Title: A test of spatial temporal decoding mechanisms in the superior colliculus

Abbreviated title: Decoding mechanism in the superior colliculus

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Conflict of interest: None

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Abstract

Population coding is a ubiquitous principle in the nervous system for the proper control of motor behavior. A significant amount of research is dedicated to studying population activity in the superior colliculus (SC) to investigate the motor control of saccadic eye movements. Vector summation with saturation (VSS) has been proposed as a mechanism for how population activity in the SC can be decoded to generate saccades. Interestingly the model produces different predictions when decoding two simultaneous populations at high versus low levels of activity. We tested these predictions by generating two simultaneous populations in the SC with high or low levels of dual microstimulation. We also combined varying levels of stimulation with visually induced activity. We found that our results did not perfectly conform to the predictions of the VSS scheme, and conclude that the simplest implementation of the model is incomplete. We propose that additional parameters to the model might account for the results of this investigation.
Introduction

With external environments rich in stimuli that continuously bombard our sensory systems, neural structures have the ability to store distributions of information that can be decoded by lower-level structures in order to execute motor behavior. The saccadic system is well studied in this respect; specifically, research efforts have focused on motor control of saccadic eye movements to study ensemble activity in the superior colliculus (SC). In the visual domain, every potential target recruits a population of activity in the SC and the distribution of information is somehow decoded to direct the line of sight to a desired object. As a result, studies have focused on target selection revealing that reorientation towards a specific target can be probabilistic, depending on factors like saliency (McPeek and Keller 2002) and relative priority (Kim and Basso 2010; Mysore and Knudsen 2011). Once a population has been selected, however, the next crucial step is to transform the ensemble of collicular activity into a proper motor command for saccade generation. Insights into such decoding computations have been facilitated, in part, by the laminar layout of the SC and the topographical organization of saccade vectors. Recordings have indicated that the neural population of saccade-related cells in the motor map is well described by a Gaussian mound, in which neurons at the center fire maximally for the executed saccade vector, while cells away from the center exhibit lower firing rates (Ottes et al. 1986; Sparks et al. 1976). This investigation focuses specifically on how population firing patterns in the SC can be decoded to specify a saccadic command.

Different computational schemes have been proposed as potential mechanisms for decoding SC activity into the saccade vector: vector summation (VS) (Badler and Keller 2002; Brecht et al. 2004; Van Gisbergen et al. 1987), vector averaging (VA) (Brecht et al. 2004; Lee et al. 1988; Walton et al. 2005), and vector summation with saturation (VSS) (Goossens and Van Opstal 2006; Groh 2001). In all three models, the central premise is that each recruited cell, \( n \), in the population contributes to the saccade by combining two factors: its activity, \( a_n \), (which could be the cell’s mean or peak firing rate, or the number of spikes in the burst), and its fixed efferent connection strengths to the horizontal and vertical brainstem burst generators, \( \tilde{m}_n \), which are solely determined by the cell’s location in the motor map. The SC population then determines the saccade vector \( \tilde{S} \) by summing all weighted cell contributions:
with $N$ the number of active cells, $\gamma$ a scaling factor, and $f[f(x)]$ the effective input-output characteristic of the brainstem. The three models differ in the way in which the scaling and the input-output function are implemented. In the VS and VA models the latter is simply the identity ($f[f(x)] = x$), whereas in the VSS model it is a sigmoid. In the VS and VSS models the scaling parameter is a constant, while in the VA model it normalizes the total population activity (Lee et al. 1988):

$$\gamma = \frac{1}{\sum_{n=1}^{N} a_n}$$

Vector averaging has garnered success by accounting for the findings from simultaneous supra-threshold microstimulation of two sites in the SC (Katnani and Gandhi 2011; Robinson 1972), and from local inactivation of the SC motor map (Lee et al. 1988). However, the VA scheme does not account for the observed relationship between the level of SC activity and saccade velocity (Berthoz et al. 1986; Goossens and Van Opstal 2000), nor for the decrease in saccade amplitude with decreasing microstimulation strength (Groh 2011; Katnani and Gandhi 2010; Van Opstal et al. 1990). Moreover, it is not obvious how to implement the normalization factor physiologically (Groh 2001). In contrast, the VS model does not need an intricate nonlinear scaling mechanism to explain saccade decoding, and readily accounts for the decrease of saccade amplitude with micro-stimulation strength. However, it cannot yield weighted vector averaging, which has been shown by dual microstimulation experiments; nor does it generate fixed-vector saccades for suprathreshold microstimulation. By including output saturation, however, the VS model becomes the VSS scheme, which accounts for suprathreshold single- and dual-stimulation results, as well as for the results of local inactivation (Goossens and Van Opstal 2006; Groh 2001). So far, the VSS model has largely been tested for a single SC population. Since the environment typically provides multiple objects of interest, it is of importance to test the SC decoding mechanism with more challenging situations. The purpose of this investigation is to study the effects on saccades by inducing and manipulating two active populations in the SC with different stimulation strengths (Groh, 2001).

Figure 1 illustrates the hypothetical results of a VSS model tested with dual microstimulation. Figure 1A provides a temporal layout of a summation with saturation output for single (red and green) and dual (blue) microstimulation at different levels of activity. The
figure illustrates that when VSS is operating at high levels of activity, summation is constrained by saturation and as result dual microstimulation resembles a weighted vector average. Figure 1B illustrates the spatial representation of a prediction that corresponds with outputs from dashed gray box B. Nevertheless, when VSS is operating at low levels of activity, summation is not constrained by saturation, and as a result dual microstimulation resembles vector summation. Figure 1C illustrates the spatial representation of a prediction that corresponds with outputs from dashed gray box C. Thus, the model predicts a transition from resembling vector summation at low levels activity to resembling vector averaging at high levels of activity (Groh 2001).

In contrast to the VSS predictions, we found that at both high and low stimulation strengths the movement elicited by dual-site microstimulation always resembled a weighted vector average of the movements evoked by the same level of activity at each site individually. This trend persisted even when low-level stimulation at one site co-occurred with activity for a visual-evoked saccade at another site. Thus, the output from two synchronous populations in the SC does not result from the independent summed contributions of the individual sites. Collectively, our results indicate that the VSS model, although appealing in its simplicity, does not explain the decoding of multiple active populations. We propose that extending the model with intracollicular interactions could account for the data observed in this study.
**Methods**

All procedures were approved by the Institutional Animal Care and Use Committee at the University of Pittsburgh and complied with the guidelines of the Public Health Service policy on Humane Care and Use of Laboratory Animals.

**Subjects and surgical procedures:**

Two juvenile, male rhesus monkeys (*Macaca mulatta*) underwent one or more surgeries in a sterile environment and under isoflurane anesthesia. The initial procedure consisted of placing a Teflon-coated stainless steel wire (Baird Industries, Hohokus, NJ) under the conjunctiva of one eye and securing a head-restraint post to the skull. In the second procedure, one cylinder was cemented over a craniotomy. The chamber was placed stereotactically on the skull, slanted posteriorly at an angle of 38° in the sagittal plane. This approach allowed access to both colliculi and permitted electrode penetrations normal to the SC surface. After each surgery, the monkey was returned to its home cage and allowed to fully recover from surgery. Post-operatively, antibiotics and analgesics were administered as indicated in the protocol.

**Experimental procedures and Behavioral tasks:**

Visual stimuli, behavioral control, and data acquisition were controlled by a custom-built program that uses LabVIEW architecture on a real-time operating system supported by National Instrument (Bryant and Gandhi 2005). Each animal was trained to sit in a primate chair with its head restrained and a sipper tube was placed near the mouth for reward delivery. The animal sat inside a dome surrounded by two alternating magnetic fields which induced voltages in the eye coil and thus permitted measurement of horizontal and vertical eye position (Robinson 1963). The animal fixated targets that were projected onto a circular mirror, which rear reflects onto the isoluminant wall of the dome. Anti-warping software obtained from Paul Bourke, University of Western Australia, allowed reflections from the mirror to appear undistorted and for distances to be properly transferred onto a curved surface. The monkey sat in the center of the dome which has a radius of 1m and spans ± 150° horizontally and ± 30° vertically of the visual field. A
photodetector, positioned outside the animal’s field of view, detected the actual time of appearance of visual objects, which was then used to correct for time shifts induced by the projector’s refresh rate.

Both animals were trained to perform the oculomotor gap task. Every trial began with directing the line of sight to a fixation point for 300-500 ms before it was extinguished. Following a 200-400 ms “gap” interval, during which the animal was required to maintain the same eye position, another stimulus was illuminated in a random location in the visual periphery. Incorporation of the gap interval permitted fixation to become disengaged prior to saccade preparation, allowing the oculomotor system to be more responsive to incoming visual and/or stimulation input (Sparks and Mays 1983). Each animal was permitted 500 ms to redirect its visual axis on the saccade target and hold gaze steady for 300-500 ms to earn a liquid reward. As the animal performed this task, two platinum iridium microelectrodes (1.0-1.5 MΩ; MicroProbes for Life Science, Inc., Gaithesburg, MD) were individually advanced with independent hydraulic microdrives (Narashigie, Tokyo, Japan). The superficial layer of the SC was first identified by the presence of distinctive bursting of background activity associated with flashes of room lights. The electrode was then driven deeper into the SC until saccadic motor bursts were identified. At this stage, stimulation (40μA, 400Hz) was delivered during the gap interval to determine the vector coordinates. The depth of the electrode was then minimally adjusted to obtain the shortest possible latency of the stimulation evoked saccade (20 - 40 ms). Train duration was manually set (range: 100-300ms) and always long enough to allow for completion of the stimulation evoked movements.

**Experiment 1: Dual Microstimulation (Figure 2A)**

The objective of the first experiment was to assess the decoding mechanism based on saccades evoked by simultaneous stimulation of two SC sites. As illustrated in Figure 2A, microstimulation was delivered 100 ms after fixation offset. Following stimulation offset, a visual stimulus was presented in a random location in the periphery, to which the animal directed its visual axis to obtain a reward. Stimulation was delivered through either one electrode (10% of the trials per electrode) or through both electrodes (another 10% of trials). Initially, the stimulation parameters were supra-threshold (always set to 40μA, 400Hz, 100-300 ms, biphasic pulses). The current intensity and/or frequency through both electrodes were then reduced to a level which yielded non-optimal saccades from each stimulation site. Table 1 lists the sub-
optimal parameters used for each paired site. Such saccades typically exhibit lower peak velocities and reduced amplitudes (Van Opstal et al. 1990), even with prolonged stimulation durations (Groh 2011; Guillaume and Pélisson 2001; Katnani and Gandhi 2010). The remaining 70% of control (non-stimulation) trials was pooled together to establish a data base of visually guided saccades that were used for comparison with stimulation-evoked saccades.

**Experiment 2: Visually induced activity with microstimulation (Figure 2B)**

Next, we examined the effect of microstimulation on visually-guided saccades. On 20% of gap saccade trials, microstimulation was delivered to one SC site during the presentation of a visual target (Figure 2B), not during the gap period as above. More specifically, the onset of the stimulation-evoked movement was timed to coincide with the typical saccade reaction time to the visual target. Following a 200 ms blank period after stimulation offset, another visual target was presented in a random location in the visual periphery, which the monkey had to fixate to obtain a liquid reward. On another 10% of trials, however, stimulation was delivered to the electrode during the gap period (see Figure 2A) to collect the saccade vector associated with the site and stimulation parameters.

The location of the visual target presented in relation to the evoked stimulation vector was loosely chosen to achieve similar distributions of distances in SC coordinates as was collected in Experiment 1. Stimulation-evoked saccades that interacted with the visual target showed no obvious signs of curvature (saccades directed first toward one target and then towards the other in midflight; Arai et al. 2004; Port and Wurtz 2003) and reflected a weighted combination of the visual and stimulation-evoked saccades; only this subset of movements was analyzed for the purpose of this study. Saccades observed on other trials clearly resembled pure stimulation movements (stimulation onset occurred well before the visually guided saccade), curved saccades (stimulation onset occurred during the visually guided saccade), or pure visual movements (stimulation onset occurred after the visually guided saccade) (McPeek et al. 2003; Noto and Gnadt 2009), and were excluded from additional analyses. We note that movement of this nature were rarely observed during each session (<1% of data removed) as the stimulation onset spanned a narrow temporal range. As before, the experiment was first performed with supra-threshold stimulation parameters and then again repeated with stimulation settings that evoked reduced amplitude saccades.
Electrical stimulation:

Constant current stimulation trains were generated using a Grass S88X stimulator in combination with Grass PSIU6 isolation units. Trains consisted of anodal phase leading, biphasic pulses (0.25 ms). For high or supra-threshold stimulation conditions, current intensity and frequency were fixed at 40 μA and 400 Hz. The lower parameter space could be as low as 10 μA and 100 Hz, and differed for each data set in order to evoke reduced amplitude saccades (see Table 1). Low stimulation settings were determined by selecting current intensities, frequencies, or both that reliably produced movements (>90% probability of evoking movement) but also significantly reduced the amplitude of the movements (~15% or more change in amplitude). Only one set of high and low stimulation-evoked saccades was collected for each data set, as the dual-stimulation protocol was only a small part of a larger stimulation study to systematically analyze the relationship between stimulation parameters and saccade features (Katnani and Gandhi 2010; Katnani and Gandhi 2011). In all cases, stimulation duration was always long enough to ensure that it outlasted the eye movement.

Data analyses:

Each trial was digitized and stored for off-line analysis. We used a combination of in-house software and Matlab 7.10.0 (R2010a). Horizontal and vertical eye position along with onset and offset times of the stimulation train were stored with a resolution of 1 ms. Component velocities were obtained by differentiating the eye position signal. Onset and offset of stimulation evoked saccades were then detected using a standard 30°/s velocity criteria, respectively.

Eye movements evoked during simultaneous stimulation or during stimulation with visual stimuli were quantified using two techniques. The first analysis uses a straightforward Euclidean metric. We compared the predictions of the VSS computation to actual data by simply calculating the magnitude of each elicited vector and the magnitude of the respective vector addition prediction.

The second analysis used a multi-linear regression:
The analysis was performed for each vector pair elicited by high and low stimulation settings. The two coefficients A and B define the single site vector ($V_1$ and $V_2$) contribution to the output ($V_3$). The sum of the coefficients describes where the vector falls in relation to the single site vectors. For example, coefficients that sum to 1 identify a weighted vector averaging response, while a sum of 2 indicates vector summation. Two pieces of information are noteworthy about the regression technique. First, a coefficient sum of 1 does not imply that each site contributes half its vector (coefficients equaling .5) as averaging movements can be rotated due to the weight/contribution from each site being different. Second, during simultaneous stimulation we do not know how the single site vectors interact to contribute to the elicited averaging movements. Therefore, we must assume that these independent vectors are conveyed by the single site stimulation trials collected under each parameter setting. To ensure that each of the individual vectors was well-characterized we bootstrapped the single site endpoint distributions, with replacement, and averaged across them.
Results

Analysis of microstimulation elicited saccade features

Here we provide a robust characterization of saccades evoked by low stimulation parameters. We demonstrate that using low versus high stimulation parameters produces significant and reliable changes in saccade properties that help to assess if such movements can be accommodated for by decoding models.

We report on a total of 30 stimulation induced saccade-vector pairs obtained from two monkeys, sampling a range of the SC motor map that spanned approximately 2° to 45° in amplitude and approximately -80° to 80° in direction (Figure 3). The vector pairs exhibited radial amplitude differences between 0° to 28° and directional differences between 20° to 100°. In order to reduce the amplitude of saccade vectors, current intensity (18 sites), frequency (4 sites), or both (8 sites) were lowered at each electrode. We found that regardless of the stimulation parameter lowered, we could reliably produce a smaller-than-optimal saccade vector for single or dual stimulation sites in the SC (see Table 1). Furthermore, the saccade always completed within the train duration. Figure 4 illustrates the radial amplitude and radial velocity of saccades produced by high (40 µA) and low (20 µA) current intensities from single (left) and dual (right) stimulation sites. The figure provides insight towards the differences generated in saccade features when stimulating at high and low levels. One can observe a reduction in amplitude, a significant shift in response latency, and more variability in the amplitude and velocity traces.

To characterize these differences across all stimulation evoked saccade vectors (single and dual stimulation sites), we categorized each data set into a high or low group based on the stimulation parameters that evoked them. Figure 5A illustrates the radial amplitude of saccades in the high versus low groups (site 1: red, site 2: green, dual site: cyan) using a log-log plot. Almost all points are below the line of unity demonstrating a significant reduction in amplitude (paired t-test, p < 0.001). To assess variability, vector distributions of radial amplitude and peak velocity were normalized by their respective mean values obtained from the same site and with the same stimulation parameters. The normalized distributions across all data sets were then pooled together and the high and low group were compared. Figures 5B and 5C illustrate the normalized distributions pooled across all sites of radial amplitude and peak velocity,
respectively, generated by high stimulation parameters versus those generated by low stimulation parameters; notice the larger variability introduced by lower stimulation parameters. Observing that the data distribution is nearly Gaussian, we performed F-tests to assess whether dual site stimulation at high or low levels produced less variability in the different saccade distributions than those generated by single-site stimulation. We found no significant differences in the distributions produced by high level stimulation. Distributions for low-level stimulation were always more variable than those produced by high level stimulation. Interestingly, however, dual-site stimulation at low levels generated significantly less variability in radial amplitude and radial velocity when compared to single-site stimulation (radial amplitude: F-test, p < 0.05, radial velocity: F-test, p < 0.05).

To characterize the kinematics of saccades produced by low stimulation parameters we illustrate the main sequence properties (Figure 6A and 6B) and the skewness of the velocity profiles, compared to visually guided saccades. Panels A and B of Figure 6 demonstrates that lower stimulation parameters generate slower and longer-duration saccades, even when elicited by dual-site stimulation (site 1: red triangles, site 2: green squares, dual site: cyan circles). All peak velocity and duration distributions generated by low stimulation parameters (single and dual site) were significantly different from visually guided distributions (peak velocity: KS-test, p < 0.001, duration: KS-test, p < 0.001); furthermore, distributions generated by dual site stimulation were not significantly different from those generated by single site stimulation (peak velocity: KS-test, p > 0.11, duration: KS-test, p > 0.34). Neither the peak velocity nor duration of saccades produced by high stimulation parameters was significantly different from visually guided saccades (KS-test, p > 0.4; data not shown).

As can be seen in figure 6A and 6B, the majority of stimulation points fall within an amplitude bin that ranges from 2° to 16°. We calculated and compared the skewness of all stimulation-evoked and visual evoked saccades within this range (Figure 6C). The velocity profiles generated from low stimulation conveyed the typical positive skewness (time to peak velocity divided by total saccade duration is usually less than 0.5; (Van Opstal and Van Gisbergen 1987)) seen in visually guided saccades. However, the inset of figure 6C provides an example of how low stimulation parameters tend to generate broader peaks as a result of lower peak velocities and longer durations. Figure 6C summarizes the result by comparing the distributions of skewness for eye movements evoked by low stimulation (blue) and those
generated by visual stimuli (red). Note that values equal to 0.5 signify symmetry, greater than 0.5 signify positive skewness, and less than 0.5 signify negative skewness. The median of blue distribution (0.44; blue dashed line) was significantly different (rank sum, p < 0.01) from red distribution (0.41; red dashed line) indicating more symmetric velocity profiles.

**Simultaneous dual microstimulation**

Having shown that lower stimulation parameters reliably reduces the radial amplitude of evoked saccades, we can now utilize different levels of microstimulation as a tool to explicitly test the predictions of collicular decoding schemes.

Figure 7A illustrates results of high and low stimulation for one vector pair. Open symbols represent high or supra-threshold stimulation endpoints (40 µA, 400 Hz). The dashed red and green traces denote the spatial trajectories elicited at each site in the vector pair; the dashed cyan lines are the result of dual site stimulation with the same supra-threshold parameters. The dashed black line connecting the single site endpoint distributions represents all possible weighted average locations between the two vectors. Note that the dual-stimulation endpoints lie close to the vector-average line. When the experiment was repeated with lower stimulation parameters at each electrode (40 µA, 200Hz), the endpoints generated by single site stimulation, as well as by dual stimulation, scaled back together (filled endpoints). The solid black line, connecting the single site endpoints, represents all weighted average locations between the two reduced amplitude vectors. Thus, Figure 7A shows that at both high and low stimulation settings, dual site stimulation produced movements that resembled a weighted vector average.

To summarize the results for all vector pairs (n = 30 paired sites), we plotted (Figure 7B) the magnitude of the sum of paired site specific movements, at both high (open circles) and low (filled circles) stimulation, versus the actual magnitude of the movement elicited by dual-site stimulation. The figure illustrates that the majority of points fall below the unity line, and lie close to the half slope of the line (dashed line) confirming an absence of linear addition and showing a dominant averaging response. The consistency of the results across all high and low stimulation parameters highlights the insensitivity of the mechanism to the chosen stimulation settings. We also performed multi-linear regression, in which the sum of coefficients derived
from the regression of each vector pair (see methods) quantifies where movements elicited by
dual stimulation fall within the spectrum of averaging (sum of coefficients equals one) to linear
summation (sum equals two). Figure 7C illustrates that the summed parameters values for almost
all low (filled circles; mean=1.09, std = 0.19) and high stimulation strengths (open circles;
mean=1.09, std = 0.08) were about 10% larger than 1. The parameter distributions generated by
high and low stimulation strengths were not significantly different from one another (t-test, p =
0.91).

In an attempt to observe any trends that could provide insight into the dominant
averaging response, the sum of coefficients generated from each vector pair was correlated to
spatial and temporal saccade features (i.e., directional separation between saccade vectors,
location on the SC motor map, radial amplitude differences, and latency differences). Due to the
minimal variability generated in the distribution of coefficient sums, the analysis revealed no
trends. Notice, however, that a single vector pair did exhibited vector summation (coefficient
sum = 2.05). Unfortunately, the saccade features for the data set did not differ from all other
vector pairs that conveyed averaging responses.

**Interactions of visually-guided and stimulation-evoked saccades**

When testing the VSS model with dual microstimulation we observed that the evoked
saccades did not meet the linear predictions of the model. Furthermore, we found that the
kinematics of movements elicited by lower stimulation parameters did not match those generated
by visually guided saccades. Being that it is unclear how microstimulation induced activity to
generate such saccades, it might be argued that the observed averaging outcome is a result of an
inadequate drive provided by dual microstimulation. Therefore, we replaced one of the two loci
with visual-target-driven activity to observe if any changes occur when part of the total SC
population is generated by natural activation.

We studied a total of 22 vector pairs, sampling a portion of the SC saccade-vector map
that spanned approximately 7° to 36° in amplitude and approximately -90° to 70° in direction
(Figure 8; gray dots: visual targets, black dots: stimulation sites). The visually guided
movements and stimulation induced movements exhibited radial amplitude differences anywhere
between 0° to 21° and directional differences between 22° to 123°. We found that stimulation
onset coinciding just before the onset of the saccade to the visual target generated a straight trajectory whose amplitude and direction were influenced by both the visual target and the stimulation evoked movement (Note: for simplicity we will call these movements, VE saccades). Accordingly, the addition of the mean stimulation site latency (high parameter setting: 29 ms, std = 9 ms; low parameter setting: 90 ms, std = 30 ms) to the onset of stimulation relative to the presentation of the visual target (high parameter setting: 171 ms, std = 27 ms; low parameter setting: 116 ms, std = 45 ms) approximately equaled the mean reaction time of the visually guided saccades (212 ms, std = 33 ms).

We reduced the evoked amplitudes for single stimulation sites by varying current intensity (12 sites), frequency (2 sites), or both (8 sites). Figure 9A illustrates VE saccades (cyan trajectories) produced at both high (40 µA, 400 Hz; open circles) and low (15 µA, 400 Hz; filled circles) stimulation parameters for a single vector pair. The red trajectories correspond to the single site stimulation at high (open triangles) and low (filled triangles) parameter settings, while the green trajectories represent saccades made to the visual target. As with the dual stimulation results, the endpoints of the VE saccades, evoked by either high or low stimulation parameters, more closely resembled weighted vector averaging responses than linear vector summation, although responses were systematically larger than the weighted average for both stimulation strengths. Figure 9B illustrates a summary of the results across all vector pairs by comparing the magnitude of the summation prediction to the magnitude of the movement elicited by stimulation. Regardless of the stimulation settings, high (open circles) or low (filled circles), nearly all points fall below the solid unity line and close to the half slope of the line (dashed line). In addition, multi-linear regression (figure 9C) revealed that almost all low (filled circles; mean = 1.13, std = 0.27) and high stimulation values (open circles; mean = 1.16, std = 0.12) were about 14% larger than one. The distributions were not significantly different from one another (t-test, p = 0.63). We note that again one vector pair exhibited summation like results (coefficient sum = 2.27) with no distinct differences to provide insight to outlying result. Furthermore, we compared the saccade features of the vector pair to dual site microstimulation pair that also conveyed summation. No similarities were found as the two pairs were different in amplitudes, directions, amount of amplitude reduction, and vector separation.

The main sequence of VE saccades (Figure 10; red triangles) were not significantly different (KS-test: p = 0.869) from those evoked by simultaneous stimulation of two sites with
low stimulation parameters (Figure 10; cyan dots). The peak velocities and durations of VE saccades were significantly smaller and longer than those of visually guided movements (Figure 10, black traces; peak velocity: KS-test < 0.001, duration: KS-test < 0.001). Furthermore, the skewness of VE saccades was also similar to the dual stimulation results, exhibiting broader peaks as a result of lower peak velocities and longer durations (data not shown).
Discussion

Vector summation with saturation (VSS) makes an experimentally testable prediction for low versus high levels of activity at two simultaneous populations in the SC motor map. Specifically, the model predicts that the low-level activities generate a vector that resembles the linear addition of the two single-site vectors, whereas the result of high activity at each site resembles the weighted vector average of the two single-site saccades (Figure 1; (Groh 2001)). We found that at both high and low stimulation levels the evoked movements always resembled a weighted vector average of the two individual saccade vectors (Figure 7). As a result, we conclude that the VSS decoding scheme in its simplest form is insufficient to properly describe spatiotemporal decoding of multiple populations of activity in the oculomotor system.

Interpreting microstimulation

Microstimulation is arguably a crude technique that requires further study to understand how stimulation parameters (i.e., current intensity and frequency, neural circuitry) relate to evoked behavior (Katnani and Gandhi 2010). Yet, stimulation studies using supra-threshold parameters have yielded saccades with metrics that closely matched the movement fields of nearby cells recorded with the same electrode and kinematics that were indistinguishable from visually guided saccades of the same amplitude. At lower current intensities (Van Opstal et al. 1990) or frequencies (Stanford et al. 1996) evoked saccades have smaller amplitudes, and velocities that fall below the normal main sequence. These findings can in principle be explained by different mechanisms. For example, microstimulation might induce an electric field around the electrode tip that results in a Gaussian activation pattern, the size and height of which depend on the stimulation parameters. Supra-threshold microstimulation then produces neural activity that resembles the activity for normal visually guided saccades. Lowering current intensity reduces the passive spread of the electric field (Ranck 1975; Stoney et al. 1968)), while lowering the pulse-train frequency reduces the local strength of the electric field (Ranck 1975; Tehovnik 1996). Both manipulations decrease the total input strength to the cells, leading to a smaller population response and thus slower and smaller saccades. An alternative explanation could be that only a few cells near the electrode tip are directly activated by the electric field (Histed et al.
2009), and that the total population response results from synaptic transmission through the local intracollicular network (McIlwain 1982). The effectiveness of this transmission could then systematically depend on both the current intensity and frequency (stimulation strength).

Either assumption can explain the dependencies of the population (and resulting saccade) output on microstimulation parameters. Importantly, the high similarities between electrically and visually elicited movements strongly suggest that SC population responses are decoded in the same manner, regardless their cause. Thus, we can utilize microstimulation to manipulate the stereotypical responses generated by the oculomotor system in order to gain more insight on spatiotemporal decoding mechanisms.

**Interpreting an absence of linear addition**

Contrary to the prediction of the VSS model, we did not observe linear addition when simultaneously stimulating two sites in the SC with low stimulation parameters. Here we discuss whether such a result is evidence against a summation mechanism, or due to the methodology. We consider two potential issues that could mask linear addition.

First, reduced amplitude saccades evoked by single and dual site stimulation could be the result from truncation due to insufficient pulse-train duration (Van Opstal et al. 1990). Stanford et al (1996) demonstrated that when using low-frequency pulse trains, stimulation duration had to be increased to yield the same saccade. However, closer examination of their results suggests that low stimulation frequencies could produce changes in saccade amplitude at all applied train durations. A recent study by Groh (2011) also demonstrated a reduction in saccade amplitude at lower stimulation frequencies (and initial eye-in-head position). Our data are in agreement with this finding, as smaller amplitude saccades evoked by low current and/or frequency were always completed well before the stimulation offset. Therefore, we consider it unlikely that a lack of linear addition would result from insufficient train duration.

Second, could averaging be an artifact of dual microstimulation? Low current intensity and/or frequency might induce population profiles that result in weak excitation. Previous research suggested a balance between local excitation and global inhibition during the execution of normometric saccades (Hikosaka and Wurtz 1985a, b). Therefore, total motor activity induced by low stimulation parameters may drive the balance between excitation and inhibition in an
inadequate fashion; this potentially could mask the true intent of decoding. To account for this possibility we performed an additional experiment in which one of the two stimulation sites was replaced with a visual target. The introduction of visually induced activity would allow the preparation of a normal motor command that should correspond to the natural excitation-inhibition dynamics of the system. We reasoned that the visually guided movement will always drive the system close to saturation, and therefore, the combination of the movement with either high or low stimulation parameters should evoke saccade amplitudes constrained by saturation. Contrary to this prediction, low-level stimulation evoked responses with smaller amplitudes than the visual saccades as a result of being the weighted average between the visual target and the reduced stimulation vector (see figure 9). Furthermore, the velocity profiles of the evoked movements exhibited lower peak velocities and longer durations, similar to saccades evoked by dual-site microstimulation. Therefore, it is unlikely that the observed averaging result is an artifact of dual microstimulation.

**Decoding Mechanisms**

Three decoding mechanisms have been proposed in literature to explain spatiotemporal decoding in the oculomotor system: vector averaging (VA), vector summation (VS), and vector summation with saturation (VSS). In this section we will discuss how each mechanism relates to the data obtained in experiments 1 and 2.

As explained in the introduction, the VA scheme in its strictest sense depends only on the stimulation site and therefore cannot account for our data, as it does not produce smaller saccade amplitudes and has no mechanism to influence saccade kinematics. To account for these findings, two mechanisms have been added to the VA model: (i) firing rates in the brainstem burst generator co-vary with SC activity levels (Nichols and Sparks 1996; Sparks and Mays 1990), and (ii) a change in the normalization factor (Eqn. 1) to $\gamma = 1/(K + \sum_{n=1}^{N} a_n)$ allows the averaging scheme to yield reduced amplitude saccades (Van Gisbergen et al. 1987; Van Opstal and Goossens 2008). In this way, the vigor of activity in the SC influences the gain of the brainstem burst generator, and the addition of K as a constant in the normalization (in spikes/s) can influence the amplitude of decoded saccades. For example, if the total population activity in
the SC is low, K can dominate the denominator to reduce the amplitude of the saccade. The scheme then resembles the vector summation model (see Eqn. 1, where $\gamma = 1/K$). If the population activity is high, K becomes negligible and the computation approaches vector averaging. Therefore, if tested with low activity levels at two simultaneously active populations in the SC, the extended VA model generates the same predictions as the VS scheme.

A recent proposal of vector summation (Goossens and Van Opstal 2006) states that the saccade goal is computed by the summation of mini-vectors elicited by each spike of active cells in a population. The SC motor map thus specifies the desired saccade trajectory, including its kinematics. As a result, saccade vectors now depend strongly on activity level. This allows the model to predict differences in saccade metrics and kinematics when tested with high versus low activity for one motor command. However, the VS model assumes that SC cells are independent units and that weighting occurs entirely downstream of the motor map; therefore, the model cannot account for multiple population decoding (i.e., experiment 1 and 2) and needs an additional criterion to constrain eye movements.

Vector summation with saturation establishes a decoding mechanism that can define how much of the total activity from the SC motor map actually contributes to a movement. However, neurons in the SC are still assumed to be independent units and the summation of their spikes is only constraining once a threshold is reached (Goossens and Van Opstal 2006; Groh 2001). As a result, the model predicts linear addition at low levels of activity when the threshold is not met, but this prediction was not confirmed by our data. To account for the findings in this investigation we speculate that excitatory and inhibitory interactions in the motor map are critical for limiting a summation mechanism. Evidence suggests that lateral interactions are involved in shaping stimulation induced activity (see Interpreting microstimulation section above); therefore, the addition of intralaminar interactions (Lee and Hall 2006; Meredith and Ramoa 1998; Munoz and Istvan 1998; Pettit et al. 1999) would allow the model to account for the possibility that multiple sites within the SC motor map compete through lateral inhibitory connections. Under these circumstances, both sites would have reduced firing rates (and hence lead to slower saccades), resulting in a reduction of the total number of spikes. Therefore, the interactions provide a method in which the summation of spikes could be constrained at both high and low activity levels. Further evidence is needed to corroborate interactions as a constraining mechanism. Nevertheless, naturally evoked saccades have been shown to land in
intermediate location relative to multiple visual stimuli (‘global effect’) (Coren and Hoenig 1972; Godijn and Theeuwes 2002). An experiment that utilizes two-site recording in the SC to correlate naturally induced neural activity to global effect behavior could potential validate the interaction mechanism. Previous experimentation in the SC (Edelman and Keller 1998; Mc Peek et al. 2003; Port and Wurtz 2003; Van Opstal and Van Gisbergen 1990) would provide a foundation for the significance of such work.

Finally, we speculate that intracollicular interactions need not be the definitive mechanism to constrain summation. For example, interactions between concurrent motor commands can occur at other nodes of the oculomotor neuraxis (e.g., frontal eye fields, basal ganglia). Also, the gating of the saccadic system by the pontine omnipause neurons (OPNs) is a function of the velocity profile (Yoshida et al. 1999). Since eye velocity is attenuated for low-frequency stimulation, the OPNs may resume earlier, thus limiting the magnitude of the stimulation-evoked movement. Additional studies are required to probe the potential contributions of these mechanisms.
Figure Legends

Figure 1 – Vector summation with saturation predictions for stimulation-evoked vectors.

**A:** provides a temporal layout of the VSS predictions (adapted from Groh 2001). The red and green lines illustrate the result of stimulation at each individual site; the cyan line illustrates the output with dual microstimulation; the dashed gray boxes illustrates the level of activity at which the model is operating to generate the predictions in **B and C. B and C:** Spatial representation of a prediction that corresponds with outputs from dashed gray boxes in **A.** Site 1 and site 2 (high/low) represent individual site-specific vectors evoked by high/low stimulation parameters and are shown as red and green lines, respectively. Simultaneous stimulation of the two sites produces the cyan vector [Weighted Average (high)/Sum (low)]. Dashed black line in **B,** represents all possible weighted average locations between the two site-specific vectors.

Figure 2 – Sequence of events for three experimental paradigms.

Timeline of events for **A:** dual microstimulation, **B:** visual activity with microstimulation. The onset, duration, and offset of each component in the all three paradigms is represented by blocked regions of different shades (fixation target, black; site stimulation, gray; peripheral target, white).

Figure 3 – Distribution of paired-stimulation sites.

The vector evoked by each site is shown by a black dot and the pair is connected by a line. All 30 paired sites are represented on the SC saccade motor map. Numbers spanning from left to right indicate saccade amplitude. Vertically aligned text (right) denotes saccade direction. **U,** up; **D,** down.

Figure 4 – Traces of stimulation-evoked saccades.
Left: Radial amplitude (top) and radial velocity (middle) for saccades evoked by high (black dashed traces) and low (solid gray traces) stimulation parameters for a single site in the superior colliculus (SC). Bottom row illustrates the different current intensity used to generate each distribution of traces. Right: The same as the left panel, but for saccades generated by simultaneous stimulation of two sites in the SC.

Figure 5 – Saccade features of stimulation-evoked movements.

A: Correspondence of mean radial amplitude between saccades evoked by high versus low stimulation parameters. Filled red triangles and green squares represent the mean radial amplitude of saccades evoked by single site stimulation (site 1 and site 2); cyan dots represent the mean radial amplitude of saccades evoked by dual site stimulation. B: Normalized radial amplitudes evoked by high versus low stimulation parameters. C: Normalized radial velocities evoked by high versus low stimulation parameters. Note the larger spread of data points along the y-axis in B and C demonstrates that saccade features evoked by low stimulation parameters have greater variability.

Figure 6 – Kinematics of saccades produced by low stimulation parameters.

Mean radial amplitude versus mean peak velocity (A) and mean duration (B). Filled red triangles and green squares represent main sequence properties for saccades evoked by low stimulation parameters at a single site; cyan dots represent properties for saccades evoked by dual site stimulation; gray circles and solid black line in A and B represents sequence properties and fit for visually guided saccades. C: Histogram comparison of the skewness values calculated for visually-evoked (transparent red) and stimulation-evoked (blue) movements that fall within an amplitude bin that ranges from 2° to 16°; dashed lines indicated the median for the color matched distribution. Inset: example velocity trace for a visually guided (transparent red) and stimulation-evoked (blue) movement of similar amplitude (~19°).

Figure 7 – Simultaneous dual microstimulation results.
A: Dashed red and green trajectories represent the individual site-specific vectors elicited by high stimulation parameters (40μA, 400Hz) and are shown with their corresponding endpoint distributions, open red triangles and open green squares. Simultaneous stimulation of the two sites produced the dashed cyan trajectories, cyan circle endpoints. Solid red and green trajectories represent the reduced amplitude vectors elicited at each individual site by low stimulation parameters (40μA, 200Hz) and are shown with their corresponding endpoint distributions, filled red triangles and filled green squares. Simultaneous stimulation of the two sites with low stimulation parameters produces the solid cyan trajectories, cyan dot endpoints. Dashed line between the two site specific-vectors, and solid line between the two individual reduced amplitude vectors represent all possible weighted average locations. B: Comparison of mean radial amplitudes elicited by dual site stimulation versus the amplitudes predicted by a VSS computation. Solid black line represents perfect correspondence between predicted summation and actual response; dashed black line represents perfect correspondence between predicted averaging and actual response. C: Collected vector pairs versus sum of multi-linear regression coefficients. Solid line at 1 indicates averaging responses; solid line at 2 indicates summation responses. B and C: Open cyan circles represents mean amplitude or coefficient sums evoked by high stimulation parameters; filled cyan circles represents mean amplitude or coefficient sums evoked by low stimulation parameters.

Figure 8 – Distribution of paired-visual and stimulation sites.

Each vector evoked by stimulation is shown by a black dot; each vector evoked by the presentation of visual target is shown by a gray dot. The pair is connected by a line. All 22 paired sites are represented on the SC saccade motor map. Numbers spanning from left to right indicate saccade amplitude. Vertically aligned text (right) denotes saccade direction. U, up; D, down.

Figure 9 – Visually induced activity with microstimulation results.
A: Dashed red lines and open red triangles represent the trajectories and endpoints elicited by high stimulation parameters (40\(\mu\)A, 400Hz); solid green lines and squares represent trajectories and endpoints made to the presented visual target; dashed cyan lines and open cyan circles represent trajectories and endpoints of VE saccades evoked with visual activity and high stimulation parameters. Solid red lines and triangles represent trajectories and endpoints elicited by low stimulation parameters (15\(\mu\)A, 200Hz); solid cyan lines and dots represent trajectories and endpoints of VE saccades evoked with visual activity and low stimulation parameters. Dashed line between the site specific-vectors and visual target, and solid line between reduced amplitude vector and visual target represent all possible weighted average locations. B: Comparison of mean radial amplitudes for VE saccades versus the amplitudes predicted by a VSS computation. Solid black line represents perfect correspondence between predicted summation and actual response; dashed black line represents perfect correspondence between predicted averaging and actual response. C: Collected vector pairs versus sum of multi-linear regression coefficients. Solid line at 1 indicates averaging responses; solid line at 2 indicates summation responses. B and C: Open cyan circles represents mean amplitude or coefficient sums evoked by visual activity with high stimulation parameters; filled cyan circles represents mean amplitude or coefficient sums evoked by visual activity with low stimulation parameters.

Figure 10 – Kinematics of stimulation-evoked saccades and VE saccades

Mean radial amplitude versus mean peak velocity (A) and mean duration (B). Filled red triangles represent main sequence properties for saccades evoked by low stimulation parameters at a single site; filled cyan circles represent properties for VE saccades; the solid black line in A and B represents a fit of the main sequence properties for visually guided saccades (gray circles).
Grants and Acknowledgments:

H.A.K. is supported by an institutional training grant from the National Institute of General Medical Science (T32 GM081760) and institutional training grant from the Nation Science Foundation (DGE-0549352). N.J.G. is supported by the National Eye Institute (R01 EY015485, P30 EY008098) and National Institute of Deafness and Communication Disorders (P30 DC0025205). A.J.V.O. is supported by the Radboud University Nijmegen and by a VICI grant from the Dutch NWO (ALW grant 805.05.003).

We thank J. McFerron for programming maintenance and G. Foster for general assistance.
References


Walton MMG, Sparks DL, and Gandhi NJ. Simulations of saccade curvature by models that place superior colliculus upstream from the local feedback loop. *J Neurophysiol* 93: 2354-2358, 2005.

A

Amplitude

Level of Activity

B - Constrained by Saturation

C - Unconstrained by Saturation

Site 2 (high)

Weighted Average (high)

Site 1 (high)

Site 2 (low)

Sum (low)

Site 1 (low)
Event Sequence

A  Dual Microstimulation

Fixation Target

Site 1 stimulation

Site 2 stimulation

Visual Target

B  Visual activity with microstimulation

Fixation Target

Site 1 stimulation

Visual Target

Time →
Radial Amplitude Evoked by High Stimulation Parameters

Normalized Radial Amplitude Evoked by Low Stimulation

Normalized Radial Amplitude Evoked by High Stimulation

Normalized Peak Radial Velocity Evoked by High Stimulation

Site 1 stimulation
Site 2 stimulation
Dual stimulation
Skewness (0.5 = symmetric)

# of Saccades

Peak Velocity (deg/sec)

Duration (msec)

Site 1 stimulation
Site 2 stimulation
Dual stimulation

Low stimulation evoked movements
Visually guided movements

A

B

C

Velocity Traces of Matched Amplitude

Velocity (deg/sec)

Duration (ms)

0 5 10 15 20 25 30 35 40

0 5 10 15 20 25 30 35 40

0 100 200 300 400 500 600 700 800 900

0 20 40 60 80 100 120 140 160 180

0 10 20 30 40 50 60 70 80

0 10 20 30 40 50 60 70 80

0 10 20 30 40 50 60 70 80
A. Graph showing the relationship between horizontal position (deg) and vertical position (deg).

B. Graph comparing actual vector magnitude and predicted summation magnitude with legends for Dual Site Stimulation - High and Low.

C. Graph showing the sum of coefficients from vector pairs with vector pair site on the x-axis and sum of coefficients on the y-axis.
A graph shows the relationship between horizontal position (deg) and vertical position (deg). The graph includes data points for dual site stimulation at high and low levels.

Another graph plots predicted summation magnitude against actual vector magnitude, with data points for each condition.

A third graph illustrates the sum of coefficients from vector pairs against vector pair site.
<table>
<thead>
<tr>
<th>Vector Pair</th>
<th>Site-specific amplitude (Site 1/Site 2/Dual site)</th>
<th>Lower stimulation setting (Site 1/Site 2)</th>
</tr>
</thead>
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<td>13.3 / 14.4 / 11.3</td>
<td>40uA, 200Hz / 40uA, 200Hz</td>
</tr>
<tr>
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<td>13.2 / 7 / 6.9</td>
<td>40uA, 300Hz / 40uA, 200Hz</td>
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<td>8.5 / 19.5 / 8.4</td>
<td>40uA, 125Hz / 40uA, 125Hz</td>
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<tr>
<td>4</td>
<td>3.9 / 12.5 / 5.8</td>
<td>10uA, 400Hz / 10uA, 400Hz</td>
</tr>
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<td>5</td>
<td>20 / 3.5 / 6.3</td>
<td>20uA, 400Hz / 20uA, 400Hz</td>
</tr>
<tr>
<td>6</td>
<td>7.7 / 8.2 / 7.7</td>
<td>15uA, 400Hz / 15uA, 400Hz</td>
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<tr>
<td>7</td>
<td>22.3 / 10.7 / 13.5</td>
<td>10uA, 400Hz / 10uA, 400Hz</td>
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<td>8</td>
<td>31.9 / 25.2 / 29.3</td>
<td>10uA, 400Hz / 30uA, 400Hz</td>
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<tr>
<td>9</td>
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<td>15uA, 400Hz / 17uA, 400Hz</td>
</tr>
<tr>
<td>10</td>
<td>27.5 / 14.1 / 12.1</td>
<td>30uA, 400Hz / 25uA, 400Hz</td>
</tr>
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<td>13.1 / 21.3 / 16.3</td>
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<td>40uA, 100Hz / 40uA, 100Hz</td>
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<td>23.5 / 8.3 / 16.3</td>
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<td>30</td>
<td>22.6 / 4.9 / 7.4</td>
<td>18uA, 400Hz / 12uA, 400Hz</td>
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Reduced amplitude (Site 1/Site 2/Dual Site)
10.1 / 10.4 / 7.5
  9 / 4.1 / 4
  5.2 / 8.2 / 5
  2.4 / 6.6 / 3
  13.5 / 2.5 / 3
  6.4 / 5.4 / 5.7
  12.9 / 2.5 / 3.6
11.8 / 14.6 / 13.7
  11.2 / 9.6 / 9.2
  12.6 / 6.3 / 6.9
   5.2 / 6 / 11.1
  12.2 / 6.1 / 8.1
  25.4 / 27 / 27.4
   9.2 / 10.7 / 7.9
  15.5 / 8.9 / 7.5
  27.9 / 10 / 12.9
   5.3 / 4.3 / 4.7
  10.2 / 8.3 / 7.9
   18 / 4.4 / 9
  2.8 / 10.6 / 5
  9.6 / 36.1 / 11.4
  13.6 / 15.4 / 12.7
  6.5 / 6.6 / 6.4
  7.9 / 5.9 / 6.4
  10.1 / 8.5 / 9.5
   5.4 / 19.7 / 7
  8.7 / 5.5 / 5.9
  24.7 / 5.8 / 14.6
  14.7 / 5.9 / 8
  13.3 / 3.6 / 7.3