Dependence on Target Configuration of Express Saccade-Related Activity in the Primate Superior Colliculus

JAY A. EDELMAN 1,2 AND EDWARD L. KELLER 2

1Graduate Group in Bioengineering, University of California at Berkeley, Berkeley, 94720; and 2Smith-Kettlewell Eye Research Institute, San Francisco, California 94115

Edelman, Jay A. and Edward L. Keller. Dependence on target configuration of express saccade-related activity in the primate superior colliculus. J. Neurophysiol. 80: 1407–1426, 1998. To help understand how complex visual stimuli are processed into short-latency saccade motor programs, the activity of visuomotor neurons in the deeper layers of the superior colliculus was recorded while two monkeys made express saccades to one target and to two targets. It has been shown previously that the visual response and perimotor discharge characteristic of visuomotor neurons temporally coalesce into a single burst of discharge for express saccades. Here we seek to determine whether the distributed visual response to two targets spatially coalesces into a command appropriate for the resulting saccade. Two targets were presented at identical radial eccentricities separated in direction by 45°. A gap paradigm was used to elicit express saccades. Express saccades were more likely to land in between the two targets than were saccades of longer latency. The speeds of express saccades to two targets were similar to those of one target of similar vector, as were the trajectories of saccades to one and two targets. The movement fields for express saccades to two targets were more broad than those for saccades to one target for all neurons studied. For most neurons, the spatial pattern of discharge for saccades to two targets was better explained as a scaled version of the visual response to two spatially separate targets than as a scaled version of the perimotor response accompanying a saccade to a single target. Only the discharge of neurons with large movement fields could be equally well explained as a visual response to two targets or as a perimotor response for a one-target saccade. For most neurons, the spatial properties of discharge depended on the number of targets throughout the entire saccade-related burst. These results suggest that for express saccades to two targets the computation of saccade vector is not complete at the level of the superior colliculus for most neurons and an explicit process of target selection is not necessary at this level for the programming of an express saccade.

INTRODUCTION

Research in the past three decades has demonstrated that the vectors of saccades are coded by neurons in the frontal eye fields (FEF), posterior parietal cortex, and deeper layers of the superior colliculus (DSC) (Andersen 1989; Goldberg and Segraves 1989; Sparks and Hartwich-Young 1989). Neurons in these saccade-related areas also have sensory properties, suggesting that they play a role in analyzing the array of sensory input and determining the location in visual space to which the saccade will be made.

To understand how the saccadic system processes multiple visual stimuli into a saccade motor program, researchers have studied saccades elicited by two targets presented in spatial and temporal proximity. Such saccades often land in between the two targets and have thus been referred to as “averaging saccades” (Coren and Hoenig 1972; Findlay 1982; Ottes et al. 1984). It is unclear where in the saccadic pathway the processing of such an array of sensory input to yield a saccade vector is complete. Indeed, the command to make such a saccade may only be evident at a level, such as at that of the excitatory burst neurons in the brain stem, where saccades are coded temporally, not spatially.

The role that the DSC plays in the sensorimotor transformations underlying the programming of saccades to two targets can be investigated by recording the activity of a class of neurons known as visuomotor burst neurons, which discharge both in response to presentation of visual stimuli, and also immediately before and during saccades (Sparks and Hartwich-Young 1989). Such neurons have both receptive and movement fields, receptive fields being the region of visual space in which presentation of a target modulates a neuron’s response, and movement fields being the loci of endpoints of saccades accompanied by neural discharge. The two-dimensional shape of receptive and movement fields refers to the dependence of cell discharge on target location or saccade vector, respectively.

Van Opstal and Van Gisbergen (1990) described three hypotheses of where in the saccadic system saccades to two targets are programmed relative to the DSC. The upstream hypothesis claims that averaging saccades are programmed in “upstream” areas that project to the DSC, such as the FEFs and posterior parietal cortex. This hypothesis predicts that, by the time the saccade generating signals pass through the DSC, they should be independent of target configuration and depend only on saccade vector. Discharge in the DSC for saccades to one target and two targets should be identical, and thus a neuron’s activity should only depend on saccade vector (Fig. 1, C and D). The downstream hypothesis claims that saccades to two targets are spatially programmed in saccade-related regions downstream of the DSC, or else that they are merely a consequence of the spatiotemporal processing downstream of the DSC. The most extreme version of this hypothesis would predict that the spatial distribution of perisaccadic activity in the DSC is identical to the spatial distribution of the visual response in the DSC, so that a neuron’s discharge should only depend on target configuration (Fig. 1, E and F). Thus, according to this hypothesis, the impending saccade vector is never represented explicitly at the level of the DSC. The collicular hypothesis claims that sensorimotor transformations underlying saccades to two targets occur within the DSC. This hypothesis predicts that while a saccade to two targets is programmed and executed, discharge in the DSC will at first depend on target configuration and then later have discharge identical to that
FIG. 1. Cartoon illustrating predictions of the upstream and downstream hypotheses. A: cartoon of superior colliculus (SC) motor map depicts recording of a neuron located on the horizontal meridian of the motor map at a position corresponding to 20° rightward saccades. B: cartoon of location in visual space corresponding to location on motor map of recorded neuron. C and D: cartoon illustrating prediction of upstream hypothesis. C: cartoon of relation of activity on motor map and neural discharge of a single neuron for 2-target (2T) saccades given that activity only depends on saccade vector. Each map of visual space depicts a saccade of a particular vector, whereas the accompanying SC motor map depicts the activity (grayish area) in the SC that would accompany this saccade. Small square on the map depicts the location in the SC of the recorded neuron. Each pair of maps is connected by a dashed line to a data point in D corresponding to discharge of this neuron for this saccade. D: taken together, these data points depict the relation between neural discharge and saccade direction. E and F: cartoon illustrating prediction of downstream hypothesis. E: cartoon of relation of activity on motor map and neural discharge recorded from a single neuron for saccades to 2 targets given that activity only depends on the locations of the 2 targets. Each map of visual space depicts a particular 2T configuration, whereas the accompanying SC motor map depicts the activity (grayish area) in the SC that would accompany this target configuration. Small square on the map depicts the location in the SC of the recorded neuron. Each pair of maps is connected by a dashed line to a data point in F corresponding to discharge of this neuron for this target configuration. F: taken together, these data points depict the relation between neural discharge and average target direction. See text for details.

for saccades to one target of the same vector. Some previous work has partially addressed the question of what role visuomotor neurons in the DSC play during saccades to two targets.

Robinson (1972) showed that simultaneous electrical stimulation of two sites in the DSC elicited saccades with a vector average of the saccades elicited by stimulation of each site alone. If we assume that electrical stimulation acti-
vates the output elements of the DSC, this result suggested that saccade areas downstream of the DSC can spatially average DSC activity. This result partially corroborates the downstream hypothesis and furthermore suggests that the resultant saccade vector is dependent on the “center of mass” of activity in the DSC and not on the total amount of activity in the DSC. However, just because the collicular–brain stem interface has the ability to create averaging saccades does not prove that saccades elicited by two visual stimuli are programmed in the same way.

Other physiological work used a paradigm in which saccades were elicited to two targets. Van Opstal and Van Gisbergen (1990) used a double-step paradigm, in which two targets were presented close together in space but separated in time, to elicit saccades that landed between the two targets. They showed that neurons in the DSC discharged less for two-target (2T) saccades than they did for one-target (1T) saccades to the same location, but also demonstrated that saccades elicited by the double-step paradigm were slower than saccades to a single target. Using a more complicated paradigm in which a monkey had to make a saccade to one of two target locations depending on the color of the fixation point and after a delay period, Glimcher and Sparks (1993) found that saccades that by mistake landed in between the two locations were coded in the DSC similarly to 1T saccades with the same vector.

We speculated that the shorter the required latency of the saccade, the more likely that lower-order structures in the saccade system such as the DSC participate in its programming, and thus that activity in the DSC may depend on target configuration only for short-latency saccades. Indeed, it has been recently shown that visual and saccade-related activity in visuomotor burst neurons in the DSC are merged for the very short latency (65–90 ms) saccades known as “express saccades” (Edelman and Keller 1996). For such saccades there may be little time to create an explicit spatial representation of saccade vector on the DSC motor map before saccade initiation. On the other hand, if the coding of such short-latency saccades does not depend on target configuration, it is unlikely that saccades of longer latencies would be so dependent.

We assessed the dependence of activity during 2T express saccades on target configuration by comparing movement fields for 2T saccades with those for 1T saccades. Differences in these fields would indicate a dependence on target configuration. We next tested quantitatively whether these neurons coded for target vector by comparing spatial profiles of activity for 2T saccades with the sum of two 1T visual responses appropriately separated in space. We also compared the metrics of 1T and 2T saccades and determined whether the distribution of endpoints of 2T saccades depended on their latency.

We found that the movement fields for 2T express saccades differed from that of 1T saccades. The discharge could be better explained as a visual response to the two simultaneously presented targets than as a motor response coding for the impending saccade. The speeds and curvatures of 1T and 2T express saccades were similar. We also found that saccades were more likely to land in between the two targets if they were of express latencies. These results are consistent with the downstream hypothesis of Van Opstal and Van Gisbergen (1990) described above.

**METHODS**

**Animals and surgery**

Neurons were recorded in the superior colliculi of two adolescent monkeys (Macaca fascicularis). All experimental protocols were approved by the Institutional Animal Care and Use Committee at the California Pacific Medical Center and complied with the guidelines of the Public Health Service policy on Human Care and Use of Laboratory Animals.

Surgery was performed under aseptic conditions. Anesthesia was induced with an intramuscular injection of ketamine and maintained with pentobarbital sodium injected intravenously. The following devices were implanted in the monkey: 1) a coil of Teflon-coated stainless-steel wire under the conjunctiva of one eye using the method developed by Fuchs and Robinson (1966) and modified by Judge et al. (1980); 2) a stainless steel recording chamber above the stereotactically determined location of the superior colliculus; and 3) two hollow bars transversely above the skull anterior to the recording chamber and a third diagonally, posterior to chamber, for use with a head-holding device. The recording chamber and transverse bars were fixed to the skull by embedding them in dental acrylic applied as liquid to the exposed skull. The dental acrylic mount was firmly anchored to the skull by the use of titanium self-tapping screws.

After surgery, monkeys were given 1 ml penicillin (Combiotic) per day for 1 wk as an antibiotic. Butorphanol tartrate (Torbutol) was used as an analgesic as needed (0.1 mg/kg im).

**Training**

After being allowed to recover from the effects of surgery, monkeys were trained to climb out of their cages into a primate chair designed to restrain the monkey during experiments. Training and subsequent experimental sessions took place four to five times per week, during which monkeys were given water as an experimental reward until satiated. Otherwise, the monkeys were water deprived. On days when training or experiments were not being performed, monkeys were allowed to drink water in their cages ad lib.

Before neurophysiological experiments began, monkeys were first trained to fixate a small target, then to saccade quickly and accurately as the target jumped in a conventional 1T saccade paradigm.

**Monitoring of single-neuron activity**

Single-neuron activity was recorded extracellularly using tungsten microelectrodes (Frederick Haer). With the use of an electrostatic device, insulation was blown off the tip to create an electrode with 0.5–1.5 MΩ impedance when tested at 1 kHz. On days of recording, the stainless steel recording chamber was opened and thoroughly cleaned under aseptic conditions. A double-eccentric micropositioning device was inserted into the chamber. A hole drilled in this device could be placed at any location within the 12-mm-diam chamber, allowing the electrode to access arbitrary but reproducible positions within the chamber. The dura mater was penetrated using a sharpened cylindrical guide tube, through which the electrode was subsequently driven hydraulically. Action potentials were detected by passing the raw neural signal through a spike discriminator (Mentor).

**Eye movement monitoring, data collection, and stimulus presentation**

Eye movement signals were obtained by placing the head-fixed monkey in horizontal and vertical magnetic fields that oscillated in temporal quadrature at 22 kHz. Electrical currents induced in the eye-coil wire by the magnetic fields were passed through a phase detector to yield separate horizontal and vertical eye move-
ment signals. Phase-detector offsets were set to account for variability in position of the coil within the eye. Before the beginning of each experimental session, the monkey’s eye position was calibrated by adjusting the gain and offset of an eye position signal amplifier while the monkey looked at visual targets projected at known locations.

Neural, eye position and velocity, and target position signals were sent to an 80386 IBM-compatible computer and sampled by a 12-bit data acquisition card (Data Translation, DT-2831) at 1,000 Hz. Resolution of the position signals was 1.5 minarc/bit.

Analog oscilloscope under computer control back-projected light spots onto a translucent tangent screen placed 40 cm in front of the monkey. Signals were generated by a D/A card at 1,000 Hz with 1.5 minarc/bit resolution. Light spots were bluish gray in color and 15 minarc in diameter. Intensity of the spots was set at 2 cd/m², 2 log units above a dim homogeneous background. To present two target lights simultaneously, the scope projected a spot at two locations alternately in the following manner: the spot was projected at one location for 4 ms, then turned off for 1 ms, then projected at the other location for 4 ms, and so on. For 2T presentations we set the voltage controlling the spot brightness at a higher level so that each of the two spots was as bright as a single spot presented alone.

**Paradigm**

On isolating a single neuron, the center of the neuron’s movement field was coarsely estimated immediately before collecting data by observing discharge during IT saccades. A variant of the standard saccade paradigm was designed to include presentations of one or two targets. Trials began with presentation of a fixation point, generally at the straight-ahead position. The monkey was required to fixate this point within 500 ms. After a variable period of fixation (400–800 ms), the fixation point disappeared, and one or two targets appeared and remained lit until the saccade terminated. To help elicit express saccades, a gap paradigm was used (Saslow 1967), in which there was a temporal “gap” between fixation point disappearance and target spot reappearance. Depending on the animal’s performance, gaps were adjusted in length from 80 to 150 ms to prevent anticipatory saccades. In one-third of our trials, two targets of identical radial amplitude and separated in direction by 45° were presented. We chose this value because we found that larger separations dramatically reduced the yield of express saccades. To discourage formation of the strategy of repeatedly making a saccade to the same of two targets as well as to gather normative data for IT saccades, single targets were presented in two-thirds of the trials. Single targets were presented randomly at one of nine possible positions near and flanking the center of the neuron’s movement field. The nine possible positions were arranged in a 3 × 3 polar grid, so that each position could be of one of three radial eccentricities and of three directions. The directions were spaced by 22.5°, whereas the radial eccentricities were spaced differently from neuron to neuron depending on the radial extent of its movement field. For two target trials, the targets were presented so that the radial eccentricity and average direction of the two targets was of one of the nine positions selected randomly. If the monkey was still well-motivated and the neuron still well-isolated after sufficient data had been obtained for each of the nine positions (~15 total trials per position), targets were presented at additional positions flanking the original nine positions.

**Latency and accuracy requirements**

To further prevent anticipatory saccades, we only rewarded saccades with latencies above a minimum reaction time of 50 or 60 ms. In most experimental sessions the maximum reaction time for saccade onset was set at 200–225 ms. We found that setting the maximum reaction time so that only express saccades were rewarded (i.e., at 100 ms) would often frustrate the monkey to the point where it did not make any express saccades. In 2T trials monkeys were rewarded for a short-latency saccade to a window surrounding both targets. This window had the shape of a radial arc with an inner radius of 0.75 × the radial amplitude of the two targets, an outer radius of 1.25 × the radial amplitude, and an angular extent of ~55°. To avoid introducing a more cognitive component to our task, we did not explicitly train the monkey to make averaging saccades. In 1T trials short-latency saccades to a small square window (4 × 4°) surrounding the single target were rewarded. Only data recorded when monkeys made saccades satisfying the latency and accuracy measures described above were analyzed.

**Saccade detection**

To enforce our saccade latency requirements, we detected saccade onset on-line. Eye velocity signals were obtained on-line with the use of a low-pass analog differentiator (cutoff: 170 Hz). Time of saccade onset was defined as the time when radial eye velocity (calculated on-line using the Pythagorean theorem) exceeded 20°/s. For data analysis, a digitally filtered eye velocity signal was filtered to obtain a more precise estimate of saccade latency. Using this off-line technique, saccade onset was defined as the time when radial eye velocity reached 10°/s. For a random sample of trials, this algorithm virtually always marked saccade onset within 2 ms of their onset as determined by visual inspection.

**Saccade classification**

In accordance with a previous report from this lab (Edelman and Keller 1996) express saccades were classified as those saccades with latencies between 65 and 90 ms, and regular saccades were classified as those saccades with latencies between 120 and 200 ms. The averaging saccades were defined as those saccades that landed closer to the midpoint of two targets than to either target; nonaveraging as those that landed closer to either target.

**Neuron classification**

The activity of 37 visuomotor burst neurons in the deeper layers of the SC was assessed using this paradigm. These neurons all displayed separate bursts of visual and perimotor activity when tested with a delayed paradigm, in which a single target was presented but the monkey had to continue fixating until the fixation point was turned off (see Edelman and Keller 1996), or during regular saccades. During or just before a saccade of optimal vector, the activity of these neurons peaked at >250 spikes/s then dropped during the saccade. Neurons with this temporal profile of activity have been referred to as clipped and partially clipped burst neurons (Waitzman et al. 1991), or burst neurons (BNs) (Munoz and Wurtz 1995). However, a few of our neurons also discharged at a low-frequency several hundred milliseconds before a saccade, a characteristic of the buildup neurons (BUNs) described by Munoz and Wurtz (1995). We applied the criterion of Munoz and Wurtz (1995) (discharge of >30 spikes/s in the 100-ms time interval beginning 200 ms before saccade onset for the saccades of the optimal vector in a delayed saccade paradigm) to the 31/37 neurons for which we collected data during a delayed paradigm, to determine how many of the neurons would be classified as BUNs. By this test we found 9/31 (~29%) tested neurons were BUNs. We have argued elsewhere that this criterion does not separate DSC into two distinct classes (Anderson et al. 1998).

According to the scheme of Sparks and Hartwich-Young (1989), the neurons we recorded would be classified neurons as visuomotor neurons because our neurons all had visual responses. In their scheme this class of neurons is distinct from burst neurons without a visual response, which they termed saccade-related burst
neurons (SRBNs), although it is unclear from their classification whether or not neurons with visual responses below a certain small criterion level would be called SRBNs. In a larger sample of neurons recorded in the SC more recently in our lab, 139/145 recorded neurons had a separate visual response (Anderson et al. 1998). This neural population consisted both of BNs and BUNs, as described above.

Spike density and summary of data analyses

To assist the quantitative analysis of DSC neurons’ burst waveform, the raw spike trace was convolved with a Gaussian of 4 ms standard deviation to yield a spike density trace (Richmond and Optican 1987).

We analyzed the spatial properties of discharge of the visuomotor neurons using two analysis procedures. We first tested whether movement fields depended on the number of targets by comparing surface fits of 1T and 2T movement fields. Second, we asked whether visuomotor discharge accompanying 2T saccades was better explained as a motor response identical to that for 1T saccades or as a visual response to two targets. To do this we first assessed how well the a scaled version of the fit of the 1T movement field, or motor prediction, fit the 2T movement field and second assessed how well the 2T receptive field was fit by a scaled version of the sum of two spatially separated 1T receptive fields, or visual prediction. We will refer to this second analysis as the visuomotor analysis.

Comparison of surface fits of movement fields

The spatial properties of 1T movement fields were estimated using a two-dimensional nonlinear surface fit with five free parameters. This process is illustrated in Fig. 2, and the detailed equations are described in the Appendix. The fields were fit as a product of a term expressing the peak discharge of the neuron, \( M \), a log-Gaussian function along a curve of constant direction, \( P(\cdot) \), which is depicted in Fig. 2E, and a Gaussian function along a curve of constant radius, \( \Theta(\cdot) \), which is depicted in Fig. 2D. The form of the equation of the fit is

\[
\hat{z} = M \cdot P(\rho; \mu, \sigma) \cdot \Theta(\theta; \mu, \sigma) \tag{1}
\]

where \( \hat{z} \) is the predicted neural discharge (spikes/s); \( \rho \) is the saccade radial amplitude (deg); \( \theta \) is the saccade direction (zero is right and horizontal; deg); and the five free parameters are \( M \), the magnitude of response at center of movement field (spikes/s); 2) \( \mu \), the radial eccentricity of center of movement field (deg); 3) \( \sigma \), the direction of center of movement field (deg); 4) \( \mu \), the spread of surface along radial dimension (unitless); and 5) \( \sigma \), the directional standard deviation, or spread, of surface (deg). A three-dimensional plot of such a surface is shown in Fig. 2B, and the contour plot of the surface is shown in Fig. 2C.

The center of the movement field is defined here as the endpoint of saccades accompanied by maximal neural discharge. The absence of a radial-directional cross-term ensured that the surface would be radially symmetrical about a line passing from the origin to the point of maximal discharge. To construct the spatial plots, mean spike density in a time window set relative to saccade onset was plotted against saccade or target vector. The specific epochs used will be described in RESULTS. These data points were then surface-fit with the use of a least-squared error criterion. The nonlinear regression was performed using the Marquardt-Levenberg algorithm (Marquardt 1963). Regressions were termed successful if over multiple iterations they mathematically converged on a stable value for each of the five parameters. We also computed the coefficient of determination \( R^2 \), a measure of goodness-of-fit for each successful regression (Glantz and Slinker 1990).

We fit the movement fields of 2T saccades using exactly the same procedure. To compare the movement field fits for 1T and 2T saccades, we compared the corresponding parameters using the Wilcoxon signed-rank test across our sample of neurons.

Visuomotor analysis: derivation of motor and visual predictions and measures of goodness-of-fit of predictions

To determine how well discharge for express saccades to two targets resembled that of the perimotor discharge for 1T express saccades, we computed for each neuron the motor goodness-of-fit (MGF), a measure of how closely the 2T movement field resembled the surface proportional (of same shape, but scaled in magnitude) to the calculated 1T movement field fit. This procedure is illustrated in Fig. 3. This surface corresponding to the contour plot in Fig. 3C was obtained by calculating the movement field fit for saccades to one target (Fig. 3A), as described for Eq. 1 above.

\[
\hat{z}_{1Tm} = M_{1Tm} \cdot P_{1Tm} \cdot \Theta_{1Tm} \tag{2}
\]

The subscript 1Tm indicates that the value is associated with the data for the 1T saccades. Next, we linearly regressed the neural discharge for the 2T data, \( z_{2T} \), against \( P_{1Tm} \cdot \Theta_{1Tm} \) to yield the coefficient, \( M_{2Tm} \). Multiplying this coefficient by \( P_{1Tm} \cdot \Theta_{1Tm} \) yields the motor prediction

\[
\hat{z}_{2Tm} = M_{2Tm} \cdot P_{1Tm} \cdot \Theta_{1Tm} \tag{3}
\]

The subscript 2Tm indicates that these values of \( \hat{z} \) are associated with the motor prediction. Note that this surface is a scaled version of the 1T movement field fit (Eq. 2). An isoradial slice through this surface passing through the center of the movement field is shown in Fig. 3D.

We will adopt as our measure of goodness-of-fit of the motor prediction the quantity one minus the ratio of the sum of squares of the difference between the data and the motor prediction to the sum of squares of the differences between the data and the mean of the data. We will refer to this measure as the MGF. For a neuron’s 2T data set, \( z_{2T} \), and the neuron’s motor prediction, \( \tilde{z}_{2Tm} \), the goodness-of-fit is calculated as

\[
\text{MGF} = 1 - \frac{\sum (z_{2T} - \tilde{z}_{2Tm})^2}{\sum (z_{2T} - \bar{z}_{2T})^2} \tag{4}
\]

where the added subscript i refers to the value for each saccade in the neuron’s data set and \( \bar{z}_{2T} \) is the mean neural discharge for all 2T saccades in the neuron’s data set. The MGF for the neuron in Fig. 3 is \(-0.68\).

To determine how well discharge for express saccades to two targets resembled that of a visual response to two targets separated in direction by 45° (the target separation used in these experiments), we computed the visual goodness-of-fit (VGF), a measure of how closely the 2T receptive fit resembled a scaled version of the expected receptive field for two targets. This procedure is illustrated in Fig. 4. The shape of the fit is calculated by first calculating the receptive-field fit for the 1T data

\[
\hat{z}_{1Tv} = M_{1Tv} \cdot P_{1Tv} \cdot \Theta_{1Tv} \tag{5}
\]

where all notation is the same as in Eq. 1. The subscript 1Tv indicates that the parameters are those for the visual receptive-field fit of the 1T data. A contour plot of this surface is shown in Fig. 4C. The 1T receptive fields were fit using the same procedure used for that of the 1T movement fields, substituting radial target displacement and direction for saccade radial amplitude and direction, respectively. As for movement fields, spike density was measured using a temporal epoch aligned with saccade onset.

For the purpose of this analysis, we assume that the visual response to two targets is the sum of the response to each target separately. If we define the receptive field as the dependence of the discharge on the average polar coordinate of the two target
locations, then the component of the receptive field corresponding to the clockwise target is
\[ M_{1Tv} \cdot P_{1Tv} \cdot \Theta_{ccw}(\hat{\theta}, \hat{\rho}, \hat{\theta}_c) \] (6)
where the subscript CCW refers to the shifting of the 1T receptive-field surface in direction by 22.5° counterclockwise and \( \hat{\theta} \) refers to the average direction of the two targets. (Note that the clockwise target’s correspondence to a counterclockwise shift in the receptive field follows from the inverse relationship between discharge on the SC map and the receptive field of a SC neuron.) Similarly, the receptive field due to the counterclockwise target is
\[ M_{1Tv} \cdot P_{1Tv} \cdot \Theta_{ccw}(\hat{\theta}, \hat{\rho}, \hat{\theta}_c) \] (7)
where the subscript CW refers to the shifting of the 1T receptive-field surface in direction by 22.5° clockwise. The detailed versions of Eqs. 6 and 7 are in the APPENDIX.

The dependence of discharge on the average position of two targets is the sum of the these two components
\[ M_{1Tv} \cdot P_{1Tv} \cdot (\Theta_{ccw} + \Theta_{cw}) \] (8)
A contour plot of this surface is shown in Fig. 4D. Note how each “mound” of the surface is shifted in direction relative to the surface portrayed in Fig. 4C. Finally, we linearly regressed the neural discharge, \( z_{1Tv} \), against \( P_{1Tv} \cdot (\Theta_{ccw} + \Theta_{cw}) \) to yield the coefficient, \( M_{1Tv} \). Multiplying this coefficient by \( (\Theta_{ccw} + \Theta_{cw}) \) yields what we will refer to as the visual prediction
\[ \hat{z}_{1Tv} = M_{1Tv} \cdot P_{1Tv} \cdot (\Theta_{ccw} + \Theta_{cw}) \] (9)
The symbols are defined analogously to those in Eq. 3. Note that this surface is a scaled version of that described by Eq. 8. An isodirectional slice through this surface passing through the center of the neuron’s receptive field is shown in Fig. 4E.

The measure of goodness-of-fit of the visual prediction, or VGF, is defined analogously to MGF
\[ VGF = 1 - \frac{\sum (\hat{z}_{1Tv} - \hat{z}_{1Tv})^2}{\sum (z_{1Tv} - \hat{z}_{1Tv})^2} \] (10)
The VGF for the neuron in Fig. 4 is 0.72. The MGFs and VGFs were calculated for each neuron’s data and then compared across our sample of neurons using the Wilcoxon signed-rank test.

**RESULTS**

**Saccade characteristics**

We were concerned about possible differences in the speed or curvature of 1T and 2T saccades, because such differences would make the results of our single-cell re-
cordings more difficult to interpret. We were also interested in the distribution of endpoints of 2T saccades relative to the positions of the two targets, and how this distribution depended on saccade latency. We therefore analyzed the eye movement data that we recorded while collecting neuronal data. We also analyzed data for regular saccades elicited by the gap paradigm.

**SPEED AND CURVATURE OF 1T AND 2T SACCADES.** It is well established that, given the same stimulus conditions, saccade peak speed is strongly dependent on saccade amplitude and that peak speed shows a soft saturation for saccades larger than ~20° in amplitude (Becker 1991). We determined that this relationship held for both 1T and 2T saccades, and that the speed of 2T saccades was virtually identical with that of 1T saccades for most saccade amplitudes (Fig. 5).

Saccades to two targets could be much more curved than 1T saccades if, for example, the saccades initially shifted toward a point in between the two targets but then curved to land near one of the two targets. We defined saccade curvature as the maximum perpendicular distance of any point on the saccade trajectory from a straight line connecting the saccade start and end points divided by the distance between these two points (Smit and Van Gisbergen 1990). The average curvature for all saccades between 10 and 20° in amplitude and 0 and 45° in direction (right to up and right) was small and only slightly greater for 2T saccades, although this difference was statistically significant (*monkey GM*: 1 target, 0.044; 2 targets, 0.057, *t*-test: *P* < 0.001; *monkey ME*: 1 target, 0.038; 2 targets, 0.049, *t*-test: *P* < 0.001).

**RELATIONSHIPS BETWEEN NUMBER OF TARGETS, SACCADE ENDPOINT DISTRIBUTION, AND SACCADE LATENCY.** The number of targets had a small effect on saccade latency in the gap paradigm. This effect was of opposite sign for the two monkeys. For example, for saccades between 10 and 20° in amplitude with directions from right horizontal to 45° right and up, 2T saccades tended to have slightly longer latencies than 1T saccades for one monkey (*GM*) (1T: 87 ms, 2T: 98 ms; *t*-test, *P* < 0.001), but slightly shorter latencies for the other monkey (*ME*) (1T: 109 ms, 2T: 95 ms; *t*-test, *P* < 0.001).

In both monkeys, the distribution of 2T saccade endpoints varied with saccade latency. The proportion of 2T saccades that were averaging saccades was higher for express saccades than for saccades of longer latencies. For *monkey GM* this relationship was quite dramatic; express saccades landed at scattered locations between the two targets, whereas saccades with latencies >100 ms tended to land near one target or the other (*Fig. 6A*). Fifty-nine percent of this monkey’s 2T express saccades but only 29% of its regular saccades were averaging (*z*-test, *P* < 0.001). The other monkey (*ME*) showed a similar, but less dramatic pattern, with 30% of express saccades and 18% of regular saccades averaging (*z*-test, *P* = 0.002). This monkey’s 2T express saccades tended to land near the upward target (*Fig. 6B*). The relatively short duration of the temporal gaps between fixation point offset and target onset generally prevented anticipatory saccades. Very few saccades (<2%) had latencies <50 ms.
Accuracy in saccade direction was defined as the mean absolute value of the difference between target direction and saccade direction for all trials. One-target express saccades (1TE) tended to be less accurate in direction than 1T regular saccades (1TR) for both monkeys (Kolomogorov-Smirnoff test, $P < 0.01$), but the scatter in direction was much less than that for 2T express saccades (2TE) for both monkeys ($P < 0.01$) (monkey GM: 1TR, 5.2°; 1TE, 6.2°; 2TE, 11.2°; monkey ME: 1TR, 2.8°; 1TE, 3.6°; 2TE, 15.0°).

The saccade amplitude gain for express saccades to two targets was slightly smaller than those to one target. We defined saccade amplitude gain as the saccade amplitude divided by the radial eccentricities of the target(s) (note that for 2T trials the eccentricities of the two targets were always the same). $t$-Tests for all trials with target eccentricities between 10 and 20° (the vast majority of our trials) during all neuronal recording sessions revealed that gains were significantly smaller for 2T saccades ($t$-test, $P < 0.001$) for both monkeys (monkey GM: 1T, 0.84; 2T, 0.79; monkey ME: 1T, 0.86; 2T, 0.80).

**Single-unit activity**

In the following sections we describe the results of our analyses of single-unit data. The results can be summarized as follows: 1) The spatial profile of discharge for 2T express saccades depends not only on saccade vector but also on the number of targets that elicit the saccade. 2) This discharge accompanying 2T express saccades is more like a visual response to two targets than a motor response preceding 1T saccades; the VGF (see METHODS) is generally greater than the MGF. 3) The MGF and VGF are comparable only for neurons with movement fields broad in direction. 4) The spatial profile of discharge for 2T express saccades is different from that of 1T express saccades for the duration of the saccade-related burst. 5) The differences between MGF and VGF are significant for both averaging express saccades and nonaveraging express saccades.

**DOES SINGLE-NEURON ACTIVITY AT SACCAD ONSET DEPEND ON TARGET CONFIGURATION?** In this section our sole aim is to provide evidence demonstrating that 1T and 2T movement fields are different. Across our sample of recorded neurons,
express saccade movement fields were clearly dependent on target configuration. Movement fields were broader along the direction axis in the 2T case than in the 1T case for all neurons tested quantitatively (see below). Data for a neuron whose discharge was greatly dependent on the number of targets are shown in Fig. 7. This neuron discharged more for 1T than for 2T saccades when saccades landed close to the center of the neuron’s movement field, as can be seen by comparing the brightness of spatially corresponding squares in Fig. 7, A and B. However, this neuron discharged much less for 1T saccades than for 2T saccades when saccades had a direction very different from that of the center of the movement field. In addition, for this neuron, 2T saccades were accompanied by more discharge when their directions were far from the movement field center than when they were close to the center. In the neuron whose discharge is portrayed in Fig. 8, such a spatially bimodal pattern was not so detectable, yet the discharge was clearly dependent on the number of targets. Figure 9 shows data for a neuron whose 1T and 2T movement fields were more similar, a finding seen for most of our neurons with larger 1T movement fields.

To confirm that 2T express saccade movement fields were broader than those for 1T, five-parameter Gaussian/log-Gaussian surfaces (see METHODS) were fit for 1T and 2T movement fields. We only analyzed neurons for which we obtained at least 10 1T saccades and 10 2T saccades. Neuronal discharge was defined as the mean firing rate in a 40-ms epoch centered on saccade onset. If movement fields did not depend on the number of targets, then the parameters of the movement field fits should be similar for 1T and 2T express saccades. However, across our sample of neurons, we found differences in the directional spread ($\theta_u$) and magnitude ($M$) parameters (Table 1A). The nonlinear regressions of the 1T data were successful for 35/37 neurons. Regressions of the 2T data were successful for 25 of these 35 neurons. The 2T saccade movement field regressions had a value of directional spread ($\theta_u$) greater than that for 1T saccades for all 25 neurons (Fig. 10A). This trend...
FIG. 7. Spatial profile of activity for a neuron with a 2-peaked movement field for 2T saccades. A: plot of movement field for 1T saccades. Horizontal and vertical axes represent horizontal and vertical saccade displacements (deg). Mean discharge rate (spikes/s) in the 40-ms epoch centered on saccade onset and averaged across all saccades landing in a 1 × 1° bin (in Cartesian coordinates) is represented by the luminance of each square. Plots in C were constructed by using saccades landing in 1 of 3 labeled sectors. Each sector spanned 22.5° in direction and a range of saccade amplitude close to the center of the neuron’s movement field. The fixation point is represented by a plus sign. B: same as A but for 2T saccades. C: rasters and spike density traces for 1T saccades. Each of the 3 plots are aligned on saccade onset (dashed line). Each horizontal tick mark represents 25 ms. Vertical bar on the left represents 250 spikes/s. All saccades landing in labeled sectors, 1, 2, and 3, in A were used to construct the corresponding plots in C. D: rasters and spike density traces for 2T saccades. Same conventions as C. See text for details. The parameter estimates and 95% confidence intervals of the parameter estimates of the curve-fit for this neuron are, for the 1T data, M: 564 ± 40 spikes/s; ρc: 9.6 ± 0.2°; ρs: 0.188 ± 0.0188 [unitless]; θc: 51.4 ± 1.26°; θs: 11.3 ± 0.92°; R²: 0.87. The regression was not successful for the 2T data.

held both for the 11 confirmed BNs and the 6 confirmed BUNs that had successful regressions. For 22/25 neurons the 2T directional spread (θs) was greater than the upper 95% confidence limit of the estimate of 1T directional spread (θc). For 20/25 neurons, 1T saccade regressions had higher peak responses values (M) than those for 2T saccades. This trend held for BNs but not for BUNs. For 17/25 neurons, the 2T peak response was smaller than the lower 95% confidence limit of the estimate of the 1T peak response. There were no statistically significant differences between the 1T and 2T fits for the other three parameters. The quality of the fits, as measured by the coefficient of determination (R²) was generally much higher for 1T data than for 2T data (Table 1A).

For comparison, we used this same procedure to test the target dependence of saccade-related discharge for regular saccades. We still found a difference in directional spread (θs) between one and two target saccades, although this difference was not nearly as large as that found for express saccades. We could not find statistically significant differences for the other four parameters (Fig. 10B; Table 1B).

As mentioned in METHODS, 2T saccades could land anywhere within a wedge-shaped window surrounding both targets, and as a result 2T saccades often did not land close to the endpoints of 1T saccades. Could such a spatial sampling problem bias the estimates of our surface fit parameters? To address this question we refit the 1T saccade data using a reduced data set equal in number with that of the 2T data set. For each 2T saccade we included in the data set the 1T
saccade whose vector was most similar. Across our population of neurons, this modified analysis yielded the same results as our original analysis (Table 1C).

VISUOMOTOR ANALYSIS: DOES ACTIVITY FOR TWO TARGETS RESEMBLE A VISUAL RESPONSE OR A MOTOR PRELUDE? Having determined that express saccade movement fields of visuomotor neurons were dependent on target configuration, we next asked whether the spatial profile of discharge for 2T express saccades could be better explained as the visual response to the two targets than as a motor prelude of a saccade with a particular vector.

Across our sample of neurons, the receptive fields resembled the visual predictions more than the movement fields resembled the motor predictions, although this was not true for all neurons. We determined quantitatively how well the 2T movement fields resembled the motor prediction, a surface proportional to the sum of two 1T receptive fields separated in direction by 45°, by calculating the VGF. Comparisons of the 2T express saccade movement fields with the motor predictions and receptive fields with the visual predictions are shown in Fig. 11 for four neurons. For each of these four neurons, we show an isoradial slice through the center of the movement fields and motor predictions (left) and through the center of the receptive fields and visual predictions (right). In the top three rows we show results for three neurons typical for our sample, in which

Next, we determined how well the 2T receptive fields resembled the visual prediction, a surface proportional to the sum of two 1T receptive fields separated in direction by 45°, by calculating the VGF. The measure of neuronal discharge for both the movement and receptive fields was the mean firing rate in a 40-ms epoch centered on saccade onset. We performed this procedure only for neurons whose 1T 5-parameter nonlinear regressions converged, and for which there were at least 10 2T trials.

Comparisons of the 2T express saccade movement fields with the motor predictions and receptive fields with the visual predictions are shown in Fig. 11 for four neurons. For each of these four neurons, we show an isoradial slice through the center of the movement fields and motor predictions (left) and through the center of the receptive fields and visual predictions (right). In the top three rows we show results for three neurons typical for our sample, in which
FIG. 9. Spatial profile of activity for a neuron whose 2T movement field was similar to that for 1T saccades. Conventions same as in Fig. 7, except that, because we were able to collect more data from the periphery of the movement field, we plot rasters and spike density traces for 4 bins instead of 3. Parameter estimates and 95% confidence intervals of the parameter estimates of the curve-fit for this neuron are, for the 1T data, $M_c = 576 \pm 56.5$ spikes/s; $\rho_c = 13.7 \pm 1.2$; $\rho_s = 0.46 \pm 0.1$ [unitless]; $\theta_c = 11.1 \pm 3.5^\circ$; $\theta_s = 27.4 \pm 3.8^\circ$; $R^2 = 0.63$. For the 2-target data, $M_c = 518 \pm 79.7$ spikes/s; $\rho_c = 15.0 \pm 2.6^\circ$; $\rho_s = 0.47 \pm 0.17$ [unitless]; $\theta_c = 15.0 \pm 5.5^\circ$; $\theta_s = 29.1 \pm 7.3^\circ$; $R^2 = 0.45$.

VGF > MGF; in the fourth row we show results for a neuron with very broad tuning whose movement and receptive fields resembled the motor and visual predictions equally well.

Across the 31 neurons for which we performed this test, the VGF was considerably greater than the MGF (Fig. 12A, Table 2A) for 2T express saccades. This result held for the confirmed BNs but was not statistically significant for the confirmed BUNs. For comparison, and to help validate this method, we computed the same goodness-of-fit measures for the 1T data, substituting 1T data for 2T data in Eqs. 3 and 9 to derive motor and visual predictions, respectively. As expected, the average MGF was much higher than VGF for 1T data (Fig. 12A, Table 2A).

We repeated the visuomotor analysis for regular saccades. In contrast to the case for express saccades, a majority of neurons (12/20) had a greater 2T MGF than VGF, although the average value of VGF across all neurons was slightly greater than that of MGF (Fig. 12B, Table 2B).

Although the 2T activity for express saccades was more dependent on target configuration than on saccade vector, for virtually all neurons the VGF for 2T saccades was worse than the MGF for 1T saccades. This suggests either that an element of saccade dependency does exist for these neurons, or else that the true shape of the receptive field for 2T saccades is more complex than the visual prediction described by Eq. 9. Across all neurons the visual prediction was generally much smaller in magnitude than the sum of two spatially separated visual responses. If the visual prediction were the same as this sum, then the magnitude coefficient in Eq. 9, $M_{TV}$, would be one. But across all neurons the average of $M_{TV}$ was 0.60 ($z$-test, relative to 1.0, $P < 0.001$). Note that the brightness of two targets and one target were equivalent (see METHODS), so that target brightness could not explain these results. A frequency analysis of the visual responses of our sample of neurons showed no peaks at 100 Hz (the rate at which the spot was flashed at a given location during
Coefﬁcient of determination ($R^2$) Radial center ($r_0$) Directional SD or spread ($\sigma_\theta$) Directional center ($\theta_0$) Radial spread ($r_1$)

<table>
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<tr>
<th>Parameter</th>
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<th>Two-Target</th>
<th>Difference</th>
<th>Wilcoxon Test</th>
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<tr>
<td><strong>A. Express saccades (n = 25)</strong></td>
<td></td>
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<tr>
<td>Response magnitude ($M$), spikes/s</td>
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<td>-0.02</td>
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<tr>
<td>Directional center ($\theta_0$), deg</td>
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<td>3.8</td>
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<tr>
<td>Directional SD or spread ($\sigma_\theta$), deg</td>
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<td>37.0</td>
<td>-16.3</td>
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<tr>
<td>Coefﬁcient of determination ($R^2$)</td>
<td>0.77</td>
<td>0.53</td>
<td>0.24</td>
<td>$P &lt; 0.001^*$</td>
</tr>
</tbody>
</table>

| **B. Regular saccades (n = 14)** |            |            |            |               |
| Response magnitude ($M$), spikes/s | 548        | 492        | 57         | $P > 0.1$     |
| Radial center ($r_0$), deg       | 10         | 10.3       | -0.3       | $P > 0.5$     |
| Radial spread ($r_1$), [dimensionless] | 0.29       | 0.28       | -0.01      | $P > 0.1$     |
| Directional center ($\theta_0$), deg | 17.7       | 19.1       | -1.4       | $P > 0.5$     |
| Directional SD or spread ($\sigma_\theta$), deg | 20.6       | 25.8       | -5.2       | $P = 0.02^*$  |
| Coefﬁcient of determination ($R^2$) | 0.85       | 0.79       | 0.06       | $P = 0.03^*$  |

| **C. Express saccades, one-target data resampled (n = 23)** |            |            |            |               |
| Response magnitude ($M$), spikes/s | 602        | 493        | 109        | $P < 0.001^*$  |
| Directional SD or spread ($\sigma_\theta$), deg | 20.7       | 37.0       | -16.2      | $P < 0.001^*$  |

A: summary across all neurons of ﬁve parameters and coefﬁcient of determination ($R^2$) obtained from ﬁtting surfaces to data for one-target (1T) and two-target (2T) express saccades. First two columns are average of each parameter across all neurons. A positive number in the third column indicates greater value for 1T saccades. Numbers in bold in the left two rows indicate the greater value when it is statistically signiﬁcant. B: summary of ﬁve parameters and coefﬁcient of determination ($R^2$) obtained from ﬁtting surfaces to data for 1T and 2T regular saccades. Conventions are in A. C: same as A, but not showing results for magnitude ($M$) and directional standard deviation ($\sigma_\theta$) parameters after resampling 1T data to address the possibility of spatial bias. See text for details. * $P < 0.05$.

the 2T trials; see METHODS), suggesting that the decrease in response was not due to the extremely rapid ﬂashing of the two targets.

Is such suppression evident for the visual response to 1T and 2T preceding regular saccades, for which the visual response is uncontaminated by the perimotor response? We used the procedure described above to compare the magnitude of the visual response preceding 2T regular saccades to the visual prediction based on the visual discharge preceding 1T regular saccades. The visual prediction was calculated as described previously, except that the temporal epoch used was 40–80 ms after target onset. The average value of $M_{2Tv}$ across the 20 neurons for which we had sufﬁcient data was 0.72, a value slightly higher than the 0.60 found above for express saccades. Again, a frequency analysis of the visual response showed no peaks at 100 Hz. This result suggests that suppression is also evident for the visual response preceding 2T regular saccades.

**IS THERE A SEPARATE CLASS OF NEURONS THAT CODES FOR THE SACCADE AND NOT THE TARGET CONFIGURATION?** Although the sample of neurons we recorded generally coded the target conﬁguration better than they did saccade vector, we sought to determine whether some subset of neurons might show the opposite preference of coding. We hypothesized that visuomotor neurons with greater perimotor than visual responses during nonexpress saccades would have a greater MGF. To temporally separate visual from motor discharges for 31/37 neurons, we used a visually guided delayed saccade paradigm, in which a target appears but a saccade cannot be made until the ﬁxation light is turned off 500–700 ms later (see Edelman and Keller 1996). For the six neurons in which we did not use the delayed saccade paradigm, we recorded activity during saccades of longer than 120 ms latency. We calculated a motor-visual index (MVI) for each neuron by comparing the perisaccadic activity of each neuron to its visual response for saccades close to the center of the neuron’s movement ﬁeld

$$MVI = \frac{(MOT - VIS)}{(MOT + VIS)}$$

where VIS is the magnitude of the peak spike density of the visual response during the epoch 50–100 ms after target onset and MOT is the magnitude of the peak spike density of the perimotor response during the epoch 40 ms centered on saccade onset. Thus a neuron that only discharged peri-saccadically in the delayed saccade task would have a MVI = 1; a neuron that only discharged in response to the visual target would have a MVI = −1. Therefore, if neurons whose discharge was almost purely saccade related coded for saccade vector, whereas neurons whose discharge was almost purely a visual response coded for target conﬁguration, then MGF should increase and VGF should decrease with increasing MVI.

We did indeed ﬁnd that MGF increased as MVI increased ($r = 0.41, P = 0.01$; Fig. 13A), but found no statistically signiﬁcant correlation between VGF and MVI ($r = -0.22, P > 0.1$; Fig. 13A). Overall, neurons with the greatest MVIs had comparable values of VGF and MGF (Fig. 13A).

But we also found that directional spread ($\sigma_\theta$) increased as MVI increased ($r = 0.35, P < 0.04$), a result consistent with the ﬁnding of Mohler and Wurtz (1976) that movement ﬁeld size and the ratio of saccade-related to target-related discharge were positively correlated. Could this result explain the dependencies of MGF and VGF on MVI? Note that if the directional spread ($\sigma_\theta$) is small then we would expect a great difference between the motor prediction, $\hat{z}_{2Tv}$, and the visual prediction, $\hat{z}_{2Tv}$, for a given neuron. These
predictions are shown for simulated data (Fig. 14A). In contrast, if directional spread (θ₀) is large then the motor and visual predictions should become much more similar (Fig. 14B). If discharge depended completely on target configuration, then the MGF should increase with θ₀ and VGF should not depend on θ₀.

Indeed, this is exactly what we found for our sample of neurons. MGF increased with increasing directional spread (θ₀) (r = 0.63, P < 0.001; Fig. 13B), whereas VGF remained nearly constant with increasing θ₀ (r = −0.08, P > 0.5; Fig. 13B). These results suggest that MGF and VGF become more comparable as the movement fields and receptive fields become larger. Thus MGF may get better with increasing MVI simply because the motor prediction more resembles the visual prediction with increasing directional spread (θ₀), not because the neurons have stronger perimotor than visual responses. Therefore our data do not support the idea that a separate class of visuomotor neurons exists that codes for the saccade vector of express saccades to two targets.

**Fig. 10.** Comparison of the directional spread parameter (θ₀) for 1T and 2T saccades found using the Gaussian/log-Gaussian surface-fit procedure. A: express saccades. Data points corresponding to the 5 neurons that had θ₀ > 50° are shown as hexagons at θ₀ = 50°. B: same as C but for regular saccades. See text for details.

**DOES ACTIVITY BECOME MORE SACCade DEPENDENT AS THE VISUOMOTOR BURST ACCOMPANYING EXPRESS SACCades PROGRESSES?** We also determined whether the spatial pro-

file of activity of visuomotor neurons during 2T saccades could become more like that for 1T saccades as the visuomotor burst continued. To do so we repeated elements of the analyses described above on specific epochs of express saccade-related activity. Because the saccades we elicited varied considerably in duration, we chose not to analyze epochs of fixed length locked to the onset of the saccade. Instead, we considered epochs whose length and position depended on saccade duration. For each saccade we defined t = 0 as 25 ms before the onset of the saccade, because the high-frequency burst of activity in visuomotor neurons begins ~25 ms before express saccades (Edelman and Keller 1996). For each saccade we defined t = 1 as 15 ms before the termination of the saccade, because the activity of visuomotor neurons during express saccades often reaches a minimum ~15 ms before the end of the saccade, before occasionally increasing (unpublished observations). We conducted the analyses for three epochs, t = 0 to t = 0.333, t = 0.333 to t = 0.666, and t = 0.666 to t = 1.0, which we will refer to as the early, middle, and late epochs.

We repeated the Gaussian/log-Gaussian surface fitting procedure on the 1T and 2T express saccade data for the three epochs. We only analyzed data from fits that converged for both 1T and 2T saccades. If the spatial profile of discharge for 2T saccades became more similar to that of 1T saccades over time, then we would expect that directional spread (θ₀) would decrease across epochs for 2T saccades. On the contrary, we found that for all three epochs directional spread (θ₀) was greater for 2T saccades than for 1T (Table 3; Fig. 15A). The difference in directional spread (θ₀) between fits for 1T and 2T saccades changed little over time, and the small decrease observed resulted primarily from an increase in directional spread (θ₀) for 1T saccades rather than from a decrease in directional spread (θ₀) for 2T saccades (Table 3).

We also repeated the visuomotor analysis described above to determine whether the MGF or VGF for 2T saccades depended on the temporal epoch. If the activity for 2T saccades becomes more dependent on saccade vector as the burst progressed, then MGF should increase and VGF should decrease over time. Again, we did not find compelling evidence that the spatial distribution of activity during the burst evolved from a target location dependence to a saccade vector dependence. For all three epochs the VGF was significantly better than the MGF for 2T saccades (Table 4). However, the MGF for 2T saccades increased slightly between the early and middle epochs, although this trend only bordered on statistical significance (paired t-test, mean difference: 0.13, P = 0.06). The 2T VGF dropped dramatically between the early and mid epochs (paired t-test, mean difference: −0.14, P = 0.001). However, by the late epoch MGF decreased close to the level observed in the early epoch. Finally, the results for 2T saccades were different from those of 1T saccades for all three epochs (Table 4). These results indicate that any change in spatial pattern of activity from target dependence to saccade dependence is likely to be small and incomplete across the population by the termination of the burst.

**DOES THE SPATIAL PROFILE OF ACTIVITY FOR 2T EXPRESS SACCades DEPEND ON HOW CLOSE THE SACCade LANDED TO
FIG. 11. Goodness-of-fits for motor and visual predictions of 2T saccade activity for 4 neurons. The pair of plots in each row shows data for 1 neuron superimposed on the motor prediction of 2T activity (left column) and on the visual prediction of 2T activity (right column). Plots show a cross-section of the motor prediction (left column; see Fig. 3D) or visual prediction (right column; see Fig. 4E). The plotted discharge was the mean discharge in the 40-ms epoch centered on saccade onset. For the left column, each dot represents the average discharge for saccades landing in direction bins of 5.625 (180/32)° width. Saccade direction is normalized with respect to the direction of the center of the 1T movement field (θ_1Tm). Solid lines are plots of an isoradial slice of the motor prediction at an amplitude equal to the center of the 1T movement field. As in Figs. 3D and 4E, only data corresponding to saccades with amplitudes close to the center of the 1T movement field are plotted. Error bars for discharge are not shown because only rarely did >1 saccade occupy each direction bin. Conventions for the right column are the same except that the variable on the abscissa is target direction normalized with respect to the center of the 1T receptive field (θ_1Tv), visual predictions are used in place of motor predictions, and bars representing standard errors of the mean are shown. Target direction for the data is defined as the average direction of the 2 targets.

DISCUSSION

Activity in the deeper layers of the superior colliculus accompanying express saccades to two targets

Edelman and Keller (1996) demonstrated that what has been considered the visual and premotor responses of visuomotor burst neurons merge during express saccades (see also Dorris et al. 1997). The experiments described here ask whether the bimodal or broadly tuned distribution of sensory activity resulting from presentation of two targets spatially coalesces into the unimodal or more sharply tuned profile of activity that is seen for saccades to a single target. By using the gap paradigm (Saslow 1967), we elicited saccades to two targets of express latency. The saccades had a high degree of endpoint scatter relative to the locations of the two targets, allowing us to dissociate saccade vector from the locations of the targets. We found evidence that the discharge of visuomotor neurons was more dependent on target configuration than on saccade vector for the duration
of the saccadic burst. The neurons that coded most similarly for 1T and 2T saccades tended to have very broad movement fields for 1T saccades.

Our results are most consistent with the downstream hypothesis of Van Opstal and Van Gisbergen (1990), which predicts that 1T and 2T express saccades with similar metrics are coded by different spatial distributions of activity in the

![Figure 12](image1.png)

**FIG. 12.** Summary data for MGF and VGF for all neurons. VGF is plotted against MGF for both the 1T and 2T data. Each dot represents 1 neuron. Dotted line represents the locus of points for which the 2 goodness-of-fit measures are equal. A: summary for express saccade data. B: summary for regular saccade data. See text for details.

![Figure 13](image2.png)

**FIG. 13.** Summary of dependence of each neuron’s MGF and VGF for express saccades on motor-visual index (A; MVI) and the directional spread parameter (B; \( \theta_s \)) for 1T saccades. For details, see text.

TABLE 2. Visuomotor analysis

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<th></th>
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<tr>
<td>One target</td>
<td>31</td>
<td>0.77</td>
<td>0.32</td>
<td>0.45</td>
<td>( P &lt; 0.001^* )</td>
</tr>
<tr>
<td>Two targets</td>
<td>31</td>
<td>-0.09</td>
<td>0.44</td>
<td>-0.53</td>
<td>( P &lt; 0.001^* )</td>
</tr>
<tr>
<td>Averaging</td>
<td>26</td>
<td>-0.12</td>
<td>0.43</td>
<td>-0.55</td>
<td>( P &lt; 0.001^* )</td>
</tr>
<tr>
<td>Nonaveraging</td>
<td>21</td>
<td>0.08</td>
<td>0.49</td>
<td>-0.41</td>
<td>( P = 0.03^* )</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>MGF</th>
<th>VGF</th>
<th>Difference</th>
<th>Wilcoxon Test</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>B. Regular saccades</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>One target</td>
<td>19</td>
<td>0.85</td>
<td>0.41</td>
<td>0.43</td>
<td>( P &lt; 0.001^* )</td>
</tr>
<tr>
<td>Two targets</td>
<td>19</td>
<td>0.36</td>
<td>0.45</td>
<td>-0.1</td>
<td>( P &gt; 0.5 )</td>
</tr>
</tbody>
</table>

*An asterisk indicates that the analyzed in the same manner the visual response preceding regular saccades, we found that the magnitude of the 2T discharge was on average \(~72\%\) of the sum of two spatially
SC ACTIVITY DURING EXPRESS SACCADES TO TWO TARGETS

Responses preceding regular saccades is less likely to be above the neuron’s maximum discharge rate than is the sum of two express saccade responses.

The VGF we found for 2T saccades was not nearly as large as the MGF for 1T saccades. It is thus unclear whether Eq. 9 is the best model of SC discharge for express saccades to two targets. Such discharge may also depend on other factors, such as saccade preparation. Indeed, it should be noted that for a particular neuron’s data set in this study, saccades were elicited to a limited region of the visual field. Although saccade endpoint was clearly dependent on the number and location of the target(s), a component of neuronal discharge may have resulted from preparatory activity.

A larger sample of data combined with mathematical modeling may be required to understand the mechanism by which the DSC integrates responses from two targets to produce the spatial pattern of discharge observed here.

We also found that perimotor discharge of DSC neurons during regular saccades to two targets was different from that during regular saccades to one target, although this difference was much smaller than that for express saccades. This finding was surprising because virtually all regular saccades to two targets were nonaveraging. Although the transient visual burst is complete before regular saccades, evidently the presence of the nonselected target has an effect on the spatial profile of DSC discharge. This suggests that sensorimotor processing is not complete even for saccades with nonexpress latencies. We did not have sufficient data to analyze regular saccades for three different epochs, so we cannot rule out the collicular hypothesis for regular saccades to two targets.

Relation to previous work on spatial coding in the DSC for saccades to two targets

Previous investigators studying the neural activity underlying saccades to two targets used more complicated tasks than the one used here, apparently because in monkey the conventional visually guided saccade paradigm elicited saccades that landed on one target or the other and not in between. Van Opstal and Van Gisbergen (1990) used a double-noise visual and motor predictions to be plotted on the same graph, saccade step paradigm to elicit saccades that landed between the two sequentially presented targets. Such stimulus presentation complicates the spatial analysis of visuomotor burst neuron activity. Indeed, the authors’ conclusions were limited to these separated 1T responses. That this number is larger than the 60% found for analysis of express saccades may result from the fact that the separate visual discharge for regular saccades is smaller than the unitary discharge for express saccades. Thus the sum of two spatially separated visual responses can be used as a measure of the spatial coding in the DSC.

TABLE 3. Directional standard deviation across epochs $\theta_s$ (express saccades)

<table>
<thead>
<tr>
<th>Epoch</th>
<th>One-Target</th>
<th>Two-Target</th>
<th>Difference</th>
<th>Wilcoxon Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early epoch</td>
<td>22</td>
<td>18.5</td>
<td>35.3</td>
<td>$-16.8$</td>
</tr>
<tr>
<td>Middle epoch</td>
<td>25</td>
<td>21.4</td>
<td>35.8</td>
<td>$-14.4$</td>
</tr>
<tr>
<td>Late epoch</td>
<td>14</td>
<td>24.1</td>
<td>37.5</td>
<td>$-13.4$</td>
</tr>
</tbody>
</table>

Summary of values of directional spread ($\theta_s$) across all neurons for different temporal epochs of the express saccade related burst. Conventions as in Table 1A. $^* P < 0.05$. 

Fig. 14. Illustration of decrease in difference of goodness-of-fit measures as neuron’s directional spread ($\theta_s$) parameter increases, assuming that discharge is completely dependent on target configuration. Simulated discharge data are superimposed on cross-sections of motor and visual predictions from 2 hypothetical neurons, one (A) with ($\theta_s = 15^\circ$), the other (B) with ($\theta_s = 30^\circ$) (bottom). Discharge values were generated by adding noise to values of the visual prediction. For simplicity and to allow the visual and motor predictions to be plotted on the same graph, saccade direction is set to target direction (as though every saccade was a pure averaging saccade). See text for details.
be that only short-latency 2T express saccades to suddenly appearing targets are coded differently from 1T saccades. Saccades with longer latencies may be coded identically.

Role of DSC visuomotor burst neurons in saccade generation

Robinson (1972) and Lee et al. (1988) provided evidence that saccades are coded by a vector average of collicular activity, such that the discharge of each neuron is associated with a saccade vector, and the ensemble of collicular activity produces a saccade that is a weighted average of these vectors. A subsequent model of the DSC implemented this idea (Van Gisbergen and Van Opstal 1989). With respect to 2T saccades, our data add support to the vector average hypothesis by showing that the two regions of activity corresponding to each of the targets produce a saccade with a vector that is approximately a spatial average of the saccade vectors that would be produced by each region acting alone.

Although it may seem surprising that saccades similar in vector could be coded by different distributions of activity in the DSC, results from a considerable body of research on the DSC are consistent with this result. It has been long known that when the superior colliculus is electrically stimulated at two neighboring positions on the motor map simultaneously, a saccade is elicited that is spatially similar to a vector average of those elicited by the electrodes individually (Robinson 1972). Our experiments indicate that such a profile of activity on the DSC motor map can accompany saccades elicited with visual targets.

Because the role of visuomotor neurons in the DSC is still not well-understood, one must exercise caution in interpreting our results. There is evidence that in the primate DSC neurons with bursts accompanying saccades project directly or indirectly to the excitatory burst neuron (EBN) region of the...
paramedian pontine reticular formation (PPRF), which contains neurons that provide the metric signal to ocular motoneurons (Keller 1979; Scudder et al. 1996). With respect to the SC classification scheme of Munoz and Wurtz (1995), both BNs and BUNs project to the brain stem, although it is unclear where exactly each SC subpopulation projects to (Istvan et al. 1994). It is also unclear, with respect to the SC classification scheme of Sparks and Hartwich-Young (1989), whether both visuomotor neurons and SRBNs project to the EBN region of the PPRF, although since work in our lab has shown that an overwhelming majority of neurons with saccade-related bursts also have visual responses and thus can be classified as visuomotor neurons, it is most likely that visuomotor neurons project to this region. But again, it is unknown whether the probability that a visuomotor neuron projects to EBNs depends on the strength of the visual response of the neuron or the size of its movement field. Such anatomic data would be crucial in interpreting our results because we found evidence that target selection has not occurred at the level of the DSC for express saccades to two targets, whether the saccades are averaging or nonaveraging, although one may argue that immediately after the onset of the visual stimuli the saccadic system construes the two lights as a single target with a large spatial extent. Indeed, express saccades may occur too quickly to take advantage of the segregation of suddenly appearing visual stimuli into distinct targets for the saccadic system.

APPENDIX

Equations used for movement and receptive-field fits

The detailed form of log-Gaussian and Gaussian components of Eq. 1 are

\[
P(\rho; \rho_1, \rho_2) = \exp \left\{ -\frac{1}{\rho_1^2} \left[ \ln \left( \frac{\rho + a}{\rho_2^2} \right) \right] ^2 \right\} \quad (A1)
\]

\[
\Theta(\theta; \theta_1, \theta_2) = \exp \left\{ -\frac{1}{2\theta^2} \left[ (\theta - \theta_1)^2 \right] \right\} \quad (A2)
\]

where \( a \) is the logarithmic scaling constant [unitless]. The other parameters are defined as in Eq. 1 in METHODS.

The parameter \( a \) ensures that the surface would pass through zero amplitude at the origin. This parameter was fixed at 3, a value taken from the result of a surface-fit procedure used to map visual space onto collicular space (Ottes et al. 1986).

Components of visual prediction

The components of the visual prediction are

\[
\Theta_{CCW}(\theta) = \Theta(\theta_{av} - 22.5, \theta_{STV}, \theta_{STV}) \quad (A3)
\]

\[
\Theta_{CW}(\theta) = \Theta(\theta_{av} + 22.5, \theta_{STV}, \theta_{STV}) \quad (A4)
\]

where \( \theta_{av} \) is defined as the average direction of the two targets. The other symbols are defined in Eqs. 5–7 in METHODS.

The authors thank J. P. Gottlieb, M. E. Goldberg, M. Pare, and the anonymous reviewers for helpful criticisms and discussions.

Address for reprint requests: J. A. Edelman, Laboratory of Sensorimotor Research, National Eye Institute, Bldg. 49, Rm. 2A50, Bethesda, MD 20892-4435.

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Previous work has supported the idea that a vector of an impending saccade is represented by a particular distribution of neural activity on the motor map of the DSC. While recent work has demonstrated that the vector of the saccade may be modified by other signals related to the memory of target (Stanford and Sparks 1994), the velocity of the target (Keller et al. 1996), and saccade adaptation (Frens and Van Opstal 1997), such work still supports the idea that the discharge of neurons in the DSC codes for a specific saccade command. The present data showing that the saccade-related activity in the DSC is dependent on the number of targets and not just their location suggests that at least for express saccades an explicit representation in the DSC of an impending saccade is not present for all neurons with saccade-related activity.

Early work showed that averaging saccades to two targets are often made when the subject is required to saccade as quickly as possible to a ‘‘correct’’ target (defined by color) in a suddenly appearing 2T array (Ottes et al. 1985). These authors suggested that the subject resolves the evidently conflicting demands of speed and accuracy by first making a short reaction time movement to land in the neighborhood of the stimuli, and only then selecting and making a saccade to the correct target. This suggestion supports the hypothesis that averaging saccades to two targets are generated by a ‘‘visual grasp reflex’’ (Becker 1991). Our results suggest that target selection has not occurred at the level of the DSC for express saccades to two targets, whether the saccades are averaging or nonaveraging, although one may argue that immediately after the onset of the visual stimuli the saccadic system construes the two lights as a single target with a large spatial extent. Indeed, express saccades may occur too quickly to take advantage of the segregation of suddenly appearing visual stimuli into distinct targets for the saccadic system.

Saccade spatial commands, target selection, and the visual grasp reflex

The components of the visual prediction are

\[
\Theta_{CCW}(\theta) = \Theta(\theta_{av} + 22.5, \theta_{STV}, \theta_{STV}) \quad (A3)
\]

\[
\Theta_{CW}(\theta) = \Theta(\theta_{av} - 22.5, \theta_{STV}, \theta_{STV}) \quad (A4)
\]

where \( \theta_{av} \) is defined as the average direction of the two targets. The other symbols are defined in Eqs. 5–7 in METHODS.

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