning was not robust enough to be seen in the task. Post hoc analyses showed that, in both areas, responses in change trials were significantly higher than responses in no-change trials ($P < 0.05$, HSD post hoc comparisons). Because V4 responses were affected by both orientation and whether the trial was a change trial or not, the responses to the nonpreferred orientation on change trials were often similar to the responses to the preferred orientation on no-change trials. So to examine how well the responses in V4 and LIP can discriminate a change or not, we restrict the following analyses to data from trials in which only the nonpreferred stimulus appeared in array 1, resulting in comparing the response to the preferred stimulus in change trials to the nonpreferred stimulus in no-change trials. So we are essentially looking at the best-case example of orientation tuning in V4 and the discrimination of a change or no-change in LIP. This is akin to the processing the animal is doing

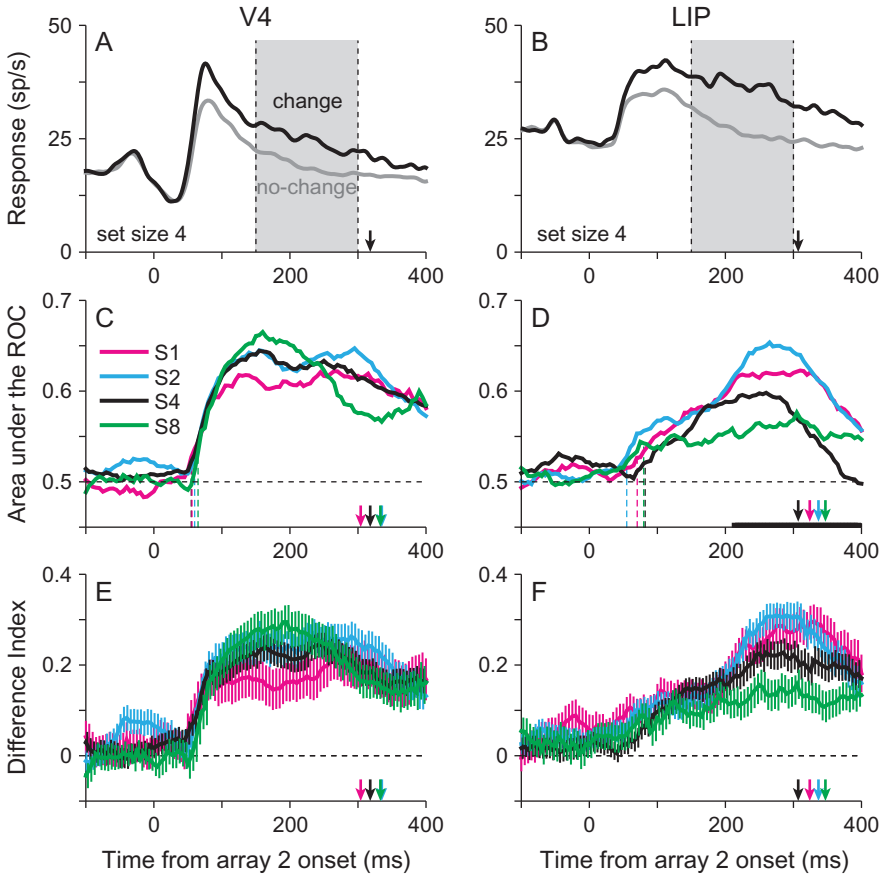

Figure 5. Response to array 2 and metrics of how well the populations could differentiate change from no-change trials. (*A*, *B*) The mean population responses from all trials in which the change occurred in the receptive field (black) and from all no-change trials (gray) as a function of time aligned on the array 2 onset for V4 (*A*) and for LIP (*B*). The shaded area shows the window in which the 2 responses were compared statistically (see text). (*C*, *D*) ROC analysis. Mean area under ROC curves for different set-sizes from responses in the V4 population (*C*) and in the LIP population (*D*). Each ROC curve was computed using the responses from change trials in which the preferred orientation was presented in the receptive field and no-change trials in which the nonpreferred orientation was presented in the receptive field. A value of 0.5 indicates chance, while a value greater than 0.5 indicates higher responses to change trials compared with nonchange trials. Vertical colored dashed lines show when the value became significantly different from 0.5 (permutation test) and the solid black line on the *x*-axis shows times when the means among the 4 traces were significantly different ($P < 0.01$, ANOVA, degrees of freedom 464 in V4 and 513 in LIP). (*E*, *F*) Mean ± SEM difference indices computed from single cells in V4 (*E*) and LIP (*F*). A difference index of 0 indicates that the neuron's mean responses in the 2 conditions were the same, while a positive index indicates that the neuron's mean response in the change condition was greater than in the no-change condition. In all panels, arrows on the *x*-axis represent the grand mean reaction times for each specific condition.

on trials in which the nonpreferred stimulus appeared in array 1: it must decide whether the stimulus presented in array 2 is the same or different to the stimulus in array 1 based on the neuronal response to the stimulus in array 2.

To examine how the activity in V4 or LIP might contribute to the performance of the task, we compared the responses during array 2 for change and no-change trials. We examined 2 metrics: the area under an ROC curve, an analysis that indicates how well an ideal observer could discriminate between the distributions of responses to change and no-change trials, and a difference index, a contrast measure that illustrates the normalized difference between the mean responses in individual cells (response to a change minus the response to a no-change, divided by the sum). For the ROC analysis, ROC curves were computed from bins of 100 ms, with increments of 5 ms. The auROC served as a measure of neuronal discriminability, that is, 0.5 indicates no discriminability between change and no-change trials while 0 and 1 indicate perfect discriminability. In our configuration, auROC values greater than 0.5 indicate that mean response on change trials was larger than the response on no-change trials.

In V4, the auROC curves started close to 0.5 and had a sharp increase about 50 ms after onset (Fig. 5*C*) and became significantly different from chance level at similar times (vertical dashed lines). Although the auROC curves appear to diverge around 150 ms and again around 300 ms, at no point were the means significantly different ($P < 0.01$, ANOVA). If anything, during the early period of the response (100–250 ms after array 2 onset), discriminability in V4 appeared to be maximal for the S8 condition. This is opposite to the animals' performance: each animal had better performance for the S2 and S4 conditions than the S8 condition. There is also a hint that the auROC values around the time of the saccade (colored arrows) mimic the behavior, with S2 being greater than S4 and S4 being greater than S8, but these differences occur too late to be driving behavior and were not significant.

The auROC data from LIP showed a very different pattern. Starting about 50 ms after array 2 onset, discriminability began to increase, but unlike V4, the curves ramped up more slowly and peaked at different levels for different set-sizes (Fig. 5*D*). For S2, S4, and S8, discriminability matched the animals' overall performance: lowest for S8, higher for S4 and highest for S2.

In each case the peak discriminability was reached roughly 50 ms before the mean saccadic latency for that condition (colored arrows). Unlike the V4 data, the mean auROCs were significantly different starting approximately 210 ms after array 2 onset ($P < 0.01$, ANOVA; black bar on *x*-axis), showing that set-size had a significant effect on our ability to tell whether a change had occurred or not based on the responses in LIP.

The difference index (DI), which utilized the mean response from each condition in each neuron, showed similar trends to the ROC analysis in both areas. In V4, the DI values started around 0 and, approximately 50 ms after array 2 onset, rose rapidly (Fig. 5*E*). The DI values then remained relatively stable for the next few hundred milliseconds. The same pattern of results was seen when we pooled the responses to both orientations (Fig. S3A). We found that the DIs were very similar for the 3 set-sizes (S2, S4, and S8); if anything there was slightly more information about whether the change had occurred in the S8 condition than the other conditions, which, as we noted above, is the opposite result that we expect based on the animals' behavior. Around the time of the saccade, there appeared to be slightly more information in the S2 condition, but the S4 and S8 conditions, which tend to produce much greater differences in performance, gave similar difference indices. In sum, both analyses suggest that V4 responds similarly under all set-sizes and that, if the animals could access this information, they should be able to perform the task as well, if not better, in the S8 condition compared with the S2 condition.

While the activity in V4 did not appear to relate to the animals' behavior, the responses recorded in LIP did. Examining the DI values in LIP (Fig. 5*F*), we found that starting about 60–70 ms after array onset, the DIs in LIP began to rise slowly, reminiscent of the accumulation of evidence seen in spike rates in LIP in the decision-making literature. As with the ROC analysis, each of the traces plateaued out at different levels that were consistent with the animals' performance: the peak DI for the S8 condition was the lowest, the peak DI for the S4 condition was in the middle and the peak DI for the S2 condition was the highest. And during the period leading up to the saccade, the error bars did not overlap. Similar, albeit less discriminable, results were seen when we pooled the responses to both orientations (Fig. S3B).

Responses as a Function of Set-Size and Behavioral Outcome

The analyses above were performed on data from all completed trials, whether the animals got the trial correct or incorrect, so it is possible that the effects we see in LIP are due to the changing proportion of correct and incorrect trials among the different set-sizes. To see whether the responses varied in V4 and LIP as a function of behavioral outcome, we sorted the neuronal data into 4 categories based on performance: hit trials, in which the bar in the response field rotated and the animal correctly made a saccade to it; miss trials, in which the bar in the response field rotated and the animal did not make a saccade to it; CR trials, in which no bar rotated and the animal correctly maintained fixation and false alarm trials, in which the bar in the response field did not rotate, but the animal made a saccade to it. Note that our definitions of misses and false alarms for this analysis are tied to behavior relative to the response field.

We start by examining neuronal responses in correct trials in the subset of neurons in which we recorded data from all 4 set-sizes. Figure 6*A*, *B* shows the mean responses of the 36 (V4; Fig. 6*A*) and 66 (LIP; Fig. 6*B*) neurons as a function of set-size and behavioral outcome: hits are represented by thick lines and CRs by thin lines. Because hits and CRs are a subset of change and no-change trials, respectively, it is not surprising that responses on hit trials are generally higher than on CR trials in either area (see Fig. 5*A*, *B* above).

In this subset of neurons, it appears that responses during hit trials and during CR trials were similar among set-sizes in V4 (Fig. 6*A*), but not in LIP (Fig. 6*B*). This is most obvious when looking at the CRs in LIP, although a close inspection of the hits in LIP shows a set-size effect early in the response. To confirm that this difference was significant in the hit trials, we ran an ANOVA in which we compared the normalized responses during a 200 ms window starting 50 ms after array 2 onset for set-sizes S2, S4, and S8. We found a significant effect of set-size ($F[2] = 9.72$, $P = 1.02 \times 10^{-4}$), with monotonically increasing normalized responses from S8 (0.782 ± 0.070) to S4 (0.952 ± 0.065) to S2 (1.26 ± 0.095). When we ran the same analysis on the V4 data from Fig. 6*A*, we found no significant effect of set size ($F[2] = 0.86$, $P = 0.425$). Notably, the response in LIP at saccade onset is similar among set-sizes (Fig. 6*C*).

To quantify these results across all the neurons, we ran an ANOVA analysis of the data using set-size, stimulus orientation and behavioral outcome as fixed variables. Set-size was implemented as a continuous variable; orientation and behavior as categorical variables and neuron as a random variable. The latter was done to effectively normalize across neurons and we will not discuss its consistent significance below. The dependent variable was the spike count in a 200 ms window starting 50 ms after array 2 onset (the "early response") or the spike

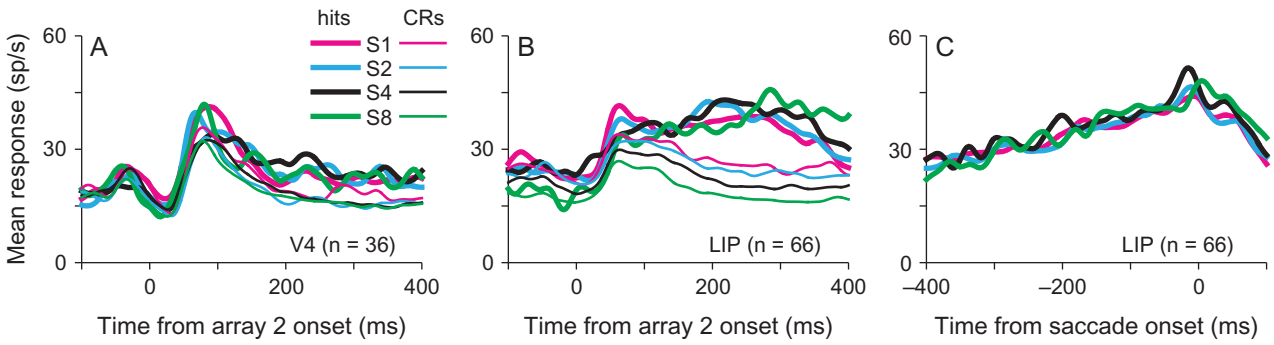

Figure 6. Response to array 2 as a function of behavioral outcome for all neurons in which all 4 set-sizes were tested. (*A*) The mean response of 36 neurons in V4 from hit trials (thick lines) and correct rejection trials (thin lines) plotted as a function of set-size. (*B*) The mean response of 66 neurons in LIP from hit trials (thick lines) and correct rejection trials (thin lines) plotted as a function of set-size. (*C*) The responses from hit trials in LIP aligned by saccade onset.

Table 1. *P*-values from the ANOVA analysis.

	Early response		Presaccadic response
	V4	LIP	LIP
Set-size	0.494	**1.78×10^{-19}**	0.850
Behavioral outcome	**2.75×10^{-3}**	**1.34×10^{-5}**	0.629
Orientation	**2.04×10^{-3}**	0.270	0.711
Set-size × outcome	0.843	0.205	**0.0296**
Set-size × orientation	0.358	0.363	0.782
Outcome × orientation	0.209	0.894	0.939

The early response refers to the spike count in a 200 ms window starting 50 ms after array 2 onset. The presaccadic response refers to the spike count in a 100 ms window starting 100 ms before saccade onset.
Bold numbers indicate significant results ($P < 0.05$).

count in the 100 ms leading up to the saccade (the "presaccadic response"); for the latter, we only included hits and false alarms as no saccades were made in the miss and CR trials.

The results of the ANOVA analysis in V4 showed that both orientation ($P = 2.75 \times 10^{-3}$) and behavioral outcome ($P = 2.04 \times 10^{-3}$) contributed to the neuronal response. The latter can be seen in Fig. 6A, where the thin lines are consistently beneath the think lines, consistent with the finding that the response to an identical stimulus was lower on a nonchange trial than on a change trial. Neither set-size nor any of the interactions were factors in driving the response (Ps > 0.20). In LIP, both the behavioral outcome ($P = 1.34 \times 10^{-5}$) and set-size ($P = 1.78 \times 10^{-19}$) contributed significantly to the neuronal response, with all other factors having *P*-values greater than 0.20 (Table 1). When we examined the presaccadic response in LIP, we found no significant effect of set-size ($P = 0.850$) or outcome ($P = 0.629$), but we found a significant interaction between the 2 ($P = 0.0296$). This was primarily driven by an effect of set-size on the false alarm responses which were slightly higher for the smaller set-sizes. An advantage of this ANOVA method is that we can establish an ANOVA model and use the coefficients to see how much influence a given factor or interaction has on the response rate. In particular, we wanted to use this as another method to see whether V4 neurons had any substantive aspect of their response driven by set-size, despite the lack of significance. We found that the coefficient for set-size in V4 was –0.047. This was an order of magnitude lower than the coefficient for orientation (0.514) and the coefficient for set-size in LIP (–0.467) and was lower than any other coefficient in the V4 data by a factor of 3.7. Thus, the results from this analysis are consistent with the hypothesis that the responses of neurons in V4 are not affected by set-size in this task.

Effect of Reward Manipulation on Responses and Discriminability

In the previous analyses, we demonstrated that when the animals have to attend multiple stimuli, the behavioral performance and LIP responses were affected by set-size, but V4 was not. Here we test the hypothesis that biasing attention to a particular location using a reward manipulation improves performance in our task and that attentional enhancement in V4 can help explain this improvement. To study this, we had the animals perform the same task with 4 stimuli with the same proportion of change and no-change trials, but presented a red fixation point and loaded one of the 4 locations with a significant larger reward (2.5 times larger than the normal). The task was identical, so the animals still had to identify changes in all 4 locations, but when they made a correct saccade to the high reward location, they received the larger reward. When the animals made correct saccades to the other 3 locations or correctly maintained fixation on no-change trials, they received the standard amount of reward.

All 3 animals consistently identified which location was rewarded with more juice: their performance was biased toward this location, both in sessions in which we recorded the responses of V4 neurons (Fig. 7A) and in the sessions in which we recorded the responses of LIP neurons (Fig. 7E). These figures show the mean percentage of trials in which a change occurred at the high reward location and the animal made a saccade to it (hits) plotted against the false alarm rate. Because false alarms can occur on both change and no-change trials, we use the false alarm rate per trial per location, calculated as the number of false alarms to that location, divided by the total number of completed trials in that block. Although we refer to this location as the high reward location, it only provided extra reward in the high reward (S4h) condition. As in all sessions, the percentage of hits decreased as the set-size increased, while the false alarm rate also decreased, but to a much lesser extent. In the high reward condition, the percentage of hits and the false alarm rate increased significantly (Ps < 1.3×10^{-5}, Wilcoxon sign-rank tests) and substantially in the high reward location compared with the same location in the S4 condition. Both changes were seen in all 3 animals.

Higher performance during the high reward conditions could be due to an increase in motivation during this block because of the overall increase in reward. If this were the case, we would expect an overall improvement in performance, however we did not find this. In the V4 sessions (Fig. 7B), the percentage of hits in the 3 locations giving the standard reward dropped slightly, but significantly ($P = 1.94 \times 10^{-5}$, Wilcoxon sign-rank test) in the high reward condition (S4h) compared with the S4 condition, but the mean false alarm rate per location did not change ($P = 0.76$). In the LIP sessions (Fig. 7F), the percentage of hits and false alarm rates per location in the remaining 3 locations were similar in the high reward conditions and the S4 conditions (Ps > 0.13). These data suggest that each animal's performance was biased toward the high reward location, while attempting to perform the task normally in the other locations.

Using the technique of Sridharan et al. (2014, 2017), we estimated criterion and d-prime, metrics from signal detection

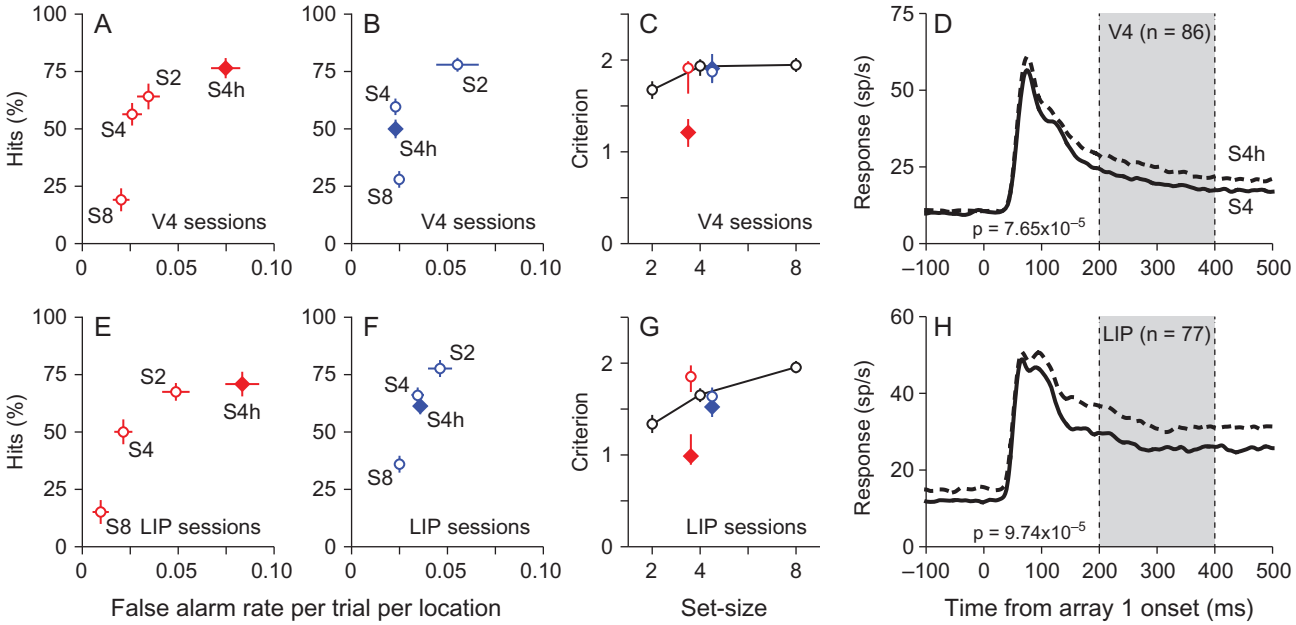

Figure 7. Effect of biasing attention to one location when 4 items were in the array. (*A*, *E*) Open circles show the mean (±SEM) percentage of hit trials plotted against the mean (±SEM) false alarm rate for set-sizes of 2, (S2), 4 (S4), and 8 (S8) in the location that would later have the high reward associated with it from V4 sessions (*A*) and LIP sessions (*E*). The solid points show the mean (±SEM) percentage of hit trials plotted against the mean (±SEM) false alarm rate at the high reward location (S4h). (*B*, *F*) Similar plots to (*A*) and (*E*), but for performance at the locations away from the high reward location in standard trials (S2, S4, and S8) and in the high reward condition (S4h) from V4 (*B*) and LIP (*F*) sessions. (*C*, *G*) Measures of criterion from the V4 (*C*) and LIP (*G*) sessions. Open black circles show criterion measures from all locations in all sessions. Red points show criterion measures from the high reward location in the S4 condition (open circles) and in the high reward block (closed diamond). Blue points show the criterion measures from the locations away from the high reward location in the S4 condition (open circles) and in the high reward block (closed diamond). (*D*, *H*) Mean responses in array 1 from blocks with 4 items in the array (S4) and from blocks with the high reward condition (S4h). The shaded area shows the window in which the 2 responses were compared statistically (*P*-values from the Wilcoxon sign-rank test are presented).

theory, from our behavioral data (Supplementary Fig. S4). In Figure 7*C*, *G*, we plot the median±standard error of the median criterion as a function of set-size (open black circles) and for the S4 and S4h conditions. At the high reward location (red points), the increased hit and false alarm rates resulted in a significant reduction in criterion in the high reward condition (solid red diamonds) compared with the standard S4 condition (open red circles; $P = 2.208 \times 10–6$ in V4 and $2.807 \times 10–5$ in LIP; Wilcoxon sign-rank tests), but d-prime did not change (Supplementary Fig. S4B, D; $P > 0.17$). Although we noted a slight reduction in hit rates at the remaining 3 locations (Fig. 7*B*, *F*), we found no difference in criterion between the high reward condition (solid blue diamonds) and the standard S4 condition (open blue circles; $P > 0.11$). There was a trend for slightly lower d-primes in the high reward condition ($P = 0.0612$ in V4 and $P = 0.0319$ in LIP; Supplementary Fig. S4B, D), but these did not pass the Bonferroni corrected threshold of 0.00625. Thus, in a signal detection theory framework, the only clear effect in the high reward condition was to lower criterion at the high reward location.

Mean neuronal responses in both V4 and LIP increased at the high reward location when the animals attended that location. Figure 7*D* illustrates the mean response to array 1 of the population of V4 neurons pooling from both the preferred and nonpreferred orientations in the S4 and S4h conditions. We focus on the response to array 1 because the activity cannot be biased by any decision-making processes that may occur after the second array appears. We found that the mean response in the S4h condition was significantly higher than the response in the S4 condition, 200–400 ms after array 1 onset ($P = 7.65 \times 10^{-5}$, Wilcoxon Sign-Rank test; gray window Fig. 7*D*), illustrating the presence of an attentional enhancement. So by biasing the animals' attention to a particular location using a high reward, we were able to induce a modulation of V4 responses that we did not see while varying the set-size. Similarly, we found a robust increase in LIP mean response in the high reward condition ($P = 9.74 \times 10^{-5}$, gray window Fig. 7*H*). In addition, we found a slight, but significant ($P = 1.68 \times 10^{-5}$) increase in the response prior to array 1 onset (from −100 to 0 ms) that was not present in V4 ($P = 0.21$), suggesting that in this task, attention not only increases the response to the stimulus, but has a modulatory effect on the baseline activity in LIP. This can occur because trials in the high reward condition were presented in a block. The responses to array 2 were also modulated by attention, giving significantly higher responses in the S4h condition than the S4 condition early in the response ($P = 0.039$ in V4 and $P = 0.0064$ in LIP, 50–200 ms after array 2 onset) and later, when the decision was being indicated ($P = 0.0096$ in V4 and $P = 0.004$ in LIP, 200–400 ms after array 2 onset).

Although manipulating the reward amount dramatically improved the animals' performance at the high reward location, we found that the information provided by the V4 population was mostly unchanged. Figure 8*A*, *C* illustrates that both the auROC and the DI measures for the S4h condition (gray traces) from the V4 population response were similar to the values in the S4 condition at the same location (black trace). There was a slight increase in the auROC starting about 300 ms after array 2 onset, but this occurred after the mean saccadic reaction time and was not significant ($P > 0.01$, ANOVA). This means that the gain change in the V4 responses had no significant effect on helping the neuron discriminate between the different outcomes (a change or no change). This is probably because the orientation difference is 90° and the population

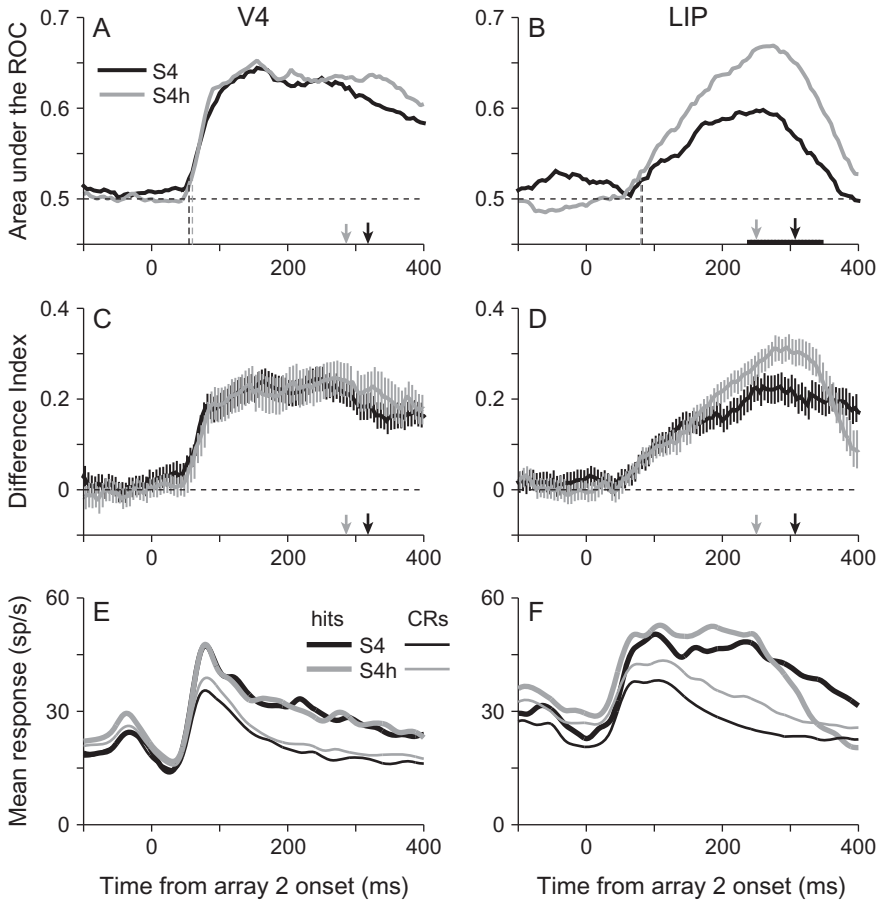

Figure 8. Discriminating change from no-change trials under conditions of spread and biased attention. (*A*, *B*) ROC analysis. Mean area under ROC curves for the standard block of set-size 4 (S4) and the block in which the animal received a higher reward for correct saccades to the receptive field (S4h) from responses in the V4 population (*A*) and in the LIP population (*B*). Vertical dashed lines show when the value became significantly different from 0.5 (permutation test) and the solid black line on the *x*-axis shows times when the means between the 2 traces were significantly different ($P < 0.01$, ANOVA; $n = 173$ and 86 for S4 and S4h in V4 and $n = 157$ and 108 for S4 and S4h in LIP). (*C*, *D*) Mean ± SEM difference indices computed from single cells in V4 (*C*) and LIP (*D*) from the same 2 conditions. Arrows on the *x*-axis represent the grand mean reaction times for each specific condition. (*E*, *F*) The mean response of 36 neurons in V4 (*E*) and 66 neurons in LIP (*F*) from hit trials (thick lines) and correct rejection trials (thin lines) in the S4 and S4h conditions.

already does a good job of differentiating between stimuli. Consistent with this, we found that the responses on hit and CR trials were very similar between the 2 conditions (Fig. 8*E*), with only a slight significant difference seen between the S4 and S4h conditions in CR trials ($P = 0.0495$, $n = 86$, paired *t*-test, 50–250 ms after array 2 onset). These data support the conclusion that performance in this task does not seem to be limited by the activity in V4. In addition, they imply that the attentional modulation seen in V4 does not directly explain the large increase in performance seen when attention is focused at a particular location.

Attending to the high reward location had a more complex effect on the LIP population response: not only did the mean response increase, but the ability to discriminate whether a change had occurred or not was substantially improved. We found that the auROC in the S4h condition (gray trace, Fig. 8*B*) ramped up at a much higher rate than in the S4 condition (black trace) and reached a significantly higher level. This illustrates a clear effect of attention on the ability of the population of LIP neurons to indicate whether a change occurred or not. Under the high reward condition, the DI initially started equal to the S4 condition, but ramped up to give much higher DI values and in which the error bars did not overlap starting approximately 200 ms after array 2 onset (Fig. 8*D*). Because these analyses include all trials, it is possible that the differences we see in Figure 8*B*, *D* are due to differences in the reaction times and proportion of saccade trials between the 2 conditions. To account for this, we plotted the neuronal activity from only correct trials (Fig. 8*F*). While we found that the high reward condition had a similar effect on hits and CRs in area V4 (Fig. 8*E*), there were several differences in LIP (Fig. 8*F*). The difference in response between the S4 and S4h conditions was clearly present prior to array 2 onset in both hit trials ($P = 0.0076$, paired *t*-test, 100 ms window from 50 ms before array two onset) and CR trials ($P = 2.52 \times 10–5$). This difference between S4 and S4h quickly disappeared in hit trials ($P = 0.139$, 50–250 ms after array 2 onset), but remained significant in CR trials ($P = 0.0034$, $n = 77$, paired *t*-test, 50–250 ms after array 2 onset), similar to the set-size effects seen in Figure 6*B*. And, consistent with the set-size data (Fig. 6*C*), the activity in hit trials ramped to an equivalent response at the time of the saccade ($P = 0.140$, 100 ms window before saccade onset). Together, our data show that the activity of single LIP neurons and the LIP population as a whole, can identify changes in orientation that

matched the animals' performance, both as the set-size changed and when attention was biased toward one location whereas the V4 data do not.

Discussion

A key aim of this study was to see whether, under conditions in which behavior in a change detection task is affected by set-size, neuronal responses in V4 or LIP matched performance. We found that the activity in V4 was relatively robust: as the number of stimuli in the array grew, the response and ability to discriminate a change in orientation remained constant even though performance dropped substantially. Further, while manipulating reward dramatically improved hit rates, the discriminability in V4 still did not change. These data suggest that in this task V4 primarily acts as a visual area and that attentional enhancement is not sufficient to explain the large increase in performance when attention was biased to one location. On the other hand, neuronal responses in LIP changed considerably and not only in magnitude: the resulting activity discriminated change from no-change trials more effectively at lower set-sizes, which matched behavior both under spread attention and when attention was biased to the high reward location.

Our finding, that attentional modulation in early visual areas is insufficient to explain performance when multiple items are present, fits well with a previous study that showed that after inactivating the SC and drastically affecting behavioral performance, attentional modulation was still present in areas MT and MST (Zenon and Krauzlis 2012). In both their study and ours, attentional modulation in visual cortex was disconnected from behavior, suggesting that another neural mechanism must be involved in underlying the behavioral benefits of attention. We believe that their data and our data can best be explained not by changes in processing in visual areas (Moran and Desimone 1985; Treue and Maunsell 1996; Reynolds et al. 1999; Fries et al. 2001; Martinez-Trujillo and Treue 2002; Cohen and Maunsell 2010), but by a mechanism that limits how much or which information from the visual system advances to other areas in the brain for further processing. Several previous studies of human cortex have shown that activity in visual areas does not limit behavioral performance (Pestilli et al. 2011; Wyart et al. 2015) and have suggested such a gating mechanism, as has a voltage-sensitive dye imaging study in primate V1, which found that attentional modulation does not vary with set-size (Chen and Seidemann 2012). Our data are not completely consistent with that study: they found that the responses in V1 under focused attention were similar to the responses with spread attention, whereas we clearly found biasing attention to the receptive field increased the response in V4. There are a number of differences between the studies that may account for this difference, such as the different recording techniques, behavioral tasks, or possible differences between V1 and V4 dynamics. Indeed, several other studies (Patzwahl and Treue 2009; Khayat and Martinez-Trujillo 2015; Mayo and Maunsell 2016) have found that the response to one of a pair of stimuli can be somewhere between the response elicited when attended and elicited when ignored. We found a hint of this in the small and marginally significant difference in response between the S1 and S2 conditions in the early period of the V4 response. However, when looking among conditions in which multiple objects were present, we found no differences in response, but a strong effect on behavior.

Two other recent studies have also opined on the limited role that attentional modulation in V4 may play in performance. By manipulating absolute and relative reward magnitudes in V4, Baruni et al. (2015) showed that changes in V4 activity could be disambiguated from changes in attentional behavior. It is worth noting that the enhancement we see in V4 in our task is consistent with their finding that the modulation is due to reward size and may not be related to attention per se. Luo and Maunsell (2015), on the other hand, used an RSVP style change detection task and modeled the behavior using signal detection theory to show that attentional modulation and noise correlation in V4 tend to correlate with shifts in sensitivity, but not shifts in criteria. Critically, they argue that the broad term "attention" may encompass many neuronal mechanisms and that it is of fundamental importance to focus on the specific mechanism that may underlie a specific behavior: a sentiment that our data fully support.

Others have previously found set-size effects in the responses of LIP neurons (Balan et al. 2008; Churchland et al. 2008; Mirpour and Bisley 2012). It has been suggested that this is due to a divisive normalization process (Louie et al. 2011; Mirpour and Bisley 2012) rather than a function of uncertainty (Basso and Wurtz 1997, 1998) because the responses in LIP vary as a function of set-size independent of stimulus certainty (Mirpour and Bisley 2012). One mechanism by which this could occur is through long range inhibition. Previous work has illustrated this sort of suppression in LIP (Falkner et al. 2010) and the response illustrated by our single neuron example (Fig. 3B) is consistent with this idea. Importantly, it was not just the raw neuronal responses that were affected by set-size and, then, positively by the high reward, but our ability to discriminate whether a change had occurred or not. We interpret this to mean that LIP, which is only one step removed from many visual areas (Blatt et al. 1990; Lewis and Van Essen 2000), or the processing that occurs in this step (Ruff and Cohen 2016) may be critical in limiting how much of the visual world we can attend to. This interpretation is consistent with studies examining the limitations of working memory (Buschman et al. 2011), which is intertwined with attention (Fusser et al. 2011; Zelinsky and Bisley 2015) and is also consistent with the finding that the detection of changes in change blindness is mediated by posterior parietal cortex (Pessoa and Ungerleider 2004; Beck et al. 2006; Tseng et al. 2010).

We tend to think of LIP as a priority map that is involved in guiding covert and overt attention (Bisley and Goldberg 2010; Zelinsky and Bisley 2015). Under this assumption, one may wonder why the set-size effect in LIP does not affect responses in V4 when attention is spread. We previously found that when activity in LIP was balanced, with 2 peaks of equal heights, there was no behavioral benefit of attention at either location: contrast sensitivity was the same at each location (Bisley and Goldberg 2003). A logical inference from that result could be that no attentional benefit should be seen when there are multiple peaks of equal height—as when attention is spread—thus, no attentional enhancement should be seen in the neuronal responses in visual cortex under the same conditions. Thus, when 4 stimuli are present, our results imply that attentional enhancement in visual areas is only present when attention is focused at a location (Moran and Desimone 1985; Reynolds et al. 2000) or to a particular feature (Treue and Martinez Trujillo 1999; Bichot et al. 2005) as we illustrated with the high reward condition.

One previous study found some set-size effects on response magnitude in V4 (Burrows and Moore 2009). There are several

differences between their stimulus arrays and ours that are likely to explain the different results. While we positioned our stimuli on an imaginary circle around fixation and just increased the number of stimuli on the circle, their stimuli were in a compact grid, with one stimulus in the receptive field and the neighboring stimuli in the surround. As they increased set-size, they increased the size of the grid, keeping separation between stimuli constant. Further, their stimuli were more akin to large versions of arrays used to induce crowding (Motter 1993; Harrison et al. 2013), than those used to test behavioral set-size effects in search or change blindness. Moreover the set-size effect they described concerned popout modulation, that is, the capacity to discriminate between popout stimuli and conjunction stimuli, and it is not clear how to interpret this set-size effect in terms of our task. Thus we think it likely that in V4, the neural mechanisms that influence crowding may be due to local inhibition, which would create a set-size effect, but that does not come into play when stimuli are spread far apart. Nonetheless, it is possible that a similar mechanism is creating the set-size effects we see in LIP, implying that lateral inhibition can differentially affect behavior depending on the cortical area in which it occurs.

Change Detection in a Decision Making Framework

Although speculative, we believe that we can explain numerous aspects of behavior that are commonly attributed to a limited capacity of attention using the data presented here combined with theories of decision making in change detection (Pashler 1988), in search (Dosher et al. 2004) and in LIP (Churchland et al. 2008). Our underlying idea (Arcizet et al. 2015) is that there is some form of a rise-to-threshold mechanism (Bogacz et al. 2007; Ratcliff and McKoon 2008; Noorani and Carpenter 2016) occurring at each location in which a bar appears. Evidence that the bar in that location changed orientation is accumulated and if it reaches a threshold, then the decision to make a saccade to that location has been made. This means that the evidence being accumulated in this task is not the raw response from whichever area LIP is receiving pertinent activity, but the evidence that a change was made. Because we include many no-change trials, we must add to our framework the idea of a temporal deadline or quitting threshold (Wolfe and Van Wert 2010); if no decision has been made to make a saccade to a bar within the temporal deadline, then the animal maintains fixation. Given the much greater chance of receiving a reward for maintaining fixation than for making a saccade to one of the 4 or 8 bars when uncertain about what response to make, we suggest that the animals have a relatively short deadline (Arcizet et al. 2015), consistent with our finding that they trade off speed for accuracy.

To explain much of the behavior, we need only incorporate the divisive normalization within LIP into this framework. In doing so, a similar input from visual cortex will have less influence in LIP when more items are present, resulting in a lower starting point (Fig. 6*B*) and slower accumulation of information indicating whether a change occurred or not. If no temporal deadline were present, then this would produce a clean set-size effect in reaction times, but given our animals' biases to trade off speed for accuracy, this results in a greater proportion of misses as more trials will lead to the temporal deadline being reached. Having a similar threshold across set-size blocks, as shown in Figure 6*C*, also explains why the false alarm rate per location, as shown in Figure 7, decreases with set-size: the activity starts at a lower level and accumulates more slowly, so it is less likely to hit the choice threshold before it hits the deadline with higher set-sizes.

Viewing our change detection data in this framework suggests a possible role for attentional enhancement in visual areas. As the normalization in LIP reduces the impact of the incoming visual evidence with greater set-size, focusing attention at one location increases the responses in V4, effectively increasing the gain from that location. This increase in input will have 2 consequences: it will reduce the accumulation at other locations, due to the divisive normalization and it will increase the starting response (Fig. 8*F*) and rate of accumulation at the attended location, increasing the probability that it will hit the choice threshold and shorten reaction times. In fact, when we compare reaction times within sessions in which we ran both S4 and S4h conditions, we found that mean ± SD reaction times dropped in the high reward location from 339 ± 104 ms in the standard S4 condition to 271 ± 78 ms with the high reward ($P = 2.21 \times 10^{-4}$, *t*-test). Reaction times in the remaining 3 locations remained similar in the 2 blocks (294 ± 56 ms compared with 282 ± 58 ms, $P = 0.211$). It also explains the increase in number of false alarm errors at the high reward location (Fig. 7*A*, *D*): increasing the input gain will increase the chance that a no-change response will result in the accumulated evidence crossing the choice threshold. Note that in decision-making theory, increasing the input gain or rate of accumulation is effectively the same as moving the choice threshold under different conditions. We expect these effects to work in parallel with any changes brought about by underlying biases in performance (Rao et al. 2012).

Although we have outlined our framework as a rise-to-threshold mechanism, it is not incompatible with our signal detection theory results. If attentional modulation in V4 only represents a change in sensitivity (Luo and Maunsell 2015) and V4 activity does not correlate with behavior in this task, then one would predict that the effects of changing set-size are due to a shift in criterion and that this might be represented in LIP. However, we found that both d-prime and criteria changed as a function of set-size (black symbols, Supplementary Fig. S4), suggesting that both can be affected outside of V4, where activity did not change. When the high reward condition was introduced, we found that activity changed in both V4 and LIP, but only a change in criterion affected performance. This suggests that modulations of activity in V4 can correlate with changes in sensitivity (Luo and Maunsell 2015) or criterion, depending on the task. Importantly, the neural mechanisms we proposed above to explain the behavior could also explain these changes in the signal detection theory metrics.

In sum, many behavioral features of set-size effects can be explained by normalization in LIP and the benefits of focused attention in change detection can be explained by the attentional modulation in earlier visual areas, but only in terms of how it affects evidence of a change occurring in LIP and not in sensory processing in area V4. We note that LIP is most likely working in concert with areas it projects to, in particular the SC and FEF, both areas involved in decision making (Kim and Basso 2008; Ding and Gold 2012; Purcell et al. 2012) and guiding covert attention (Moore and Armstrong 2003; Ignashchenkova et al. 2004; Cohen et al. 2009; Lovejoy and Krauzlis 2010). We use LIP here as an exemplar of this circuit.

Supplementary Material

Supplementary data is available at *Cerebral Cortex* online.

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