Title:
Saccadic Momentum and Attentive Control in V4 Neurons During Visual Search

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Abstract

Saccadic momentum refers to the increased probability of making a saccade in a forward direction relative to the previous saccade. During visual search and free viewing conditions saccadic probability falls in a gradient from forward to backward directions. It has been considered to reflect an oculomotor bias for a continuing motor plan. Here we report that a saccadic momentum gradient is observed in non-human primate behavior and in the visual responses of cortical area V4 neurons during a conjunction style visual search task. This result suggests that saccadic momentum arises in part from a biased spatial distribution of visual responses to stimuli. The effect is independent of feature selective attention and overridden by directed spatial attention. The implications of saccadic momentum for search guidance are much broader and robust than the inhibition-of-return’s presumed role in preventing re-fixation of recent locations.
**Introduction**

Do saccadic momentum or inhibition of return (IOR) phenomena result from underlying changes in the sensory representation of the stimulus field? The present study investigates this issue and differentiates effects associated with saccade momentum and IOR conditions from known attentive effects in visual cortical area V4.

The guidance of search is modulated by both task strategy and attention to stimulus properties, and ultimately depends on the current sensory representation of the surrounding space. Models of visual search generally proceed by identifying relevant, salient items or their likely locations within the scene during fixations. Search models often incorporate a measure that reduces the probability of returning to previous fixations either by using a memory strategy or by reducing the salience of items/locations that have been recently inspected (Itti & Koch, 2001; Zelinsky, 2008). The IOR phenomenon (Klein, 2000) is often employed as the agent that reduces the probability of returning to previous fixation locations. Initially described as an increase in reaction time to targets placed at previously attended locations (Posner & Cohen, 1984), the oculomotor inhibition of return (O-IOR) refers to the observation that returning to a recently fixated location is less likely and takes longer than to other locations in the scene (Klein, 2000).

Klein and MacInnes (1999) proposed that the IOR could be viewed as facilitating a foraging search by preventing the revisiting of prior fixation locations. Smith and Henderson (2009) reported that there was a reduced probability of making a saccade to a much broader area in the direction of the previous fixation position relative to the current. Furthermore, they drew attention to the forward progression of saccades, describing their observations as saccadic momentum; defined as the tendency for saccades to continue the trajectory of the previous saccade. They reported such forward saccades to be preceded by shorter fixation durations than backward directed saccades. Further work has established saccadic momentum as a gradient for both saccade direction and fixation duration under various viewing conditions (Bays and Husain, 2012; Luke, Smith, Schmidt, & Henderson, 2014; Smith and Henderson, 2011; Wilming, Harst, Schmidt & Konig, 2013). Debate continues to surround the IOR and its relation to saccadic momentum and their respective mechanisms.
Behavioral measures spurred early speculation that IOR effects were tied to oculomotor control systems with interest centering on the superior colliculus (SC). A series of studies culminated in the report that while IOR components are clearly present in the discharge activity of superior colliculus neurons, the source of the IOR signal is antecedent to the superior colliculus (Dorris, Klein, Everling, & Munoz, 2002). High on the list of potential sources are frontal and parietal cortical areas involved with oculomotor control (Dorris et al., 2002; Mayer, Seidenberg, Dorflinger, & Rao, 2004). The confluence of both attentional and motor control systems in both frontal and parietal cortex raise the possibility that saccadic momentum and IOR arise from active attentional efforts that bias attention toward new or forward locations and away from prior locations (Bichot, Heard, DeGennaro, & Desimone, 2015; Bichot & Schall, 2002; Mirpour, Arcizet, Ong, & Bisley, 2009; Zhou and Desimone, 2011). The known connections and feedback of frontal and parietal areas to visual association cortex, particularly area V4 (Blatt, Andersen & Stoner, 1990; Schall, Morel, King, & Bullier, 1995), present the possibility that there are sensory correlates of saccadic momentum and the IOR in visual association cortex. Furthermore, these correlates may directly modulate the neural representation of objects in the visual scene and thus influence the guidance prioritization for visual search.

It is widely established that the visual salience of an object can be modulated by visual attention and the strategy employed for the search task. The emphasis to date has been on forward looking attentive processing at the site of the next fixation. In this study, though not exclusively, the emphasis is on what has happened in the recent past to influence the current neural representation of the surround. The behavioral and physiological correlates of these questions are examined using a visual search paradigm employing arrays of conjunction style stimuli (Treisman and Gelade, 1980; Wolfe, 1994) and measuring the activity of cortical area V4 neurons. Spatial crowding and background effects were minimized by using simple stimulus arrays with spacing set to the receptive field (RF) eccentricity as has been previously employed (Bichot, Rossi & Desimone, 2005; Shen and Pare, 2014). Search strategies that may bias the temporal stimulus sequence analyses were defeated by using random placement of the target and distracters within these arrays.

Visual processing in V4 can be modulated by attentive mechanisms even when the stimuli are in the periphery and not the target of a following saccade (Bichot, Rossi & Desimone, 2005; Motter, 1994; Reynolds and Chellazi, 2004; Qiu, Sugihara & von der Heydt, 2007). Here we explore the responses to stimuli after the first saccade in visual search and contrast them to the responses at the onset of the
visual search array. Peripheral stimuli that share behaviorally relevant features with a target are important in the guidance of saccade selection during search. This report addresses changes in the neural response to those stimuli that result from the search process itself and, in turn, potentially alter the guidance of the next steps in search. Understanding the factors that alter the neural response to stimuli during visual search provides insight into the mechanisms that determine where we look next.

This report establishes that during visual search non-human primates demonstrate saccadic momentum behaviors, and that the sensory response to stimuli in area V4 of cortex is correlated with saccadic momentum behavior. Neural correlates of saccadic momentum in V4 are shown to be independent of feature selective attention, and are overridden by directed spatial attention.
Materials and Methods

Data were obtained from two monkeys trained for behavioral neurophysiological recording experiments. Standard electrophysiological techniques were used to obtain recordings from neurons in extrastriate area V4 (Motter, 2006, 2018). The impulse activity of single cortical neurons was recorded with glass-coated Elgiloy microelectrodes inserted transdurally into the cortex. Waveforms were isolated by adjusting the position of the electrode during recording. Post-mortem examinations confirmed the neurophysiological recording locations. All experimental protocols were approved by the IACUC's at the VA Medical Center and at SUNY Upstate Medical University. The study adhered to the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research.

Behavioral paradigms. The monkeys performed two different behavioral tasks for these experiments. The first task was a standard fixation paradigm that required the monkey to fixate steadily on a small spot of light for several seconds while at the same time ignoring stimuli presented in the near periphery (1-15 degrees from fixation). This task was used to locate and map each neuron’s receptive field and determine each neuron’s response preferences for stimulus shape, size, orientation, color and position with the RF. The monkeys were required to keep eye position inside a 1.0 deg window centered on the fixation spot. Eye position was measured with a scleral search coil system. Viewing was binocular.

The second task was a conjunction style visual search task used to examine the neural responses to stimuli entering the receptive field as the result of a saccade. Stimuli were arranged on a grid pattern with the grid spacing, grid orientation, and number of elements in the array based on each cell’s RF size and eccentricity, limited by the 35x25 degree display boundary. Figure 1A illustrates the basic search display, with the spacing and orientation of the grid determined by the position of the center of a RF; depicted by the dashed circle to the lower right of the initial central fixation spot. Arrays typically had 20-36 items, subject to limitations of the display screen to fully display each item and for the RF to always be within the display boundary during search; items clipped by the display boundary were eliminated entirely. Because saccades go item-to-item in the arrays and disproportionately to nearby items (Figure3), we elected to group saccade amplitudes into three groups based roughly on the saccades to immediately surrounding items, or the next closest, or those beyond that distance. These

[ INSERT FIGURE 1 ABOUT HERE ]
Figure 1. Array construction and saccade amplitude grouping. A. The eccentricity of the receptive field (RF -dashed circle) center and its location with respect to the point of fixation (fovea) defined the interstimulus distance and orientation of the stimulus array. Because the eccentricity can vary for each neuron, distances are normalized with respect to RF eccentricity across neurons and expressed in grid units. Stimulus shape, size, orientation and color varied based on the neurons' tuning preferences. Trials began with fixation on a solitary target (plus) at center of the screen. That fixation target was replaced briefly (300 msec) with a cueing replica of the trial's target stimulus, after which the cue was removed and the full stimulus array appeared. As search for the target progressed, each fixation resulted in a stimulus appearing in the RF except for fixations that placed the RF outside of the array. B. Saccade amplitudes were measured in grid units and for behavioral analysis they were segregated into three amplitude groups. These 3 groups were determined by rings around the current fixation point having radii of 1.7 and 2.6 grid units. The location of the current fixation clearly determines the number of items in each ring group.
“ring groups” are depicted in Figure 1b, and are in that manner defined for saccades from each location in the array. The groups are based on distances of 1.7 and 2.6 grid units and are used for the behavioral data analysis.

The search task required the animals to find and fixate a stimulus (always present) in the array. The trial started with a fixation spot at the center of the screen. Once fixation was established (within 0.5 deg for 300 ms) the spot was replaced by a replica of the target stimulus for the trial. After 300 msec the replica was removed and the array was simultaneously presented without a stimulus at the center location. Subjects searched through the array until the target was found. Fixation of the target for 600 msec terminated the trial as correct, resulting in a liquid reward. Trials were terminated as incorrect if the final target fixation had not begun within 6 seconds. The search array remained on until the trial was declared as either correctly or incorrectly completed. The shape and size of stimuli depended on the neuron being studied. The eye position window that identified final fixation was variable and defined to be a circle that was centered on and just encompassed the edges of the target stimulus plus 0.25 degrees in radius. Targets were randomly selected from four stimuli (see below) on a trial-by-trial basis; a target on one trial could be a distracter on the next. The animals worked daily for about 1200-1500 trials at correct performance levels of >85%.

Stimulus presentation. Stimuli were presented on a CRT monitor (22 pixels/degree) located at a viewing distance of 57 cm. Stimulus generation and presentation was controlled by custom software using standard graphic routines with stimulus timing synchronized with the vertical refresh of the graphics display system (Motter, 2006, 2009). The stimuli consisted of letter-like figures, such as T, I, E, L, F, O, Z and their non-rotationally invariant, mirror images. Each stimulus could be varied in orientation, length, width, and color. Stimuli were presented on a gray background of 8 cd/m². A standard set of color levels was used, based on the use of individual RGB guns, combinations of two guns, or white. These colors were adjusted to an average value of 20 cd/m² using an EG&G model 450 photometer fitted with a photometric filter. Individual frames were measured to assure that each frame of a presentation was identical. No attempt was made to select isoluminant colors for individual animals or neurons. A black stimulus (<1cd/m²) was also used.

Receptive field properties. During the initial characterization of RF properties, fixation was maintained throughout the trial on a fixation target. During this period letter-like stimuli having different
orientations, shapes, sizes, colors, luminances, or stimulus positions were sequentially delivered to the area of the RF on each trial. These trials characterized an optimal/preferred stimulus for each neuron. A stimulus duration of 200 msec and an inter-stimulus interval of 400 msec were used for presentation timing (Motter, 2006). The number of stimulus presentations delivered per trial as well as the sequence order was pseudo-randomized to avoid prediction of both trial duration and stimulus type. RF's were mapped using a reverse correlation technique employing a slightly faster sequential presentation of stimuli at each location in a 16 x 16 grid placed over the area of the RF (Motter, 2009).

Search stimulus selection. Single neurons were initially selected for study if they responded to flashed stimuli during electrode advancement. Computer controlled stimulus sets were then used to define the RF location and preferences for size, color/luminance, shape and orientation of stimuli. Based on the neuronal response rate, a preferred color and shape was chosen to define one feature pair. A second pair of color and shape features was chosen that elicited reduced but clear responses, described here as non-preferred features. Thus four stimuli were chosen: one stimulus combining both preferred (PR) color and shape, two stimuli combining either the preferred color (CL) or preferred shape (SH) with the non-preferred second feature, and one stimulus that combined the non-preferred features (NP). In the simple conjunction search task, the target is defined by two features, color and shape, whereas distracter stimuli each share only one of the target features. The target for each trial was randomly selected without replacement from a pool containing equal numbers of the four possible stimuli to equate presentations. The positions of the stimuli, both target and distracters, within the array grid were randomly assigned. The proportions of the two distracter stimuli were balanced for each trial.

The interstimulus spacing and orientation of the search array grid was set to equal the RF center eccentricity and visual field elevation so that fixation on one stimulus resulted in the placement of another stimulus at the center of the RF (Bichot et al., 2015; Mazer and Gallant, 2003). For area V4, optimal letter-like stimuli are typically much smaller than the RF (Motter, 2018). RF’s did not include the fovea, thus only one stimulus appeared in the RF on any fixation. The trial started with fixation at the center of the array. A stimulus was always in the RF at the time of the array onset. Typically 4 different search sets were used per day during recording.

Eye movement analysis. Data are reported with respect to two different time points. The first is the time of onset of the stimulus array during the initial fixation period. The response to the stimulus in the
RF at the onset of the array measures the relative responsiveness to a stimulus after a prolonged period without any stimulus in the RF. The second time point(s) is the beginning of each midtrial fixation occurring between the initial and final fixations which represent the bulk of the data. Data during the final fixation on the trial target at the end of the trial are not used in this report. The beginning of a new fixation was defined as the time of the beginning of a 60 msec time window where the instantaneous eye movement velocity fell below and stayed less than 16 deg/sec. Saccade onset was defined as the beginning of a 20 msec interval where velocity exceeded 16 deg/sec. A minimum fixation duration of 120 msec was required for neural analyses. If a secondary, error correcting saccade was made, the ensuing fixation was merged with the prior fixation if it began less than 60 msec after the end of the prior fixation and was localized to the same stimulus (Wu & Kowler, 2013). This method was applied to 2% of midtrial fixations and was done primarily to clarify re-fixation accounting.

Saccadic momentum

Behavioral analyses. For the behavioral analysis of saccadic momentum two measures are made. The first measure is the duration of the fixation between the two saccades. The second measure is the vector angle between one saccade with respect to the immediately preceding saccade. The angle is defined in a counter clockwise fashion. A return to the previous fixation position is an angle of 0 degrees, and a forward progression, in the same direction as the previous saccade, is an angle of 180 degrees. The momentum angles were evaluated against the set of all possible saccade angles; obtained by measuring all possible saccade vector angles from each actual fixation location to each stimulus in the array. These measures define the expected angle frequencies for a Chi-square hypothesis test.

Neural analyses. With respect to saccadic momentum, what are the analogous conditions for examining sensory neurons? Consider the diagram of Figure 2A showing an initial saccade (thick arrowed line) to a central stimulus location. Saccadic momentum states that a continuing forward saccade to a location in the lower oval is more likely than a backward saccade to a location in the upper oval. Given that the stimuli at locations in the lower oval are the same as those in the upper oval, a neural sensory correlate of saccadic momentum can be defined as a difference in the responses to the stimuli based on which locations they occupy with respect to the just completed saccade. Ideally one would like to examine the
Figure 2. What is Saccadic Momentum for a neuron? Arrowed lines portray saccades. Circles portray receptive fields (RF). A. Saccadic momentum states that a subsequent forward saccade to a location in the lower oval is more likely than a backward saccade to a location in the upper oval. B. Instead of simultaneously recording neurons with RFs at all grid locations marked by the dots in A, the evidence for saccadic momentum is derived from repeated measures from a single neuron. The direction of saccadic momentum for a single neuron (a single RF) is derived from a consideration of the angle between each saccade vector and the neuron’s RF vector. The RF vector is represented as the line between the RF center and the fovea (the fixation point). A saccade from F1 to F2 with the accompanying shift of the RF from P1 to P2, results in a large angle indicated by $\alpha$. Whereas, a saccade from F3 to F4 with the accompanying shift of the RF from P3 to P4, results in a small angle indicated by $\beta$. In this manner, although there is only one RF location, an entire range of saccade angles can be associated with the response to an item appearing in the RF. C. The different angles can be classified based on whether the RF leads saccade, trails behind the saccade, or is displaced sideways with respect to the saccade away from the current fixation at F0.
neural response at all stimulus locations simultaneously, but to make comparisons one also needs to
record from neurons with identical response properties at each location, and that is not practical.
Instead we examine the responses from a single neuron’s RF when it falls in a leading, trailing, or any
other position with respect to the direction of the just completed saccade (Figure 2B). At the sensory
level the question is whether there is an overall response imbalance that favors the forward
progression. The measurement is made relative to the saccade vector, and not relative to a direction in
external space. The diagram in Figure 2C shows how a RF at a specific retinotopic location can be used to
gather information about saccadic momentum from a consideration of the angle made between the
saccade vector and the RF vector (the line between the fovea and the center of the RF). The coordinate
scheme used defines an angle of 180 degrees to represent a leading saccade toward the RF (the RF
leads/moves in front of the saccade) and an angle of 0 deg to represent a trailing saccade that goes
away from the RF (thus the RF trails behind the saccade advance). Symmetrical directions to the right or
left are pooled across the 0-180 axis in the data analysis.

Neural activity summaries. The activity of each neuron was normalized with respect its response to the
preferred stimulus (preferred shape and color) in the RF at the initial onset of the stimulus array. The
average response activity in the interval from 50 to 150 msec after array onset was used for the
normalization (Motter, 2006). For all other spike rate analyses the 200 msec response interval from 50
to 250 msec after array onset or after the beginning of a fixation is used. The analysis duration was
constrained by the minimum response latency and the average initial saccade latency of 210 ms.
Because the animal subjects were unconstrained in their search patterns, the number of specific
stimulus and/or behavioral combinations varied, a minimum of 5 such occurrences per combination per
neuron were required for analysis. After rate normalization data were averaged across neurons. Activity
rates for histograms illustrating the time course of events are binned in 10 msec intervals. For
population analyses the average spike rate for each condition was used in a repeated measures (RM)
ANOVA design using neurons as subjects. Pairwise multiple comparisons (Holm-Sidak method) were
made between treatments. When warranted a RM ANOVA on Ranks was used, or paired t-tests.
Results

The results are organized around three main observations: (1) behavioral evidence of saccadic momentum and fixation duration as a function of saccadic direction in non-human primates, (2) neurophysiological evidence for a correlation between area V4 neural activity and saccadic momentum parameters, and (3) differentiation and comparison between feature selective attention and spatially directed attention components during visual search. The behavioral data are derived from the same sets of trials used to collect the neuronal data. All behavioral data are based on midtrial saccades and fixations, thus excluding the initial saccade after array onset and the final fixation on the target.

Behavioral results

Where do saccades go?

Saccades preferentially targeted nearby stimulus locations of stimuli that share the target color rather than target shape. Figure 3 summarizes the distribution of saccade amplitudes and saccade targeting outcomes for visual search in the regular grid array. Because the grid spacing is based on the RF eccentricity (see Methods and Figure 1) and varied from neuron to neuron, measurements of saccade amplitude are normalized and expressed in grid units. Figure 3A shows that the midtrial saccades mostly targeted grid locations within the first ‘ring’ of items (see Figure 1b) surrounding each fixation either along major axes, centered at 1.0 grid units, or along diagonal axes, centered at 1.4 grid units (groups a&b). A second grouping (c) centered around 2.0 and 2.3 grid units represent item locations in the second ring. A third ring group (d&e) represents the saccades greater than 2.6 grid units. Although the subjects were not trained to use color for guidance, they clearly did so (Figure 3B). Saccades landed on stimuli that matched the target in color about 82% (83% and 81% for the two subjects separately) of the time, while landing on stimuli that matched the target shape only 13% (12% and 15% separately) of the time and landing in empty areas of the display (fixation locations > 1.5 degrees from a stimulus center) 5% (6% and 4% separately) of the time. In previous work preferential selective attention to stimulus
Figure 3. Where do saccades go? A. Most saccades target grid locations within the first or second ring of items surrounding the current fixation point. When saccade amplitudes are expressed in the unit length of each array grid, then saccades to the first ring of items along major and diagonal grid axes are centered around 1.0 and 1.4 grid units. Groupings around 2.0 and 2.3 represent item locations in the second ring, and groupings at 2.8, 3.0 and greater define the third ring. Dashed line is the cumulative proportion of saccades. B. The vertical dashed lines in A delineate binning boundaries for the analysis of targeting as a function of saccade amplitude in B. Most saccades land on items having the same color as the trial’s target. The preference for items sharing the color of the target is independent of saccade amplitude. As saccade amplitudes increase, the relative number of landings on empty areas (> 1.5 degrees from center of any grid item) increases. These analyses excluded the first saccade of each trial.
color has been correlated with the modulation of the neural response in area V4 (Motter, 1994; Bichot et al, 2005). Saccades that landed on shape matching stimuli, as well as empty areas, occurred sporadically within trials that otherwise appeared to be guided by color. Figure 3B shows these results to be largely independent of stimulus eccentricity with the exception of landing on an empty area where probability of landing increases with eccentricity (longer saccades). Whether the latter represents targeting errors or strategy is uncertain, the longer saccades may have represented a strategy of resetting the search to a new area of the grid. These midtrial analyses excluded the initial saccade and the final saccade onto the trial’s target.

**Saccadic Momentum**

In addition to targeting preferentially nearby items that share the trial target’s color, we have found that the saccades also display saccadic momentum - the tendency for saccades to continue the trajectory of the previous saccade. Saccadic momentum was initially defined for human performance using search tasks that typically employed a target placed on a natural photographic scene. Here we establish that it also is present for monkey subjects on a regular grid search task. The grid placement also provides a more restricted framework for saccade targets thereby reducing the uncertainty of what item is targeted. The trial by trial random placement of all stimuli on the grid defeats any particular search strategy that might account for saccadic momentum.

Saccade momentum was investigated by measuring the angle between two consecutive midtrial saccades. These angles were binned in 45 deg increments centered on the major grid axes and diagonals. An angle of 180 degrees implies a saccade in the forward direction, a continuation of the direction of the previous saccade. Data were analyzed separately for each subject and then averaged across subjects for presentation. Data were grouped by amplitude according to whether the second saccade of the pair targeted an item in the first, second, or beyond grid rings (Figure 1b) with respect to the fixation location between the two saccades. The count totals for each direction within each amplitude group formed the observed outcome measures. Saccades to items in the first ring account for about 60% of all midtrial saccades (Figure 3a) and have a bias for the forward direction as shown in Figure 4a. In Figure 4a the radial extent for each direction is the percentage of counts for that direction.
Figure 4. Saccadic momentum. Relative saccade directions for midtrial saccade pairs grouped by saccade amplitude. A. Polar plot shows percentage of observed counts for the different saccade angles grouped by amplitude. Dashed gray circles in A and B indicate 10% and 20% of total count levels. B. Percentage of counts for possible saccade angles in each amplitude group. Possible angles based on the vector of the prior saccade and vectors to all other array item locations. C. Ratio of observed / expected within each amplitude group. Ratios greater than 1.0 (dashed black circle in C) indicate increased probability of occurrence, those less than 1.0 indicate decreased probability. Saccade amplitude groupings as depicted in Figure 1b.
relative to the total counts measured for that amplitude group. Because the search arrays are limited in
spatial extent, the probability of a saccade being made in any given direction depends on the starting
position within the array, e.g., saccades from fixations along the edge of an array are limited to
directions back into the array. Of course, in an item-to-item sequence of fixations it is always possible to
go back to the previous fixation location, thus possible outcomes will be biased for the return position.
The observed saccade directions need to be evaluated with respect to the possible saccade directions.
Bays and Husain (2012) employed similar reasoning. To determine the distribution of possible saccade
directions, we determined for each actual fixation the angle between the prior saccade and the angles
formed to all other array item locations. These measurements yielded expected outcomes under the
hypothesis of a random selection of possible saccade directions (Figure 4b). The expected counts,
(grouped by amplitude), were normalized with respect to the total observed counts within the same
amplitude group. A ratio index was then computed as ‘observed’ divided by ‘expected’ for each
direction, yielding a value greater than one for observed direction exceeding expected direction
outcomes. This data is plotted in Figure 4C for the three saccade amplitude groups. Chi-square statistic
evaluation of the difference between expected and observed outcomes were significant for each plot
(p<0.001). In Figure 4C saccades to items in the first (black) or second (red) ring indicate a clear bias
favoring a continued forward progression (180 degree) over a return direction (0 degree). Display
boundary conditions probably play a prominent role in the third (cyan) ring data that disrupted the
saccade momentum effect somewhat. Saccadic momentum accounts for a significant aspect of guidance
in these types of displays.

Simple counts of saccade directions in Figure 4a can be very misleading about the probability of
saccades in those directions, in this case particularly the intermediate distances (dashed line). Of the
44,771 mid-trial fixations, saccadic returns to the 1-back fixation positions occurred 1308 times of
33,716 opportunities, or 3.9%, where an opportunity is defined as a midtrial fixation sequence across 3
items. This is similar to our previous reports (Motter and Belky, 1998; Motter and Holsapple, 2007),
where we considered this consistent with a moderate IOR phenomenon. What was not appreciated
before was how saccade amplitude and the spatial distribution of saccade directions as shaped by
display boundaries produce a very uneven distribution of possible saccade directions for sequences of
two saccades. When the sequence and spatial structure of search is taken into account, saccadic
momentum (Smith and Henderson, 2009) is revealed as a forward based gradient as shown in Figure 4C.
Saccadic momentum analysis coupled with amplitude grouping establishes a broad gradient of
Figure 5. Saccadic momentum control array. A. Search array of 48 items, with 50/50 distribution of distracter types. Items randomly placed in display with only a non-overlap constraint. Same trial procedure as main experiment. B. After measurement of observed and expected counts of saccadic angles, the polar plot shows the observed/expected ratios for saccade amplitudes in 0 to 10 degree range binned in 2 degree steps. C. Polar plots of observed/expected ratios for saccade amplitudes in 10 to 20 degree. As saccades exceed 10 degrees the observed/expected ratio shifts from forward (180) to backward (0) directions due in part because of display boundary constraints. In legend ‘A’ stands for saccade Amplitude. Black dashed circle marks ratio of 1/1.
probability favoring the forward (180 degree) direction with a greater than chance ratio (1.5) in the forward direction as well as a smaller than chance ratio (0.5) in the reverse direction (0 degree). The implication for search guidance is much broader and robust than the IOR’s presumed role in preventing re-fixation of recent locations.

[INSERT FIGURE 5 ABOUT HERE]

Consideration was given to the hypothesis that the appropriate control might be the distribution of only the target color matching stimuli, given the preferential targeting behavior. Although the random placement of stimuli actually results in essentially identical distributions, nevertheless, that procedure was done and the outcome did not differ. A second concern was the possibility that the regular grid spacing or its associated normalization across the axis length or orientation changes was specific to the saccadic momentum effect observed. A control experiment was performed with data collected from the same two subjects for search through arrays of 48 stimuli whose positions were randomly determined from trial to trial within the 35x25 degree display area (Figure 5a); there were no grid axis changes in this experiment. The same conjunction style conditions using red and blue, Ts and Ls stimuli were employed (see also, Motter & Holsapple, 2000). Analyses were performed in the same manner as before but using saccade amplitudes expressed in degrees. A very similar set of results were found for saccade amplitudes less than 10 degrees (Figure 5b), which covers the range of the first grid ring of stimuli in the main experiment. Longer saccades become more likely to be regressive, even exceeding the random probability of a regressive direction (Figure 5c), perhaps implying a reset of search away from an edge or corner.

The symmetry of the polar plots with respect to clockwise (CW) versus counterclockwise (CCW) directed saccades for both experiments allowed the data to be collapsed across CW versus CCW directions for analysis. The data were thus collapsed, mirrored across the 0 to 180 direction axis, and reanalyzed using 22.5 degree bins. The results for the two subjects are plotted in Figure 6a for both the regular grid (solid lines) and control random placement (dashed lines) experiments. Saccade amplitudes were limited to less than 1.7 grid units for the regular grid experiment and less than 10 degrees for the random placement experiment. Despite the differences in the experiments and subjects the lines overlay each other, with a large linear gradient emphasizing forward saccades (50% > chance) over backward saccades (50% < chance). By these measures saccadic momentum is a robust phenomenon.
The saccadic momentum effects are neither due to the regular grid array arrangement nor to the normalization of grid axis orientation or grid length.

[ INSERT FIGURE 6 ABOUT HERE ]

**Fixation Duration Correlate of Saccadic Momentum and O-IOR**

There is a reported delay in the making of a saccade to a previously fixated location, termed an oculomotor IOR (O-IOR). The delay is measured as an increase in fixation duration in the return to a previously fixated item relative to items in other directions. In most cases this has been measured using a probe target stimulus delivered with respect to the current fixation position (Klein & MacInnes, 1999; Smith & Henderson, 2009, 2011; Luke et al., 2014) or during tasks employing fixed patterns of eye movement (Hooge & Frens, 2000) with the result that the fixation duration prior to a return saccade was found to be longer than to other locations. However, other studies have examined sequences of fixations during a visual search for a target embedded in a natural scene (Mills, Dalmaijer, Van der Stighel & Dodd, 2015; Smith & Henderson, 2009) and find a gradient of fixation durations from shortest for those preceding forward saccades to longest for return saccades.

Measurements were made of the duration of the fixation between consecutive pairs of midtrial saccades as well as the angle between the two saccades. Analysis was limited to cases where the amplitude of the second saccade was less than 1.7 grid units. This choice limits the targeting to items in the first ‘ring’ of stimuli surrounding fixation, and it reduces the influence of the display boundary in the sample. Like the plots of saccade probability (Figures 4 and 5), polar plots of fixation duration as a function of relative saccade direction were symmetric with respect to CW versus CCW directed saccades. This symmetry allowed the data to be collapsed across CW vs CCW directions for analysis. In Figure 6b the fixation duration as a function of saccadic momentum direction is plotted for each subject separately. The upper two solid lines show the data for the regular grid array, and the dashed lines show the data for the control random position array of 48 items. Both solid line plots show an increase in fixation duration as a function of direction from forward to backward, although the data for Subject A is a considerably steeper function. The dashed lines, on the other hand, show a much shallower, if any, trend for longer durations in the backward direction.
Figure 6. Saccade momentum gradients.  

A. Observed / Expected ratios were recalculated after collapse of data across the 0 – 180 direction axis. Ratios are plotted for each subject for the main experiment (solid lines) and the control experiment (dashed lines) in 22.5 degree increments. Overlapping, essentially linear functions reveal a common saccadic momentum gradient favoring forward (180) directions over backward (0) directions. 

B. Average fixation duration prior to second saccade as function of angle between consecutive saccades. Average fixation duration is shortest for forward direction and slowest for backward directed saccades, although the slopes varied considerably between subjects in the main experiment (solid lines) and between the main experiment and the control experiment (dashed lines). Solitary points along the right show that fixation durations in the control experiment for actual saccade return to previous item (O-IOR) were longer than other backward direction saccades. Standard error bars are often hidden behind symbols.
Fixation duration does not provide as robust a measure of saccadic momentum as saccadic probability. Many factors not directly related to saccadic momentum can affect the measurement. For example, a time constraint for making a decision to saccade can influence the distribution of made saccades and either hide or expose an underlying time accumulating assessment of saccade direction. If subject A in Figure 6b, has a more relaxed time constraint for making a saccade this could explain the steeper slope observed, and would be consistent with a longer average fixation duration as is apparent in Figure 6b. It is also clear that differences in the array structures or in the variability of the array structures in the regular grid arrays versus the random placement arrays result in different fixation durations for the same subjects.

Do specific O-IOR cases provide a further increase in fixation duration? With regard to returns to the previously fixated object, the far right data point for the regular grid arrays (solid lines) represent actual O-IOR events. The 22.5 degree binning and the saccade amplitude limitation to less than 1.7 grid units within the regular grid array constrains those saccades to just the previously fixated object, contaminated possibly by a few fixations on a empty areas > 1.5 degrees from the refixation object. Neither subject shows a particular change away from the slope of the line for other saccade directions, i.e., nothing special for the O-IOR event. However, for the random placement data there is a difference. Here a 22.5 degree binning and the saccade amplitude limitation to less than 10 degrees contain possible backward saccades to objects that are not the previously fixated object. When analysis is limited to just the actual O-IOR events, the fixation durations are slightly longer as shown by the two disconnected symbols at the far right of the dashed lines. Thus increased fixation duration prior to actual O-IOR events can be detected, just not consistently across these experiments. The reason for the difference is not clear, although the degree of crowding is certainly a major difference in the two experiments.

In summary, fixation durations are subject to a variety of factors, including the direction of the saccade relative to the preceding saccade. These observations serve a cautionary note to an oculomotor interpretation of the relation between saccadic momentum and fixation duration. In the regular grid search task we did not find fixation duration evidence consistent with an independent O-IOR behavior.

Area V4 neuronal responses during visual search
The responses of 85 area V4 single neurons were collected from two monkey subjects while they performed the visual search task in the regular grid arrays described above and in Figure 1. The interstimulus spacing and orientation of the search array grid was set to the RF center eccentricity and elevation so that a fixation on one stimulus resulted in placement of another stimulus at the center of the RF. The results presented below first examine the response to the stimulus in the RF at the initial onset of the array of stimuli. These “Onset” responses provide comparisons to previous work and provide a critical comparison framework for the responses during the midtrial fixations. Following these results the responses associated with midtrial fixations are examined with respect to feature attentive and saccadic momentum correlates, and finally with respect to spatially directed attention correlates.

V4 neural response at array onset

The stimulus in the RF at the onset of the array occurs with only a blank background preceding the stimulus in the RF, and before any search saccade takes place. Array onset is the principal time point used in many search tasks. The stable conditions afforded by array onset were used to assess the response to the four different stimulus types, PR (preferred color and shape), CL (preferred color), SH (preferred shape) and NP (neither preferred color nor shape) used in the search task (see Methods). For comparisons across neurons, the response rate of each neuron was normalized with respect to the response to the preferred stimulus (see Methods). Figure 7a&amp;b show peri-stimulus time histograms of the average population response at array onset to the four different physical stimuli, also sorted by color matching condition. The amplitude differences in response to the four stimuli were expected because the stimuli were chosen to be different based on the tuning properties of the neurons. The neural response has an onset latency of about 50 msec and a mean peak latency of 115 msec that precedes the onset latencies of the initial saccades whose mean latency is 210 msec. For analysis, spike rates are computed over a 200 msec interval starting 50 msec after array onset. The box plots of Figure 7c show the median and average raw spike rate as well as the range of Onset response rates from the 85 neurons to each of the four stimulus types, additionally sorted according to the color match between the RF stimulus and the target for the trial. Only onset stimuli that were not the target of the first saccade are included.
Figure 7. Response to array Onset. A. Response histograms for PR stimulus (upper pair) and SH stimulus (lower pair). For each pair the black line represents the response when the stimulus matched the color of the trial’s target and the red line when it did not. Small upward triangle along baseline indicates average saccade latency following array onset. Short vertical tics along baseline (at 50 and 250) mark the time window used to measure the response activity. B. Same for histograms of CL stimulus (upper pair) and NP stimulus (lower pair). C. Box plots of raw spikes/sec activity for each stimulus and for each attentive (color matching) condition; M – matching, NM – non-matching. Red bar within the 25th -75th percentiles box is the mean, black the median response. Whiskers are the 10th and 90th percentile response rate limits. D. Response histogram to array onset when next saccade is away from receptive field stimulus (black), response when next saccade is onto the receptive field stimulus (gray). Upper pair for the PR stimulus, lower pair for SH stimulus.
In the histograms of Figure 7 a&b there is a clear enhancement of the response for stimuli that matched the trial’s target color. In previous work (Bichot et al, 2005; Motter, 1994) subjects were trained to attend to color in order to identify the target, resulting in an enhanced neural response for color matching stimuli. Here (and e.g., Zhou and Desimone, 2011), the subjects were not trained to use color, but did so overwhelmingly (Figure 3b). In the histograms the target color matching condition results in both an amplitude increment and broader response duration as compared to the target color non-matching condition. Although the overall response diminishes as a function of the tuning sensitivity, the feature selective ratio (match/non-match) between match conditions remains steady at about 116% across the PR, CL and SH stimuli, and decreases to 105% with the less effective, less preferred NP stimulus as reported by Bichot et al. (2005). Interestingly despite the SH stimulus having the preferred shape, it is the match of its non-preferred color to the target that controls its response dynamic. Note that the NP stimulus, even though selected to differ from the preferred stimulus in both color and shape, still averages a substantial response of about 60% of the PR stimulus. A repeated measures ANOVA showed both stimulus type and match condition had significant (p<0.001) differences, but also a significant (p<0.001) stimulus x match interaction. Two outlier neurons were dropped from this overall analysis to meet normality and equal variance test requirements. Six other neurons did not have sufficient data in one of the 8 conditions, resulting in an analysis with 73, 3, and 1 degrees-of-freedom. Post comparisons (Holm-Sidak) between the color match/non-match conditions were significant (p<0.001) for each stimulus type except the NP stimulus (p=0.13). Post comparisons were also significant for stimulus type (p<0.001) within each match condition except for the SH vs NP conditions (match p=.02, non-match p=.09).

What about spatially directed attentive influences at array onset? For stimuli whose color matched the trial target there were sufficient trials in about 58% of the neurons (49/85) to examine the response to the stimulus when, in fact, it was the destination of the next saccade; and therefore, presumably the recipient of focal, spatially directed attention around the time of the initial saccade (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser , 1995). There were too few instances of saccades to non-color matching stimuli to examine that combination. Figure 7d shows the time histogram curves for the PR and SH stimuli (when matching the target color) at onset when they were (black) or were not (gray) the target of the next saccade. In contrast to the feature selective difference, there was no significant population difference attributable to spatially directed attention at array onset. This array onset result contrasts with observations in Bichot et al. (2005) and in midtrial search below, but is consistent with
Motter (1993) where stimulus onset differences in the spatially directed attentive condition became significant only with encroachment of additional stimuli into the RF. An alternate and encompassing view is that the stimulus conditions at onset produced a maximal response for each stimulus type, and directed attention effects may only come into play under conditions that otherwise produce diminished responses (see below).

Zhou and Desimone (2011) also separated the Onset response from the midtrial data, differentiating them as early and late search, based on the differences in the pattern of response and latency of attentive effects. Here we examine this difference further, interpreting the differences as the adaptation, or forward suppression, effects found in Motter (2006).

**Neural correlates of feature selection during midtrial fixations.**

Midtrial fixations are fixations after the first saccade and before the final fixation on the target for the trial (see Methods). The responses to stimuli appearing in the RF as the result of a saccade were synchronized to the onset of each fixation, averaged across responses for each neuron, and then across neurons for the population response. To examine potential attentive feature selection during the midtrial fixations, the stimuli appearing in the RFs were sorted by the stimulus type and whether the stimulus matched the target color for that trial. Figure 8a-d shows the population response of V4 neurons to each stimulus type, and the blank (> 0.33 grid units from any stimulus) condition. For comparison purposes the array Onset response (Figure 7) for the color match condition is also shown as the gray dashed line.

The average midtrial response is reduced compared to the average Onset response for the four stimulus types as seen in Figure 8a-d and summarized in Figure 8e. Across all stimulus types, the feature selective advantage for target color matching stimuli remains clear and is present earlier in the response than in the Onset case. In some cases, it may even persist across the interval from one fixation to the next. For each stimulus type the average midtrial activity for color match and non-match conditions are about 75% of their respective Onset response levels (Figure 8f). The constant ratio suggests a
Figure 8. Response to stimulus during midtrial fixations. A-D. Peri-event response histograms for each stimulus type, synchronized to the onset of the midtrial fixation at time zero. Black lines represent response to the RF stimulus when it matches the color of the target, red lines when the stimulus does not match the target’s color, and blue lines for the blank condition where there is no stimulus in the RF. Gray dashed line is response to target color matching stimulus at array onset (from Fig. 7). The two short vertical tics along baseline mark the analysis window. E. Comparisons of response rates for Onset versus midtrial, broken down according to the target color matching condition for each stimulus type. F. A nearly constant 75% ratio of midtrial responses to onset responses as a function of both match condition and stimulus type. G. Feature attentive selection advantage for color matching is comparable for Onset and midtrial conditions.
multiplicative scaling; however, the reduction is also consistent with the loss of the transient component of the V4 response as observed in flashed sequences of stimuli during maintained fixations (see Motter, 2006, Figures 4&7). The effectiveness of feature attentive selection (the match / non-match ratio) has a steady 18% increment (Figure 8g) for PR, CL and SH stimulus types, and less (~6%) for the NP stimulus. The decreased effectiveness for the NP stimulus confirms the Bichot et al., 2005 report that effects of attentive feature selection are more pronounced in cases where the features align with the tuning properties of the neuron. This bears re-emphasis; in assessing the presence of feature attentive effects, it is necessary to evaluate the feature’s effectiveness with respect to the neuron’s tuning properties. The NP stimulus in this study elicits an average response of about 50 spikes/sec (Figure 7c), yet there is little feature attentive differentiation in the response to the NP stimulus. The responses to all stimuli are significantly greater than the blank condition. Although the response to the NP stimulus in Figure 8d is rather unimpressive, especially considering the activity prior to fixation onset, it is clearly different than a blank condition (blue line). A repeated measure ANOVA on ranks with multiple comparisons showed that the response to the target color matching stimulus (black) in the RF is greater than the non-match (red) for the PR, CL and SH stimulus type (p<.01), but not the NP stimulus (p>.01). The feature attentive related observations, where comparable, agree with those drawn by Bichot et al. (2005) and Zhou and Desimone (2011).

The baseline activity is elevated during search compared to the baseline prior to array onset. This is primarily due to averaging activity, elicited by other stimuli, that is not synchronized to the chosen fixation onset. For example, in the post-response period > 250 msec after the synchronization (and likely into the next fixation period) the activity converges toward the same, ~0.4, response level. The activity prior to the synchronization point needs to be viewed somewhat differently because it represents the tail end of the previous response indirectly synchronized to fixation onset because saccade durations (20-40 msec) are nearly constant. However, because the fixation durations vary over a larger range, the onset of the prior response is lost in the averaging; making the prior response appear to be truncated. Given that the search arrays contained only stimuli that were effective in eliciting a response, a response should occur on each fixation. The exception is the blank condition where there is no stimulus in the RF; there the response (blue line) decays toward the pre-onset baseline. The blank condition activity decays at a rate consistent with the decay of the sustained response after stimulus offset which lasts around 150 msec (Motter, 2006).
Neural correlates of Saccadic Momentum

While the behavioral data for saccadic momentum demonstrate a clear bias for directional heading, the mechanisms of this action are unclear. It could be a downstream oculomotor hysteresis, but given a frontal cortical origin for the attentive strategies of search, it could also arise from a biasing of sensory information. What constitutes a neural sensory analogy of saccadic momentum? Using Figure 2, a rationale was outlined in the Methods for examining the differences in sensory responses in relation to saccade direction. The hypothesis is that responses from RFs that lie forward (leading) of the saccade direction should produce a more vigorous response than those that lie in a backward (trailing) direction. For a single neuron’s RF, the analysis is based on the position of the RF with respect to the saccade trajectory.

Directional data were mirror reflected across the 0 to 180 degree directional line and subdivided into three groups (Figure 2c; leading, sideways, and trailing) containing approximately equal numbers of possible target locations in the regular grid arrangement. Figure 9a-c sorts the V4 population response to the PR stimulus into these three groups. Figure 9a depicts the response when the position of the RF is in a leading direction, Figure 9b a sideways direction, and Figure 9c the trailing direction each with respect to the direction of the prior saccade. The responses are synchronized to the onset of fixation at time 0. For comparative purposes both the response when the RF falls on a blank area (blue), and the response to the color matching stimulus at the onset of the array (dashed gray) are shown. A diminishment in both response amplitude and duration is apparent in the response to the PR stimulus from leading to trailing positions. This change is observed for both the target color matching (black) and non-matching (red) conditions. Instances where the stimulus in the RF was targeted on the next saccade are specifically excluded here. That exclusion does bias the peak response in the leading direction by altering the distribution of available observations. However, it is specifically that condition where it is most likely that attention is directed to the RF during selection and initiation of a saccade (see below). In contrast the responses depicted in Figure 9a-c are all cases where attention is not directed at the RF. In the absence of spatially directed attention there is a clear difference in the response to the PR stimulus that is dependent on saccadic direction relative to the RF position. On the other hand, the non-spatial,
Figure 9. Neural correlates of saccadic momentum. A. Peri-event response histogram when the preferred (PR) stimulus appeared in the RF as a result of a leading direction (LD) saccade. Note the amplitude and breadth of the response in comparison to B & C. B. Response histogram when stimulus appeared in RF as result of a sideways direction (SD) saccade. C. Response histogram when stimulus appeared in RF as result of a trailing direction (TR) saccade. Lines in A-C represent conditions as in Figure 7. D. Population responses to the four stimulus types appearing in RF; grouped in 30-degree increments of the angle between the saccade vector and the line between the fovea and RF center. Response means and standard errors for feature attentive conditions corresponding to target color matching conditions (black) and non-matching conditions (red).
feature selective attentive influence is present, and the directional diminishment applies to both the
color match and non-match selective conditions.

Figure 9d summarizes the population responses for all four stimulus types showing in each case a
gradient of response to an identical stimulus as a function of saccade direction in 30-degree increments.
The responses are measured during the 200 msec interval starting 50 msec after fixation onset, as
demonstrated by the baseline markings in the peri-event time histograms. Figure 9d shows a decline in
response amplitude from leading (180 deg) to trailing (0 deg) positions for the PR, CL and SH stimuli, and
a suggestion of such for the NP stimulus. The directional effects appear to be independent of the
attentive, feature selective effect that separates color matching and non-matching conditions, with one
clear exception. At 0 degrees they converge, feature attentive differentiation is not present in the return
direction. Why the color matching and non-matching curves converge at 0 degrees is puzzling. An
explanation is elusive. Instances of a return to previous fixation (O-IOR) do fall in this bin, but the
convergence remains when each actual O-IOR event is specifically excluded.

The finer grain analysis of saccade direction presented in Figure 9d came at the cost of a reduction in
the number of neurons with sufficient data for the comparisons. The matching by direction partitioning
(2x6) reduced the number of participating neurons from n=73 in Figure 9a-c to n=60 for PR, n=54 for CL,
n=54 for SH, and n=58 for NP stimulus groups. Two-way repeated measures ANOVAs on matching and
direction factors were made for each stimulus type separately. Main effects for both color matching and
direction were significant at the p<.001 level for PR, CL and SH stimuli but only for direction for the NP
stimulus. There were significant interactions between match and direction factors (p<.01) for each
stimulus type, that are consistent with the departure from the approximately parallel black and red line
slopes depicted in the plots for each stimulus type. In post-comparisons and as seen in Figure 9d the
leading (120-180 degree) points had higher response rates than the trailing (0-60 degree) directions.

In summary, the results provide a clear indication that stimuli falling in RFs in the leading direction
result in a larger response, particularly in the neurons tuned for those stimuli. Thus those stimuli are
potentially more salient and likely to attract attention or priority in visual search. These results
demonstrate a sensory based correlate of saccadic momentum.

**Neural Correlates of Spatially Directed Attention**
During visual search, when the RF stimulus is the destination of the next saccade, the response is enhanced compared to when the saccade goes elsewhere (Bichot et al., 2005; Hayden and Gallant, 2005). The goal here is to provide an examination of whether the enhanced response can be viewed as an extension of saccadic momentum or feature attentive processes, and whether the enhanced response exceeds the initial array Onset response. Figure 10a shows the midtrial response (blue) to the PR stimulus in the RF when it was the destination of the next saccade, and the response (black) when the saccade went elsewhere. The enhanced response nearly matches, in both amplitude and duration the initial Onset response (dashed gray). The data are for 54 neurons where sufficient midtrial data were available for saccades into the RF for the color match condition. Non-match conditions were not available as there were too few saccades made onto color non-match stimuli that happened to be in the RF. Saccades onto versus saccades away from the stimulus in the RF were associated with significantly different responses for all four stimulus types in the 50 to 250 msec interval after the beginning of fixation. The analysis, repeated measures ANOVA on ranks (RM ANOVA), was made for the target color matching condition for treatments of initial Onset, midtrial onto and midtrial away conditions. Post comparisons of midtrial onto versus away responses (Figure 10e, triangles vs squares), were significantly different, p<0.01). This observation concurs with that of Bichot et al. (2005), although examined here for individual stimuli. For the PR, CL and NP stimulus types, spatially directed attention enhanced the response for the saccade onto the RF stimulus condition, resulting in responses rates that approached the response to that stimulus in the Onset condition (Figure 10e, circles vs triangles) and were not significantly different (RM ANOVA ranks, p>0.05) from it. The maximum firing rates did not exceed the Onset response. The response to the SH stimulus, however, was significantly less than the Onset response (RM ANOVA ranks, p<0.01). For the CL, SH and NP stimuli this is not the result of a simple saturated neuronal firing rate, as those same neurons gave greater responses to the PR stimulus. The result is consistent with a saturation limit for each separate stimulus. There was no apparent difference in the response latencies for Onset, onto and away responses, with the differentiation between them all occurring in the 75-85 msec interval post-event onset (Figure 10a). Despite the SH stimulus result, the general outcome suggests that directed attention accompanying a saccade to a RF stimulus overrides the diminishment (forward suppression) of midtrial responses that are observed when the RF stimulus is not the destination of the next saccade.

[ INSERT FIGURE 10 ABOUT HERE ]
Figure 10. Neural correlates of spatially directed attention. A. Peri-event response
histogram showing response to target color matching distracter in receptive field when
next saccade goes to it (blue) versus away (black) from it. Population response based on
54 neurons. B. Response histograms showing subdivision of blue response in A, into
leading (black), sideways (gray) and trailing (light gray) directional groups. Responses
are based on different numbers of neurons as indicated due to limitations in availability of
different combinations of stimulus and saccade events. C. Response histograms for
target color matching (black) and non-matching (red) stimulus conditions when the next
saccade was to the RF stimulus; for a subset of 10 neurons. D. Response histograms to
the actual trial target in the RF when the next saccade was to the target (blue) and when
the next saccade was away from the target (green). A reduced data criterion was used to
include neurons for D, as explained in main results section. For A-D the gray dashed line
represents response to target color matching distracter at array onset. E & F. Mean
population responses to the four stimulus types in various conditions detailed in the inset
legends and main text. Onset refers to array onset response. Onto refers to condition
where next saccade goes to stimulus in the RF. Away refers to condition where next
saccade goes away from the stimulus in the RF. Dist = distracter, m = matching, nm =
non-matching condition.
Moore and Chang (2009) reported that stimulus discrimination by area V4 neurons differed depending upon whether a saccade went to or away from the RF. Figure 10e compares stimulus discrimination using the differential responses to the four stimulus types, and shows that the curve for the saccade onto a stimulus in the RF (triangles) is much steeper, i.e., increased discriminative power, than that for the saccade away case (squares), confirming Moore and Chang (2009). The differences in stimulus discrimination imply a loss of stimulus information in the response during midtrial fixations. Note, in counterpoint, differences in the feature attentive conditions (squares vs diamonds) did not change the slopes of the tuning curves in Figure 10e, nor at array onset (circles and triangles, Figure 10f).

Next we examined whether either saccade momentum or feature selective differences are still in play for responses to the RF stimulus when it is the destination of the next saccade. For these comparisons the data were limited to much smaller subsets due to insufficient numbers of the specific stimulus or saccade direction combinations in most neurons. Figure 10b presents the saccade momentum analysis for the PR stimulus in cases where the RF stimulus matches the target color, and is the destination of the next saccade. The histograms are formed individually from the set of data available where leading, sideways, and trailing effects were supported by n=20 (black), n=32 (gray), and n=9 (light gray) neurons respectively. A tiered pattern comparable to that seen in Figure 9 (where the saccade does not go to the RF) is not apparent here, and particularly, there is no evidence for a decreased response in the trailing case. Thus saccadic momentum differences are quashed when the RF stimulus is the target of the next saccade. This also appears to rule out any notion that saccadic momentum determines directed attention.

Similarly, feature selective differences between the target color matching and non-matching conditions are greatly diminished when the RF stimulus is the destination of the next saccade. Because saccades to non-matching color stimuli are infrequent, only a small subset of neurons had sufficient data to examine feature selection under these conditions. Figure 10c shows the averaged midtrial responses for 10 neurons when the PR stimulus in the RF becomes the destination of the next saccade. In this case there is little difference between the target color matching and non-matching responses (p>0.05, t-test, n=10). In addition, there is no significant difference between the match condition response and the Onset response recalculated for those same 10 neurons (p>0.05, t-test). Similar insignificant differences
were observed for the remaining stimulus types. By driving the responses to a maximal limit, directed attention appears to quash both saccadic momentum and feature selective effects.

Occasionally the actual target for the trial appeared in the RF. By reducing the minimum number of required responses to this relatively rare stimulus combination to two, a comparison can be made between responses when the trial’s target was in the RF and became the destination of the next saccade versus when the saccade went elsewhere. It is this latter case that is quite rare and required the criterion of two in order to obtain at least 30 neurons in all stimulus types. The results for the PR stimulus are shown in Figure 10d, and for all stimulus types in Figure 10f. The response to the PR stimulus when it is the trial’s target is not different from the response to the PR stimulus when it is one of the distracters and both stimuli are the destination of the next saccade. And, in turn, both are no different from the response to the PR stimulus at array onset for the color matching condition. This result is true for all 4 stimulus types (Figure 10e, circles and triangles; 10f, circles and squares).

Interestingly the response to the target stimulus when the next saccade goes elsewhere is like the response at array onset when the stimulus is a color non-matching condition (Figure 10f, diamonds and triangles). Earlier in the results (Figure 7d) no difference was found between Onset responses when the stimuli were or were not the destination of the next saccade. Here for midtrial responses there is a difference, both for distracters (Figure 10e, triangles and squares) and targets (Figure 10f, squares and diamonds). It is important to recognize that the response to array onset for the color match condition appears to be an upper limit across all conditions described above.

In summary, spatially directed attention overrides saccadic momentum and feature selective attention phenomena during the processing of stimuli that are the destination of the next saccade. Furthermore, the equivalence of responses under target color matching conditions at array onset, and to stimuli in the RF that are the destination of the next saccade (whether a distracter or the actual target) argues that these responses reach a saturating level of activity. Thus an enhanced response might actually be a return to standard, rather than an active process of augmentation. By comparison with previous work (Motter, 2006) the midtrial responses that do not reach this saturation level lack a significant initial transient component, suggesting that directed spatial attention may somehow restore that component of the visual response in V4 neurons.
Discussion

In this report, saccadic momentum, the tendency for saccades to continue the trajectory of the previous saccade during visual search is confirmed for conjunction style search by non-human primates. The results confirm a gradient from higher probability for forward progression to lower probability for backward regression. The saccadic momentum gradient is robust. Here the use of trial-by-trial randomization of array items defeats any particular search strategy that might account for saccadic momentum, and establishes saccade momentum at some intermediate level of control, consistent perhaps with a foraging facilitator role but absent a higher cognitive strategy associated with picture viewing. The implications for search guidance are much broader than the IOR’s presumed role in preventing re-fixation of recent locations. The saccade momentum gradient was complemented by a similar gradient based on fixation duration in some cases, but no robust evidence for an independent oculomotor IOR based on fixation duration and acting in addition to the saccade momentum gradient was found. Saccadic momentum and O-IOR have been dissociated across different visual tasks (Bays and Husain, 2012; Dodd et al. 2009, Luke et al. 2014; Smith and Henderson 2009). Whether our result is due to the specifics of this visual task, a sparse array of objects (versus a visual scene) or the task requirement of search (versus free viewing, memorization, or patterned saccade) is unknown. Wilming, et al., 2013, also did not find evidence of an O-IOR beyond the saccade momentum gradient when salient areas were segregated in their analysis.

Our previous results with repeated flashed stimuli indicated there should be a significant diminishment of area V4 neural responses during visual search compared to the initial array onset response contingent on the repeated presence of an effective RF stimulus across fixations (Motter, 2006). The present results confirm this observation (Figure 8). The amount of reduction is consistent with the loss of the transient component of the V4 response (Motter, 2006). Feature attentive selection based on color matching was present in both initial onset and midtrial responses, generally confirming previous reports (Bichot et al., 2005; Zhou & Desimone, 2011), and suggesting feature attentive selection effects are not reliant on the transient response component. After excluding the initial fixation, no correlation was found between the neural activity and the number of fixations prior to finding the target.

In this study there was not an enhanced response to stimuli that became the target of the next saccade at array onset. But there was an enhanced response to stimuli that became the target of the
next midtrial saccade, and that enhanced response matched but did not exceed the initial array onset response. This was the case for each of the four stimulus types (Fig. 10e) suggesting that the array onset response represents a maximum response for each stimulus. Directed spatial attention can apparently enhance/restore the response up to this level. It is also significant that the directed attention enhancement quashes the feature selective differentiation (Figure 10c) as has been reported for pop-out modulation in a saccade task (Burrows and Moore, 2009).

A description of the geometry of saccadic momentum with respect to the movement and positioning of neuronal RFs during search was developed (Figure 2). The response of area V4 neurons to stimuli that entered the RF as the result of a saccade was found to be a function of the angle between the saccade vector and the line between the fovea and the center of the RF. The results agreed with the saccadic momentum geometry, finding that the responses from RFs that lie forward of the saccade direction were increased relative to responses from RFs that lie behind the saccade direction. Indeed, the response amplitude measures formed a monotonic gradient varying as a function of the directional angle that matched the behavioral saccadic momentum gradient (Figure 9). The gradient establishes a salience bias that predicts saccade direction (Mazer and Gallant, 2003) and is correlated to the previous saccade. These findings establish a saccadic momentum correlate in the sensory response of extrastriate area V4 neurons. How is that possible?

Is saccadic momentum the result of attentive guidance? The attentive differences attributable to feature selection between match and non-match conditions did not differ as a function of the saccade momentum gradient (Figure 9d). Thus, there appears to be no general linkage between feature attentive selection and saccadic momentum. Consequently, spatially directed attention would seem to be the most likely candidate. It and feature selective attention are postulated to arise in the frontal cortex and pass to V4 via the frontal eye fields (Bichot et al, 2015; Bruce and Goldberg, 1985; Gregoriou et al., 2009; Ninomiya, Sawamura, Inoue and Takada, 2012; Schall, 2015; Zhou and Desimone, 2011), thus providing a possible linkage to oculomotor events. However, the analysis establishing the gradient specifically excluded any stimulus that was the target of the next saccade. Furthermore, analysis of spatially directed attention indicated that it generated a spatially narrow profile, limited to the object/location that is the target of the saccade. If FEF activity building before the next saccade impacted V4 neurons it could bias the V4 sensory response (Thompson, Hanes, Bichot and Schall, 1996; Moore and Armstrong, 2003), however, the timing seems wrong with the V4 response occurring very
early in the fixation period before the next saccade and not building within the period prior to the saccade (see also, Mazer and Gallant, 2003). Furthermore, some studies (Gregoriou, Gotts, and Desimone, 2012; Ninomiya et al., 2012; Thompson, Bichot and Sato, 2005) conclude that V4 receives information only from the visual neurons in FEF and not visuomotor or motor FEF neurons. A similar argument can be made for saccade related influence derived from frontal to lateral parietal to V4 (Blatt, Andersen and Stoner, 1990; Ipata, Gee, Goldberg and Bisley, 2006; Ninomiya et al., 2012).

These attentive based considerations are all forward looking without a clear linkage to the previous saccade. However, such a linkage exists if we postulate that the activity in FEF (or LIP) associated with the prior saccade is what biases the response of V4 neurons to the stimuli present after the saccade. The peak visual activity in FEF occurs at the location of the saccade goal in the retinotopic map irrespective of the target’s actual salience (Sato, Murthy, Thompson and Schall, 2001; Thompson, Bichot and Sato, 2005). This activity peaks at the time of the saccade and outlasts the saccade for a short interval. Therefore, the retinotopically organized feedback to V4 immediately after a saccade is greatest in the direction of the saccade and falls away to either side. Even covert saccade conditions generate this activity (Thompson, Biscoe and Sato, 2005). Thus FEF (or LIP) feedback to V4 could underlie the bias in responsiveness to stimuli appearing in the RFs of V4 neurons on the next fixation, thus providing the saccadic momentum gradient observed in this study. Convergence from the large overlapping RFs in FEF and LIP (Hamed, et al., 2002; Mayo, et al., 2015) may provide the graded response bias that underlies the saccadic momentum gradient with the distribution of the feedback onto V4 being the critical parameter. Interestingly the pre-saccadic enhancement but not feature discriminability of V4 neurons survives FEF inactivation suggesting the LIP feedback may play the critical role (Noudoost, Clark, & Moore, 2014). More information is needed about the linkage between posterior parietal and area V4. Posed in this manner saccadic momentum seems to be an unintentional effect, yet this relationship is a variation on priming effects that play significant roles in modifying behavior. Longer fixations prior to reverse direction saccades may result from having to work against this gradient. Although little evidence supporting a separate sensory IOR mechanism was found, saccadic momentum alone provides a mechanism to bias stimulus salience in a forward direction and against a return to the recently fixated locations in models of visual search.
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