Activity in V4 Reflects the Direction, But Not the Latency, of Saccades During Visual Search

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Gee AL, Ipata AE, Goldberg ME. Activity in V4 reflects the direction, but not the latency, of saccades during visual search. J Neurophysiol 104: 2187–2193, 2010. First published July 7, 2010; doi:10.1152/jn.00898.2009. We constantly make eye movements to bring objects of interest onto the fovea for more detailed processing. Activity in area V4, a prestriate visual area, is enhanced at the location corresponding to the target of an eye movement. However, the precise role of activity in V4 in relation to these saccades and the modulation of other cortical areas in the oculomotor system remains unknown. V4 could be a source of visual feature information used to select the eye movement, or alternatively, it could reflect the locus of spatial attention. To test these hypotheses, we trained monkeys on a visual search task in which they were free to move their eyes. We found that activity in area V4 reflected the direction of the upcoming saccade but did not predict the latency of the saccade in contrast to activity in the lateral intraparietal area (LIP). We suggest that the signals in V4, unlike those in LIP, are not directly involved in the generation of the saccade itself but rather are more closely linked to visual perception and attention. Although V4 and LIP have different roles in spatial attention and preparing eye movements, they likely perform complimentary processes during visual search.

INTRODUCTION

In everyday life, we are constantly confronted with an overwhelming amount of visual information. We naturally shift our eye gaze to focus on behaviorally relevant objects in the scene at the expense of others. This search behavior allows us to place the object of interest on the high acuity region of the retina for further processing. The mechanisms in the brain that underlie how we select a search target still remain unclear. In most natural environments, the viewer rarely knows the location of a relevant object but rather searches for it based on features such as shape and color.

Previous studies showed that V4, a prestriate visual association area, has presaccadic activity. In highly constrained tasks, Fischer and Boch (1981) showed presaccadic activity in area V4 to preferred line orientations. Tolas et al. (2001) documented a shift in receptive field toward the location of the impending saccade. In more naturalistic free viewing visual search tasks with less constraints on eye movements, selection of the stimulus in the receptive field for a saccade led to enhanced activity in V4 (Bichot et al. 2005; Mazer and Gallant 1983) and is selective for complex attributes such as shape and color (Gallant et al. 1993; Gattass et al. 1988; Pasupathy and Connor 1999; Schein and Desimone 1990). V4 also projects mainly to inferior temporal cortex (Ungerleider et al. 1983) and is selective for complex attributes such as shape and color (Gallant et al. 1993; Gattass et al. 1988; Pasupathy and Connor 1999; Schein and Desimone 1990). V4 also projects to areas important for spatial information and oculomotor planning to pin visual attention to the saccade endpoint. V4 and LIP can complement each other in their roles of spatial attention and saccade generation during visual search.

METHODS

We used two male rhesus monkeys (Macaca mulatta) weighing 8–14 kg. All experimental protocols were approved by the Animal Care and Use Committees at Columbia University and the New York State Psychiatric Institute as complying with the guidelines established in the Public Health Service Guide for the Care and Use of Laboratory Animals.

Behavior

We trained two experimentally naïve monkeys on three tasks: standard visually guided and memory-guided delayed saccade tasks and a free-viewing visual search task. These tasks were used to

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address a variety of questions concerning visual search in both LIP and V4. For this particular experiment, the visually guided saccade task was used to select V4 neurons for recording, and the search task was used to address the role of V4 during visual search. We trained the monkeys on the search task before any surgery so there were initially no fixation constraints. In the search task, they had to report the orientation of a target among distractors (Fig. 1A, Ipata et al. 2006). Each trial started when the monkey grabbed two bars, one with each hand. A small white central fixation point appeared in the center of a black background. If the monkey maintained fixation inside a 3 × 3° window for 1–1.75 s, the fixation point disappeared and an array of six or eight stimuli appeared, depending on the eccentricity of the receptive field of the isolated neuron. The array consisted of a target and five or seven distractors that were positioned symmetrically around an imaginary circle, centered on the former fixation spot, such that one object was always in the center of the neuron’s receptive field. On each trial, the relative position of all the stimuli changed randomly. The target was a white capital T that could be upright or inverted. The orientation of the target and its location on each trial were unpredictable. All but one of the distractors had the same dimensions, color, and luminance as the target but differed only in the position where the horizontal component crossed the vertical component. In certain sessions, one of the distractors, designated the popout distractor, had the same dimensions as the other distractors but popped out by virtue of its color and luminance. In this study, we did not examine the responses to this stimulus. Monkeys were rewarded for reporting the orientation of the target by releasing one of the two bars (the left bar when the target was the upright capital T and the right bar when the target was the inverted capital T). An error trial occurred only if the monkey released the incorrect bar. Monkeys were free to move their gaze and did not need to fixate the target to receive the reward. They were given 3 s to respond correctly. After that time period, the trial aborted. After the monkey reached asymptotic performance (~98% correct), we prepared them surgically for head restraint, eye position tracking, and neuronal recording and then trained them on the delayed saccade tasks. In the delayed saccade task, the monkeys fixated a small white central fixation target. After fixating for 1–1.75 s (chosen pseudorandomly), a saccade target appeared for 50 ms (for the memory-guided task) or for the duration of the trial (in the visually guided task). After a delay period of ~1,000 ms after the onset of the saccade target, the fixation point disappeared, and the monkeys were rewarded for making a saccade to the location of the target within 500 ms. We controlled all experiments using the REX system (Hays et al. 1982).

**Surgery**

After the monkeys learned the search task, we implanted subconjunctival scleral search coils for the measurement of eye position, a head restraining device, and recording chambers (either a 2-cm circular chamber or a 2 × 3-mm oval chamber) implanted during aseptic surgery under ketamine and isoflurane anesthesia. Each monkey in this study had a chamber also implanted over LIP. In one monkey, we recorded from LIP before we recorded from V4. We positioned the chambers over ventral area V4 at 25 mm lateral and 8 mm posterior from the midpoint guided by MRIs.

**Recording**

We recorded single neurons from area V4 with glass-insulated tungsten electrodes (Alpha Omega Engineering). We introduced the electrodes through a guide tube positioned in a 1-mm spaced grid. To amplify, filter, and discriminate action potentials, we used an amplitude window discriminator (MEX, developed by Dr. John McClurkin at the Laboratory of Sensorimotor Research of the National Eye Institute, running a Dell Optiplex PC running the QNX operating system).

Once we isolated a neuron, we mapped the receptive field by positioning an object in different locations in the visual field while monkeys performed the visually guided saccade task. We studied a total of 111 neurons in V4 (60 from monkey A; 51 from monkey R). After we mapped the receptive field location, we characterized the response of the neuron to orientation, shape, and color. Every neuron we studied responded significantly to at least one set of target and distractors used in the search task.

After we mapped the receptive field and characterized the neuron, we recorded from the same neuron while the monkey performed the free-viewing visual search task. In this study, we analyzed the activity of the neurons during the interval between the onset of the array and the onset of the first saccade.

**Data analysis**

We wrote all data analysis programs in Matlab (Mathworks). To examine the pattern of activity, we calculated spike-density functions by convolving the spike train, sampled at 1 kHz, with a Gaussian of σ 10 ms. We defined the neuronal response for an interval of interest as the mean of the spike density over the interval. To create the population data, we took the square root of every data point from all the spike-density functions for that cell. We divided each value by the total mean of the square-rooted values from all the functions. We used this square root normalization method to decrease the effect of outliers, which is a standard way of normalization (Wilson and Martinez 1997). We performed more detailed analyses on actual spike counts taken from 50-ms epochs.

We mapped receptive fields using a visually guided delay saccade task and by adjusting the target position by hand. We used this task to characterize the visual response of the cells and found that all neurons had significant visual activity. We identified the receptive field of a neuron as the locations in which the visual response was significantly different from background activity and ≥75% than background activity. The 75% criteria allowed us to position the object in the receptive field and classify locations that were not in the receptive field. In some cells, the visual response at adjacent locations (flanks) was significantly greater than background but was not 75% greater than the background activity. In our analysis, we used data from the array position that evoked the maximal response, and we excluded from all analyses the flank array positions that evoked significant but submaximal responses. All of the remaining locations have been classified as outside the receptive field, and we will refer to these positions when we want to specify that the direction of the saccade is outside the receptive field. We also excluded from the analysis trials in which the first saccade had a latency of <80 ms to remove saccades that had been planned before the array appeared. These exclusions were all post hoc so that, during the session, the probability that the search target appeared in each location was equal, and the monkeys’ performance was similar for targets at each location.

When the fixation point appeared, the monkey had to maintain fixation in a 3 × 3° window. We noted that the monkey actually maintained a fixation window in a smaller portion of space. *Monkey A* on average had a fixation span including 2 SE of 0.16 × 0.87° and *monkey R* had a fixation span including 2 SE of 0.15 × 0.58°. Both are well within the fixation limits used for V4 experiments, which have been documented. For instance, Reynolds and Desimone (2003) used a window of 1.2 × 1.2° and McAdams and Maunsell (1990) used a window of 1.4 × 1.4°. Therefore small changes in fixation position are unlikely to affect the neural response. More detailed analysis of fixational eye movements are described in **RESULTS**.

We compared trials in which the monkey made a saccade to the receptive field with trials in which the monkey made a saccade away from the receptive field and the flanks. To calculate the time at which the activity from these two types of trials started to separate, we used a sliding window test. For each millisecond, we calculated the activity in a 50-ms bin centered at that time for each class of response. We
compared the activity in each pair of bins using a two-tailed \( t \)-test. We performed a Lilliefors test for normality that showed that the data have a normal distribution, which allowed us to use the two-tailed \( t \)-test. We defined the time of separation as the first bin of 20 of 25 consecutive bins that all had \( P < 0.05 \). Cells that showed separation after the onset of the first saccade were excluded from additional analysis.

**RESULTS**

**Behavior**

Both monkeys performed the visually guided saccade task correctly on \( \geq 99\% \) of the trials and the search task correctly on \( >95\% \) of the trials. On average, they made 1.7 saccades. Both monkeys always fixated on an object in the array and often fixated the target on the first saccade even though they were not required to do so. In the search task, monkey A had an average saccadic latency of 163 ± 19 ms and monkey R had an average saccadic latency of 184 ± 27 ms (Fig. 1, B and C, histograms).

**V4 activity and saccade goal selection**

We recorded the activity of 111 neurons in area V4 from two monkeys (60 in monkey A and 51 in monkey R). The activity in area V4 distinguished the direction of the upcoming saccade (Fig. 1, B and C). The responses diverged such that the population was more active when the monkey was going to make the saccade to the receptive field (solid trace, Fig. 1, B and C) rather than when the monkey was going to make the saccade away from the receptive field (dotted trace, Fig. 1, B and C). This effect of the saccade direction was significant both when there was a target in the receptive field and also when there was a distractor in the receptive field (Wilcoxon signed-rank test; monkey A, \( P = 0.015 \); monkey R, \( P = 0.01 \)). Thus we combined all trials regardless of the object inside the receptive field and only grouped trials according to saccade direction.

This response modulation for saccade direction was not dependant on fixational eye movements. The average fixation position during 0–50 ms after the array appeared was not significantly different for trials in which saccades were made to the receptive field versus away from the receptive field for 101/111 cells (standard \( t \)-test, \( P > 0.05 \)). If we eliminate the 10 cells that showed significance for average fixation position from the upcoming population analysis, the results remain the same. In addition, individual analysis of these cells shows that they reflect the overall distribution of cells in the population. The population data showed similar results. The average fixation position was not significantly different at the 0.05 level for trials in which saccades were made to the receptive field versus for trials in which saccades were made away from the receptive field during 0–50 ms after the array appeared (standard \( t \)-test: \( P = 0.75 \) and 0.90 for \( x \) and \( y \) positions, respectively, for monkey A; \( P = 0.87 \) and 0.78 for \( x \) and \( y \) positions, respectively, for monkey R). There was also no significant difference at ±20 ms surrounding the average time at which the saccade goal was selected (standard \( t \)-test: \( P = 0.20 \) and 0.48 for \( x \) and \( y \) positions, respectively, for monkey A; \( P = 0.55 \) and 0.08 for \( x \) and \( y \) positions, respectively, for monkey R). We did not find a significant difference in mean fixation position that reflects average eye movements made during the fixation period. Thus fixational eye movements did not affect the response of V4 neurons in the selection of the saccade goal.

We calculated the time at which the monkey’s choice of the saccade goal was clearly present in V4 by using a sliding window analysis described above. We call the time at which there was a reliable discrimination in the direction of the upcoming saccade goal the “selection time.” This corresponds to the time at which the two spike-density functions significantly diverge in Fig. 1, B and C. In monkey A, the selection time of the saccade goal emerged in the population at 112 ms after the onset of the array, and in monkey R, it occurred at 114 ms after the onset of the array. Under conditions of free-viewing visual search, activity in the population of V4 neurons clearly correlates with the monkeys’ selection of the saccade goal.

The majority of the neurons showed enhanced activity when the monkey made a saccade into the receptive field relative to...
when the monkey made a saccade away from it. This effect can be seen in the population level in the interval from 100 to 150 ms after the array onset \((P < 0.0001\) for both monkeys by Wilcoxon signed-rank test; Fig. 2, A and C). This effect was also evident at the single neuron level: 21/60 cells in monkey A and 26/51 cells in monkey R showed a significantly higher activity when the monkey made a saccade into the receptive field during the same interval from 100 to 150 ms after the array onset (standard \(t\)-test, \(P < 0.05\)). This difference became more evident during the 50-ms time window directly preceding the saccade. All but 12 cells in monkey A and 5 cells in monkey R had higher activity when the monkey made a saccade into the receptive field, which was significant at the population level \((P < 0.0001\) for both monkeys by Wilcoxon signed-rank test; Fig. 2, A and D). Twenty-two of 60 cells in monkey A and 38/51 cells in monkey R showed a significant difference in activity depending on the saccade goal selection (standard \(t\)-test, \(P < 0.05\)). Both at the population level and at the single neuron level, it is clear that activity in V4 predicts the direction of the upcoming saccade.

**V4 activity and saccadic latency**

The time at which V4 reliably distinguished the direction of the impending saccade did not correlate with the latency of the saccade for the majority of the neurons. To show this relationship, we divided trials from each neuron into two groups based on the latency of the saccade: a short and a long latency group (Fig. 3A). This grouping allowed us to ask if the time at which the activity in V4 identified the saccade goal, the selection time (the time at which the 2 activities significantly diverged according to saccade direction; solid and dotted traces in Fig. 1, B and C) is tied to the initiation of the saccade (Fig. 3A). If the activity in V4 is completely unrelated to the saccade, the selection time calculated from the array onset should be the same for both short and long latency saccade trials (cf. gray and dotted lines in Fig. 3A). The selection time calculated relative to the array onset or the saccade onset. Two hypotheses are shown. Dotted line: selection time is constant for short and long latency trials. The variability in saccadic latency does not come from variability in selection time in V4, so V4 would not directly initiate the saccade. Solid line: selection time is longer for long latency trials. The variability in saccadic latency comes from variability in selection time in V4 so V4 could initiate the saccade. B: selection time from array onset is plotted against the saccade latency for the 2 above hypotheses. A–C modified from Bisley et al. (2008). D: the time from array onset to selection time is plotted against the mean 1st saccadic latency for each group for each cell for both monkeys. E: the time from selection time to saccade onset is plotted against the mean 1st saccadic latency for each group for each cell. Lines connect points from the same cell. The solid red lines connect the population means. The dotted lines show example slopes of 0 and 1, respectively.
the initiation of the saccade with a slope of 1 (Fig. 3C, dotted line). In these conditions, the identification of the saccade goal in V4 would not predict the initiation of the saccade, nor would it be directly involved in the genesis of the saccade. Instead, V4 would be closer to the perceptual decision process occurring at the onset of the array.

In the extreme opposite scenario, the identification of the saccade goal in V4 may be closely correlated to the initiation of the saccade. Under these conditions, the selection time calculated from array onset would correlate with the initiation of the saccade (Fig. 3, A and B, solid black line). All the variability in saccadic latency would be introduced before the selection time in V4. The time needed to generate the saccade, the period from the selection time to the saccade onset, would remain constant for both short and long latency trials (Fig. 3, A and C, solid line). The time at which V4 selects the saccade goal would predict the saccadic latency, which would suggest that V4 is involved in the initiation of the saccade. Of course, it is also likely that saccade goal selection times in V4 neurons may be correlated with both array onset and initiation of the saccade, suggesting contributions to both visual processing and saccade generation.

When we calculated the selection time aligned with array onset, we found no correlation between the selection time and the initiation of the saccade at the individual neuron and population level. We used only neurons in which we could get significant saccade goal selection times in both groups (22 cells in monkey R; 7 cells in monkey A). Of these neurons, 18/29 did not show a correlation between the selection time and the saccadic latency (ANOVA, \( P = 0.667, F = 0.19, \text{df} = 35 \)). This result can be seen by the black lines in Fig. 3, D and E, which connect the two individual data points for a single neuron. The red lines in Fig. 3, D and E, connect the population means from all the data presented. We also found no correlation between the selection time and the initiation of the saccade in the population as seen by the flat slope (\( m = -0.09 \); Fig. 3D, red line). We further validated this result by performing a bootstrap analysis. For each cell, we took 80% of the trials randomly and calculated a selection time for short and long latency groups. We repeated this calculation 100 times for each cell to find average selection times. This analysis confirmed our results. Seventeen of 29 cells showed no correlation between the saccade goal selection time aligned with the array onset and saccadic latency (ANOVA = 0.9902, \( F = 0, \text{df} = 33, \text{slope} = -0.002 \)). The lack of correlation is unlikely to be caused by noisy data.

In contrast, when we calculated the selection time aligned with saccade onset, we found a strong correlation with the saccade onset for the same individual neurons (ANOVA: \( P < 0.0001, F = 25.5, \text{df} = 35 \)) and in the population as seen by the slope close to 1 (\( m = 0.83; \) Fig. 3E, red line). We confirmed these results using the bootstrap analysis described above. The same cells showed a strong correlation between selection time aligned with saccade onset and with the initiation of the saccade (ANOVA = 0.0002, \( F = 16.99, \text{df} = 33, \text{slope} = 0.81 \)). This correlation also shows that our statistical analysis is strong enough to detect a correlation based on divergence of neuronal responses in our data. These data are similar to the hypothetical situation with the dotted lines in Fig. 3, B and C. This result suggests that most of the variation in the saccadic latency occurs after the saccade goal is selected in V4 and thus downstream from area V4. Therefore the activity in these V4 neurons does not directly initiate the saccade.

**DISCUSSION**

In this study, we showed that, during free-viewing visual search, V4 activity predicts the direction, but not the latency, of the upcoming saccade. These results suggest that presaccadic activity in V4 is not involved in driving the saccade but rather represents a spatial attention signal. We will discuss these findings in context of the role of saccadic modulation in V4 and the source of this signal during visual search.

**Role of V4 saccadic modulation**

V4 has long been known to have saccade-related activity. Fischer and Boch (1981) showed that, when a monkey makes a visually guided delayed saccade, V4 neurons increase their activity before the saccade. During free-viewing visual search tasks, V4 neurons also show enhanced activity when an impending saccade was directed into the receptive field of the neuron (Bichot et al. 2005; Mazer and Gallant 2003). However, the contribution of the saccade signal in V4 to visual search remained unclear. One possibility is that the V4 signal is critical in driving the saccade. This signal may originate in earlier visual areas or in V4 and use complex visual features such as shape and color (Gallant et al. 1993; Gattass et al. 1988; Pasupathy and Connor 1999; Schein and Desimone 1990) to enhance activity at a particular spatial location. Areas further upstream such as LIP and FEF, which are not necessarily selective for object features (although, see Sereno and Maunsell 1998), can use this signal for the generation of saccades (Ibata et al. 2006; Thompson et al. 1996).

Alternatively, the saccadic signal in area V4 that we and others show could be a spatial attention signal. Saccade plans facilitate attention psychophysically in both humans (Deuel and Schneider 1996) and monkeys (Bisley and Goldberg 2003). Perceptual thresholds improve at the goal of a visually guided saccade. The presaccadic activity in V4 could contribute to visual attention. Moore and Armstrong (2003) showed that subthreshold stimulation of FEF increases the visual response of V4 neurons and also improves perceptual ability at the corresponding location. Previous studies showed that it takes \( \sim 100–300 \) ms for an attentional benefit in V4 to emerge (Ghose and Maunsell 2002; Hamker 2005; Motter 1994). Our data show a saccade selection at \( \sim 113 \) ms, which is within a reasonable range for showing attentional enhancement in V4. Presaccadic activity in V4 may therefore be an attention signal that reflects activity in other areas involved in spatial attention and saccade planning rather than contributing to the generation of the saccade.

We found that, although V4 has a presaccadic signal in visual search, the time at which most V4 neurons and the population distinguish the saccade goal is unrelated to the latency of the saccade. This finding is in contrast to activity in LIP, where the time at which LIP neurons distinguish the saccade goal predicts the latency of the saccade (Ibata et al. 2006; Thomas and Pare 2007). These results showed that V4, unlike LIP, is not likely to contribute directly to the generation of the saccade. Furthermore, we found that LIP reliably predicts both the direction and latency of the upcoming saccade at


Source of the saccadic signal

The source of the saccadic signal in V4 could arise from an area related to saccade generation, such as LIP. Although LIP is capable of informing V4 of the impending eye movement, it is unlikely that V4 simply receives all of its saccadic information from LIP for two reasons. First, V4 does not show a correlation with saccadic latency such as that seen in LIP. This relationship could possibly be caused by a synaptic delay from LIP or a disconnect from LIP and the oculomotor system. Second, V4 activity reflects where the eyes will move before a long saccadic latency. This is evident because there is a time at which the saccade direction is identified in LIP and V4. The saccadic signal in LIP ranges from ~85 to 140 ms and V4 from ~75 to 125 ms. On the trials with a long saccadic latency, V4 signals where, but not when, the saccade will occur before LIP does.

A saccadic signal could arise in other cortical areas besides LIP. One source of presaccadic information could be the FEF. FEF is a saccade-related structure that has been shown to have effects on visual attention (Ekstrom et al. 2008; Moore and Armstrong 2003; Moore and Fallah 2004; Thompson et al. 2005). FEF specifically has direct connections to V4 (Baizer et al. 1991) and has been shown to increase activity in V4 neurons representing the endpoint of the saccade goal (Moore and Armstrong 2003). Another source may be the superior colliculus, which also connects to V4 via the pulvinar (Baizer et al. 1991) and shows presaccadic enhancement to the search goal (McPeek and Keller 2002).

Eye movements generated from these saccade-related areas are also affected by visual attention (Schafer and Moore 2007). Thus V4 may initially receive signals from these saccade-related areas for spatial attention during our task and can later project to these same areas to provide visual information for upcoming saccades if necessary. Although LIP and V4 clearly have different roles in saccade generation and visual perception, they can complement each other in these two functions.

It is clear that there are enhanced modulatory effects for the locus of spatial attention throughout the visual stream. Traditionally, it was thought that information flowed from lower sensory levels to higher processing areas. Here, however, we show that the signal selecting the saccade goal, and spatial attention, occurs in LIP before V4. In this case, modulation occurred in a higher cortical area before a lower sensory visual area. Furthermore, the saccadic signal in V4 differs from that of LIP. Saccades have two functions: they move the eyes and they focus attention. The saccade goal can specify the locus of attention even before the eye moves (Bisley and Goldberg 2003). Unlike LIP, the V4 saccadic signal is not tightly correlated to the saccadic latency, suggesting that V4 does not contribute directly to the generation of the eye movement in the same manner as LIP. Instead, the saccadic signal in area V4 likely reflects the locus of spatial attention as generated by the eye movement plan. The saccade to that location brings the object onto the fovea for enhanced perceptual analysis.

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Disclosures

No conflicts of interest, financial or otherwise, are declared by the authors.

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