Pallidal Discharge Related to the Kinematics of Reaching Movements in Two Dimensions

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Turner, Robert S. and Marjorie E. Anderson. Pallidal discharge related to the kinematics of reaching movements in two dimensions. J. Neurophysiol. 77: 1051–1074, 1997. Movement-related discharge of neurons in the internal and external segments of the globus pallidus (GPI and GPe, respectively) of two monkeys was studied during reaching movements in a two-dimensional workspace. Discharge was studied during movements to targets in eight directions and at three distances from the starting position under three behavioral conditions that manipulated target visibility and movement triggering. A total of 73 neurons (57 in GPe and 18 in GPI) with changes in discharge in concert with arm movements were included in a quantitative analysis. Of these, 83% also changed their discharge during manipulation of the contralateral arm outside of the task. Although 73% of changes in discharge began before the initiation of movement, they seldom preceded the initial activity of the agonist muscles. Decreases in discharge were more common than reported previously, constituting 40% of the changes in discharge detected. In GPe neurons, decreases also tended to begin earlier than increases. Changes in discharge in GPe neurons were of larger magnitude than those in GPI, and increases in discharge were larger than decreases. Onsets of changes in discharge were temporally linked to movement onset in 69% of neurons. Time locking of neural onsets to trigger presentation and movement termination was found in only 30 and 1% of neurons, respectively. Direction of movement influenced the magnitude of changes in discharge in 78% of cells. Directional modulations were broadly tuned and preferred directions were uniformly distributed across the range of directions. When directional modulations were large, preferred directions were consistent for different amplitudes of movement and for different behavioral conditions. Amplitude of movement influenced the magnitude of changes in discharge in 78% of cells, and in 80% of cases that relation had a significant linear component. Amplitude effects were not more common or stronger for movements in directions close to a cell’s preferred direction. Linear relations to movement amplitude were more common and accounted for more of the trial-to-trial variance in discharge rate than relations to either average velocity or movement duration. The relation to movement amplitude was consistent for two behavioral conditions when the change in discharge was scaled strongly with movement amplitude. Movement-related changes in discharge of neurons in the skeletonmotor portions of both pallidal segments reflect the kinematics of movement. This information, encoded in combination with sensory and contextual information, may play an on-line role in the selective facilitation and suppression of different frontal thalamocortical circuits.

INTRODUCTION

The role of the basal ganglia in normal motor control remains unclear, although disorders of movement are the cardinal signs of parkinsonism and other conditions characterized by anatomic and biochemical changes in the basal ganglia. It is clear, however, that a subsection of the basal ganglia circuitry is devoted to somatomotor functions (Alexander et al. 1990). Cells in the ‘‘motor’’ territory of the internal segment of the globus pallidus (GPI) carry basal ganglia output signals related to somatomotor activity (DeLong et al. 1985), and these neurons exert a direct inhibitory influence on target neurons in the ventrolateral thalamus and midbrain (Anderson and Turner 1991a; DeVito et al. 1980; Harnois and Filion 1982; Uno and Yoshida 1975). The activity of neurons in the motor territory of the external segment of globus pallidus (GPe) can also influence motor centers by way of inhibitory projections to the subthalamic nucleus, GPI, and the nucleus reticularis of the thalamus (Hazrati and Parent 1991; Hazrati et al. 1990; Kim et al. 1976). Thus movement-related signals carried by neurons in both GPI and GPe could influence movement execution via their indirect action on neurons of motor-related areas of the cerebral cortex or the brain stem.

The information contained in the discharge of individual pallidal neurons constrains any model of the potential role(s) of basal ganglia output in the control of movement. Prior studies established that the discharge of single cells in the caudal lateral portions of both pallidal segments is often modulated during active and/or passive movements of the contralateral limb (Anderson and Horak 1985; Anderson and Turner 1991b; DeLong 1971) and it is usually related to the movement of individual joints (Hamada et al. 1990). In some studies it was reported that movement-related changes in pallidal discharge are often influenced by kinematic and kinetic variables, including the direction of movement, the force being exerted, the movement duration (MT), and the amplitude and/or velocity of the movement (Anderson and Turner 1991b; Georgopoulos et al. 1983; Mitchell et al. 1987). Others, however, have reported that the relations of pallidal discharge to specific parameters of movement are weak and inconsistent across different task conditions (Brotchie et al. 1991a; Mink and Thach 1991b). Although a preferential relation of pallidal discharge to fast movements has been reported (Mink and Thach 1987, 1991b) and the magnitude of modulation may be enhanced during rapid movements, pallidal movement-related discharge is present during both fast and slow movements (Hamada et al. 1990).

According to current concepts of basal ganglia function, movements in GPe and GPI neurons have contrasting effects on frontal thalamocortical circuits (Alexander et al. 1990). Reductions in GPe discharge are hypothe-
sized to facilitate movement planning or execution by disinhibiting thalamic and brain stem targets. This action parallels that proposed for pauses in substantia nigra reticulata (SNr) discharge in facilitating saccadic eye movements (Hikosaka and Wurtz 1983c). In contrast, pauses in GPe discharge would suppress movements by increasing inhibition of the same targets via indirect pathways. Thus possible differences in the movement-related discharge of GPe and GPi neurons are of interest for models of basal ganglia function.

Because movement-related increases and decreases in the discharge of neurons in either GPe or GPi are predicted to have opposing effects on motor centers, it also is important to examine how these opposing changes in discharge are related to parameters of movement. To date, the only consistent difference that has been found, in both GPe and GPi, is that movement-related increases in discharge are at least twice as common as movement-related decreases (Anderson and Horak 1985; DeLong 1971; Georgopoulos et al. 1983).

We have expanded studies of the movement-related signals carried by pallidal neurons by recording pallidal activity during multijoint arm movements of different amplitude and direction made in a two-dimensional workspace. Because several studies have reported strong influences of behavioral context on the movement-related discharge of basal ganglia neurons (Brotchie et al. 1991b; Hikosaka and Wurtz 1983b; Mink and Thach 1991a; Mushiake and Strick 1995), we also have compared the discharge of individual pallidal neurons during similar movements made in different task contexts. We have found that GPi neurons have early decreases and late increases in discharge compared with the timing of changes in GPe discharge. The movement-related discharge of most pallidal neurons is related consistently to the direction of movement, irrespective of movement amplitude and task context. Relations of discharge to movement amplitude were also common. Preliminary results and an analysis of the task-related kinematics and electromyographic (EMG) activity have been presented previously (Turner and Anderson 1991; Turner et al. 1995).

Methods

Animals and apparatus

Two juvenile male *Macaca fascicularis* monkeys, weighing 2.3–2.8 kg when obtained, were used in these experiments. Animals were cared for in accord with the Guiding Principles in the Care and Use of Animals (American Physiological Society, 1991). The monkeys were trained to perform three related visuomotor reaching tasks to obtain apple sauce or fruit juice rewards.

The behavioral apparatus and tasks were described in detail in Turner et al. (1995). Briefly, target light-emitting diodes (LEDS) could be illuminated and visible as virtual images in the workspace of the arm via a mirrored sheet of Plexiglas positioned in front of the animal. Twenty-four peripheral targets were arranged in eight spokes separated by 45°, with the three targets in each spoke at 1, 2, and 3 in. from a center light. When the LEDs were not lit, their locations were not visible to the monkey.

The work surface was a digitizing pad (Scriptel) inclined 5° from horizontal toward the monkey. The digitizing pad extended from just below the axilla so that, with hand and forearm prone on the surface, movements of the hand across the digitizing pad entailed predominantly adduction and abduction of the shoulder and horizontal flexion and extension of the elbow. Little trunk movement was possible with this arrangement.

The animal’s working forearm was held in a splint that extended on the palmar surface from just below the elbow to the first phalangeal joint. The splint 1) prevented movement around the wrist and finger joints, 2) contained the antenna for monitoring the X and Y position of the hand on the digitizing pad, and 3) contained a small magnet used to close reed switches that were mounted below the digitizing pad in register with target locations displayed via the mirrored surface.

The digitizing pad controller and subsequent D-A converter sampled hand position at 10-ms intervals with an accuracy of ±0.6 mm. Throughout the training and experiments described here, the monkey’s arm was visible through the Plexiglas sheet because the work surface and the monkey’s arm were illuminated with small incandescent lamps.

In the nomenclature adopted, targets directly to the right of the monkey were at 0° and those directly away from the animal were at 90°. Magnets in the splint closed a reed switch at the target locations if the center of the distal end of the splint was within an ellipsoidal area of ~2.4 × 1.2 cm (the target zone) centered on the LED images, with the major axis aligned with the arm’s axis. When well trained, the monkeys performed movements with an accuracy much higher than that required by the size of the target zones (Turner et al. 1995).

The color and intensity of the LEDs provided the monkey with feedback as to whether the hand was within a target zone. The central LED was lit continuously throughout an experiment, and its color changed from red to green when the hand entered the center target zone. All of the other LEDs were red when lit, and their luminence doubled when the monkey’s hand entered the correct target zone. Movements were triggered by a tone presented through a speaker mounted above the behavioral apparatus.

Behavioral tasks

Both animals were trained to make arm movements under three conditions designed to manipulate the cognitive requirements of a basic reaching task. The monkey was required to 1) hold the hand within the central start position zone for an initial hold period (H to T, “start position time,” Fig. 1); 2) move its hand quickly to a specified target location at the end of the start position time (T to E, “response time”); and 3) hold its hand at the target location for ≥0.4 s (“target hold time”). The monkey received a drop of apple sauce or fruit juice (“reward”) on approximately half of the trials that were performed correctly.

Sensory condition (Fig. IE1)

Under the sensory condition, the target location was visible during the movement and the time at which movement was to be made was cued overtly. At the end of a start position time 1.5, 2, 2.5, or 3 s in duration, one of the target lights was illuminated and the trigger tone sounded simultaneously (T). Both the target position and the start position time were selected pseudorandomly. The monkey was required to move its hand to the target zone for the illuminated LED within 0.8 s and remain within the target zone for ≥0.4 s.

Precued condition (Fig. IE2)

Under the precued condition, the target position was indicated in advance but was not visible during the movement, and a trigger tone was presented to signal movement initiation (M). One target light was presented (Q) for a short time (0.5 or 0.1 s) at 0.7 s after the beginning of the start position time. As in the sensory condition, the monkey was required to keep the hand in the start zone until the trigger tone sounded at the end of the variable start
position time. Response time and target hold time were the same as in the sensory condition.

Self-timed condition (Fig. 1E3)

Under the self-timed condition a single peripheral target light and the central LED were both illuminated continuously and no trigger tone was presented. The monkey was required to initiate movement to the peripheral target within a time window of 1.5–3 s after acquiring the central start position. The permitted start position time was therefore roughly equivalent in range to the variable start position times of the other two conditions. After training, however, animals adopted start position times that were much less variable than under the other two conditions.

Trials of each behavioral condition were performed in blocks. For sensory and precued trials, either three or six of the peripheral targets were presented in pseudorandom sequences of trials until ≥15 valid trials for each target location were collected. If a trial was performed incorrectly, the target presented in that trial was presented again at the end of the sequence of trials. Self-timed trials were performed in multiple blocks with one peripheral target location visible continuously throughout a block. In most cases, a block of sensory condition trials was followed by blocks of precued and self-timed condition trials. Only then was a second block of sensory condition trials presented that used a different set of targets than presented in the first sensory block.

Surgery

After completion of training, a cylindrical stainless steel chamber (10 mm diam) was surgically implanted with the use of standard techniques (Anderson and Turner 1991b) to allow access to the globus pallidus from a 45° lateral approach (Szabo and Cowan 1984). The monkey was given Tylenol analgesic immediately after surgery and was allowed ≥2 days to recover before the first exploratory electrode penetrations.

Neural recording

The activity of neurons in globus pallidus was recorded extracellularly as described previously (Anderson and Horak 1985; Anderson and Turner 1991b). The first neurons encountered had the low tonic firing rates typical of cells in the putamen (Crutcher and DeLong 1984a). The passage of the electrode into the pallidum was marked by a sharp increase in the background neural activity, and isolated action potentials characteristic of pallidal neurons were of short duration (~0.3 ms from onset of initial negativity to peak positivity) and had high tonic firing rates (DeLong 1971).
Penetrations were placed initially in an 0.5-mm grid throughout the chamber, but the areas in which neurons with activity related to arm movement were encountered were sometimes explored on a finer grid.

Recorded activity was amplified (gain = 5,000–20,000), filtered (band-pass = 0.5–10 kHz), displayed on-line, and stored on a pulse-code-modulated VHS-based data storage system (Vetter 4000). Isolated action potentials were identified with a time/amplitude window discriminator (BAK DIS-1), and acceptance pulses were converted with custom electronics to an analog signal that reflected instantaneous firing frequency (1,000/inter spike interval in ms = spikes/s), which was displayed on a storage oscilloscope. If a unit had a distinct and consistent perimovement change in activity during at least one of the three tasks, then the unit was studied further.

Data recorded on tape included the amplified neural recording, analog signals reflecting X and Y hand position on the work surface, and behavioral logic reflecting times of target, tone, and reward presentation.

Sensorimotor examination

On completion of data collection in the behavioral tasks, the activity of all neurons was examined for responses during a detailed sensorimotor examination in which the experimenter manipulated the arm around the shoulder, elbow, forearm, wrist, and finger joints. The leg, back, tail, and neck were manipulated in a similar manner, and orofacial areas were explored by manipulating the inside of the mouth with a cotton swab soaked in applesauce. Neural activity was also evaluated while watching spontaneous eye movements and targeted eye movements to small bits of apple.

Data analysis

Data were digitized off-line at a 2-kHz sampling rate for each channel with the use of the ComputerScope ISC-67 system from RC Electronics (Santa Barbara, CA). Digitized channels included pulses from the spike discriminator, instantaneous firing frequency, behavioral logic signals, and X and Y arm position.

Arm X and Y position signals were filtered with the use of a cubic spline smoothing routine (Hutchinson 1986), and tangential arm velocity was calculated with the use of Eq. 1

$$V_t = \sqrt{V_X^2 + V_Y^2}$$  \hspace{1cm} (1)

In Eq. 1, $V_X$ and $V_Y$ are smoothed X and Y arm velocities and $V_t$ is the resulting tangential velocity.

With the use of custom programs, behavioral events of interest were detected automatically with the use of a series of position, velocity, and duration thresholds. As illustrated in Fig. 1, times were defined for trigger presentation (T), M, and movement termination (E). The automatic process was monitored visually, and on rare occasions the results were corrected. Movement amplitude and direction were calculated as the straight line distance and direction between the hand positions at times of M and E.

During data processing each digitized instantaneous firing frequency value was shifted back in time to fill the interspike interval from which it was computed. It then was binned into average frequency during 5-ms intervals aligned on time of M. The binned instantaneous frequency was used in all subsequent data analysis (Fig. 1A).

The baseline discharge rate of a neuron was calculated from the mean instantaneous firing frequency during the 500 ms before T, averaged across all valid sensory condition trials collected for that neuron.

Detection of perimovement changes in discharge

Significant changes in discharge rate were detected in perimovement averages of a neuron’s firing frequency. A “search period,” extending from 300 ms before M until 200 ms after M, was tested for changes from the mean rate measured during a 500-ms control period ending 300 ms before M. The average firing frequency was considered to have a significant “movement-related change” if four of eight consecutive 5-ms bins in the search period were significantly above or below the baseline discharge rate (2-tailed t-test, 1 sample vs. baseline discharge mean, $P < 0.02$). The time of the first significant bin was taken as the onset time of a movement-related change in averaged discharge. The time of offset of a change in averaged discharge was detected in a similar way by searching the average after response onset for at least four of eight consecutive bins that were not significantly different from the control rate ($P > 0.02$). These detection criteria were arrived at by screening the efficacy of a wide variety of potential detection criteria applied to all perimovement averages for all cells studied.

The present criteria were chosen because they allowed determinations, in a straightforward and nonbiased way, of the onsets of perimovement changes in discharge that were in close agreement with estimates based on visual inspection. All of the changes in discharge detected with the use of these criteria were of relatively large magnitude and long duration, with peak changes in discharge $>3$ SD away from the baseline discharge rate and durations $>80$ ms.

For each neuron the detection procedure was performed on averages of all successful trials to each target presented under the sensory condition. A neuron was considered to have a significant movement-related change in activity if a significant change was detected in any of these averages.

Measures of perimovement discharge

Maximum and minimum discharge rates were extracted for each valid trial from a perimovement epoch of smoothed frequency of firing data (300 ms before to 200 ms after M). The frequency of firing data for a single trial were low-pass filtered with a cutoff at 2.5 Hz with the use of a digital filter algorithm (Fig. 1A) (Hamming 1983). The filtering process preserved in the single-trial frequency of firing waveform the main features of changes in discharge observed in perimovement averages. These measures (maxima and minima) provided a way to analyze separately both components (increases and decreases) of the biphasic changes in discharge that were common for many pallidal neurons and were used for all subsequent analyses.

To test the temporal locking of discharge to different task events, onset times of single-trial changes in discharge were detected with the use of the modified Komolgorov-Smirnov algorithm described in Anderson and Turner (1991b). Briefly, onset and offset times of a change in discharge (a “response”) were shifted iteratively to find the epoch with a maximum difference between the distributions of response and control frequencies of firing. The control period extended from 800 ms before M to response onset. Onset times were allowed to shift between 300 ms before and 200 ms after M. Although onsets and offsets of multiple response phases could be detected with the use of this technique, only the onset times of the earliest increases and decreases in discharge are discussed in this paper.

The onset times of single-trial changes in discharge (onset) were tested for significant temporal correlation (i.e., time “locking”) with the times of T, M, and E. Such time locking has been considered to be evidence for an underlying functional linkage between the behavioral event and the linked neural discharge (cf. Comenges and Seal 1985; Hanes et al. 1995). If a neuron’s discharge has a close temporal relation to M, then the time between the
trigger and the neuron’s initial change in discharge (onset-T) should co-vary with the behavioral reaction time (RT, the T to M interval). If, on the other hand, its initial change in discharge shows a tighter temporal linkage to the trigger, then the time between its onset and M (M-onset) should co-vary with the RT. To test for these linkages, Pearson product-moment correlations were calculated for the behavioral RT versus onset-T and M-onset.

A significant positive correlation between RT and onset-T in the absence of a correlation between RT and M-onset was taken to indicate that onsets were time locked to the time of M. Conversely, a significant positive correlation between RT and M-onset, but not onset-T, implied that the onset was time locked to T. If neither or both correlations were significant, then the time locking was considered to be indeterminant. We recognize that this technique actually tests for the relative temporal linkage of neural onsets to two behavioral events and that the sensitivity is strongly influenced by the absolute variability in the interval between the two behavioral events. For instance, the more variable the RT interval, the easier it is to detect a temporal linkage to M or T.

The same technique was used to test for time locking of neural discharge onsets with the times of E. In this case, however, the correlations between MT (the interval from M to E) and onset-M and E-onset intervals were tested.

Movement direction effects

The relation of a cell’s discharge to movement direction (directionality) was determined independently for increases and decreases in activity. Target direction, which correlated very closely with movement direction (Turner et al. 1995), was used as the independent variable in statistical tests for directionality because of its discrete nature. Significant unimodal directionality in a cell’s minimum or maximum perimovement discharge was determined with a nonparametric randomization test adapted from Lurito et al. (1991). First, mean resultant length, \( \bar{R} \), was calculated for the absolute magnitude of a cell’s dynamic increases and decreases in discharge (Fisher 1993; Mardia 1972). (Absolute dynamic changes in discharge were calculated as the absolute value of maximum or minimum discharge minus the neuron’s baseline discharge rate.) The value \( \bar{R} \) is essentially the length of the vector sum of all target direction by discharge rate vectors, and its magnitude reflects the unimodal directionality of the data. A distribution of 5,000 “control” mean resultants was produced from random shufflings of the data, in which single-trial discharge rates were reassigned to one of the target directions selected at random. If the actual mean resultant, \( \bar{R} \), was greater than the 95th percentile of the distribution of 5,000 control mean resultants, then the increase or decrease in discharge was considered to have a significant unimodal directionality (\( P < 0.05 \), approximate). The mean direction, \( \hat{\theta} \), of a significant mean resultant was taken as the preferred direction of that increase or decrease in discharge. Because absolute changes in discharge from the control discharge rate were used in these calculations, preferred directions always reflected the direction in which the change in discharge was maximal, regardless of whether the change was an increase or decrease. The mean angular deviation, a circular equivalent to the SD, was calculated from the mean resultant and was used as a measure of the angular breadth of a cell’s directional tuning (Fortier et al. 1993).

Single-trial values of discharge with a significant unimodal directionality were subsequently modeled by regression analysis (SYSTAT, Evanston, IL) with the use of the first-degree periodic (cosine) function presented in Eq. 2 (Georgopoulos et al. 1982).

\[
y = a + b + g \cdot \cos(\theta - \theta_{\text{mb}})
\]

In Eq. 2, \( \theta \) is target direction (the independent variable), \( a \) is the baseline discharge rate of the cell (measured before T, as described above), and \( y \) is the predicted sinusoidal model of discharge rate.

The coefficients resulting from this analysis reflect \( b \), the mean change in discharge rate across all directions included in the analysis (i.e., offset); \( g \), half-wave amplitude of the sinusoidal function (i.e., gain); and \( \theta_{\text{mb}} \), the direction in the sinusoidal function with a maximal change in discharge from the resting rate (e.g., regression preferred direction). The component of a perimovement change in discharge that was not modulated by movement direction (i.e., the unmodulated component) was estimated by subtracting the gain coefficient \( g \) from the offset coefficient \( b \). This gave the difference in discharge from baseline rate to the point on the tuning curve closest to baseline firing. The coefficient of determination \( (R^2) \) from the regression analysis was used as an estimate of how much of a cell’s trial-to-trial variability in discharge could be accounted for by the cosine function.

The peak-to-peak magnitude of a directional modulation in discharge was calculated as the difference in mean maximum or minimum discharge rates for the directions with the highest and the lowest actual mean rates.

Movement amplitude, velocity, and duration effects

The influence of the target distance on perimovement discharge was first tested with one-way analyses of variance (ANOVAs) (target distance vs. maximum and minimum discharge) for each direction in which targets were presented at three eccentricities from the start position. The nature of the relation between discharge and movement amplitude, target distance, and other correlated kinematic variables (MT or mean tangential velocity during movement) was explored with regression analysis. The linear model presented in Eq. 3 was tested with the use of least-squares regression (SYSTAT).

\[
y = a + b \cdot D
\]

In Eq. 3, \( D \) is the predictor variable and \( y \) is the predicted maximum or minimum discharge rate. Coefficients \( a \) and \( b \) represent the \( y \)-intercept and slope (spikes \( \cdot s^{-1} \cdot cm^{-1} \)) of the model.

Histology

Marking lesions were made at selected positions (e.g., presumed border between GPIs and GPi, 1st location of optic tract activity) by passing DC (30 \( \mu \)A for 10 s) through the recording electrode.

After the last recording session each monkey was deeply anesthetized (pentobarbital sodium) and killed by transcardial perfusion with saline followed by 10% Formalin in phosphate buffer. The brains were blocked in place in the stereotaxic coronal plane, removed, fixed in buffered Formalin, cryoprotected with sucrose, frozen and cut into 50-\( \mu \)m sections, and stained with cresyl violet.

The anatomic location of penetrations was reconstructed with the use of marking lesions and electrophysiological landmarks as well as dark lines of gliosis that showed recording tracks entering the globus pallidus. The approximate location of each recorded neuron could be estimated by comparing the location of a penetration in the chamber, the position of the neuron along the recording penetration relative to electrophysiologically identified borders, and the position of marking lesions made in the same and/or adjacent penetrations.

Results

Neurons sampled

The discharge of 293 pallidal neurons was monitored during a sensorimotor examination, 74 neurons in monkey \( F \) and 219 in monkey \( I \). In agreement with previous studies (DeLong 1971; DeLong et al. 1985; Hamada et al. 1990), many of these (123 of those examined) responded to passive
rotation or manipulation of one joint or body segment, often to very small movements of specific joints or palpation of selected muscles. Because the neurons documented in this study were those encountered during search for pallidal "arm" neurons and regions with these neurons were explored intensively, the numbers of neurons found responding to different body parts do not reflect the true proportions in the overall population of globus pallidus neurons.

Seventy-five neurons studied during both sensory and precued conditions were selected for inclusion in the following quantitative analyses. Cells included were those with high tonic discharge rates (>50 spikes/s) that either responded to manipulation of the contralateral forearm, elbow, or shoulder (arm cells, n = 62) or were found within 0.5 mm of arm cells, as defined above, but were nonresponsive or not tested in the sensorimotor examination ("near-arm" cells, n = 13). For 56 of the 75 neurons, data were also collected under the self-timed condition.

Most of the high-frequency arm and near-arm cells (57 cells, 76%) studied were in GPe. The baseline discharge rates were similar for high-frequency cells in GPe and for the 18 cells in GPi (87.5 and 86.5 spikes/s, respectively). The approximate anatomic locations of these 75 neurons are illustrated in Fig. 2, A and B, for monkeys F and I, respectively. The locations of the arm responsive neurons that were included in this analysis are indicated with filled circles (n = 62). Many additional arm responsive neurons (open circles, n = 61) were not included in the population of neurons analyzed here because 1) they responded to manipulation of distal arm joints that were not free to move in the present task; 2) stable recordings were not maintained; or 3) the neuron did not have movement-related changes in discharge during any of the tasks. Circles with crosses denote the locations of near-arm neurons (n = 13). Small dots indicate pallidal neurons that either responded to manipulations of body parts other than the arm or did not respond in the sensorimotor examination and did not qualify as near-arm cells.

Movement-related discharge under the sensory condition

Under the sensory condition, 73 of the 75 cells had significant movement-related changes in average firing rate around the time of M. The remaining 2 had movement-related discharge only under precued or self-timed conditions and will not be included in this description. The general characteristics of pallidal movement-related changes in discharge resembled previous descriptions (Anderson and Horak 1985; DeLong et al. 1985; Mitchell et al. 1987).

Significant increases were detected in the discharge of 88% of the cells (64 of 73) for at least one movement direction, and decreases were detected in 66% (48 of 73). In about half of the cells, both increases and decreases in discharge were found (39 cells, 53%) consisting of biphasic changes in discharge (32 cells) or pure increases in discharge for some target directions and pure decreases for other directions (7 cells). The remaining 34 cells had only increases (25 cells) or decreases (9 cells) in discharge. Overall, across all directions tested in every cell, 60% of the detected changes in discharge were increases and 40% were decreases.

The onset times of the earliest movement-related changes in discharge were clustered around the time of onset of earliest EMG activity, with decreases in discharge tending to begin earlier. Figure 3A shows the distribution of onsets in perimovement discharge relative to the time of M for every first change in discharge detected under the sensory condition. The earliest EMG activity recorded for monkeys performing this task had a mean onset time 60 ms before the time of M (−60 ms) (Turner et al. 1995). Although the latency distributions for increases and decreases overlapped nearly completely, the distribution for decreases was skewed toward earlier onset times (medians: −50 and −40 ms for decreases and increases, respectively), and the two distributions were significantly different (Komolgorov-Smirnov 2-sample test, P < 0.03).

This difference in the two onset latency distributions was accounted for by delayed onsets for increases, relative to the onsets of decreases, in the discharge of GPi neurons. Figure
FIG. 3. Distribution of onsets of initial perimovement changes in discharge including all changes detected (i.e., multiple target directions per neuron). Distributions for increases and decreases in discharge are plotted above and below the 0 axis, respectively. A: distributions of onsets for all pallidal neurons. Binwidth: 20 ms. B: cumulative distributions of onsets for GPe ( — — — ) and GPi ( – – – ) neurons.

3B shows cumulative distributions of onset latency for the first detected increases and decreases separated by cell type. Although the distributions again overlapped substantially, it can be seen that in GPi neurons, nearly all decreases (91%) began before the time of M (0 ms), whereas a considerable proportion of increases (33%) began after M. In GPe neurons, however, decreases in discharge were more likely to begin after M than were increases (30 vs. 22% for decreases and increases, respectively). The latency distributions for increases and decreases were significantly different for GPe neurons (komolgorov-smirnov 2-sample test, \( P < 0.02 \)), but not for cells in GPe (\( P > 0.7 \)). When the onsets of increases or decreases were compared between cells in GPe and GPi, there was a trend for decreases to begin earlier and increases later in GPi neurons, but these differences were not significant (2-tailed \( t \)-test, \( P > 0.1 \), Table 1).

Peak changes in movement-related discharge also showed the same pattern of early decreases and late increases only in GPi neurons. The mean time at which decreases in discharge reached a minimum was significantly earlier in GPi than in GPe (Table 1, Peak times). Increases in discharge tended to reach a maximum later in GPi than in GPe. The difference in the timing of minima and maxima was highly significant for GPi neurons (2-tailed \( t \)-test, \( P < 0.005 \)), but not for those in GPe.

Decreases as the first change in discharge tended to be more common in GPi than in GPe, especially when the movement-related discharge was composed of a biphasic change. Decreases composed 43% of the first changes detected in GPi and 37% in GPe, but this difference was not significant (\( \chi^2 \) test, \( P > 0.3 \)). When biphasic changes in discharge were detected, however, a decrease in discharge was the first change in nearly all GPi discharge (i.e., the ‘‘+/–’’ type accounted for 14 of 15 cases, 93%). Increases began the majority of biphasic changes in GPe discharge (‘‘+/+’’ type accounted for 22 of 39 cases, 56%). This constituted a significant difference between GPi and GPe neurons in the incidence of ‘‘+/+’’ type biphasic changes (\( \chi^2 \) test, \( P < 0.001 \)).

The high prevalence of early decreases in the movement-related discharge of GPi neurons was particularly evident in a population average of their perimovement discharge (Fig. 4). Separate population averages were constructed for GPi and GPe neurons by including the perimovement average discharge for all movement directions in which a significant movement-related change in activity was detected. In the population average for GPi neurons (Fig. 4, – – – ), the first change from baseline discharge was a decrease in discharge starting at –55 ms, which was followed by an increase starting at +35 ms. In contrast, the population average for GPe neurons (Fig. 4, — — — ) showed only an increase in discharge starting at –75 ms.

In the majority of cells in which time locking could be determined, the onset time of the first movement-related change in discharge was linked to the time of M rather than to the time of T or E. Figure 5 illustrates an example of a

**TABLE 1. Timing of changes in discharge**

<table>
<thead>
<tr>
<th>Onset Times</th>
<th>GPi</th>
<th>GPe</th>
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<tr>
<td><strong>Onset Times</strong></td>
<td>Increases</td>
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<tr>
<td>Means</td>
<td>–20</td>
<td>–54</td>
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<tr>
<td>( P &lt; 0.03 )</td>
<td>NS</td>
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<td>Medians</td>
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<td>Peak Times</td>
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<tr>
<td>Means</td>
<td>76</td>
<td>22</td>
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<td>( P &lt; 0.005 )</td>
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Mean times in milliseconds relative to the time of movement initiation. Significances according to two-tailed \( t \)-tests.
discharge in another cell in GPe. This neuron had a small early decrease in discharge that began as early as 140 ms before movement, followed by a large increase in discharge that began up to 60 ms before movement and lasted throughout the movement. The small decrease was maximal for movements toward the body (270°) and the increase was maximal for movements made directly away from the body (90°). A plot of mean maximum and minimum discharge versus target direction (Fig. 7A), shows that the small early decrease (○) was only slightly modulated with movement direction, compared with the dramatic directional modulation of the later increase (■). The randomization test found a slight directionality in the early decrease (0.02 < P < 0.05, preferred direction at 223°), whereas the directionality of the late increase was highly significant (P < 0.0004, preferred direction at 89°). Cosine functions (Fig. 7, solid lines) accounted for 69% of the trial-to-trial variance in this cell’s perimovement increases, but only 6% of the variance in decreases.

FIG. 7. Population averages of perimovement discharge for all GPe (— — —) and GPi (— — —) neurons. Averages include data from each neuron for all target directions in which a perimovement change in discharge was detected. Each neuron’s baseline discharge rate was subtracted from individual averages before averaging across directions and neurons.

Close temporal linkage for one neuron between the onsets of movement-related discharge and the time of M. Rasters aligned on the time of M and sorted according to RT show that the movement-related increase in discharge did not begin earlier when RTs were longer (Fig. 5A). As a consequence, the M—onset interval (○) was relatively constant and showed no correlation with RT, whereas the onset-T interval (Fig. 5B, ■) showed a positive correlation with RT (Pearson product-moment correlation, P < 0.001).

Significant correlations between RT and onset—T or M—onset were found in only 30 of 73 cells (41%). Of these, 21 (70%) were linked with M (significant RT vs. onset—T correlation). A similar fraction (69%) was linked with M when the linkage to M was determined by the correlation between MT and E—onset.

Only nine cells showed a significant linkage to T (significant RT vs. M—onset correlations), and only one cell showed linkage to E (significant MT vs. onset—M correlation).

Influence of direction on perimovement discharge

Perimovement averages and rasters revealed directional modulations in movement-related discharge that were smoothly and broadly tuned for most pallidal cells. Figure 6A illustrates the movement-related discharge of a cell in GPe that responded to elbow manipulation and had a large decrease in discharge beginning as early as 100 ms before M. Rasters and averages for movements to targets at 2 in. from the start position are arranged according to the eight target directions. The decrease in discharge, although present for movements in all eight directions, differed in magnitude with movement direction (randomization test, P < 0.0004), with the maximum decrease accompanying movements directly to the left (preferred direction 183°).

Figure 6B shows the directionality of movement-related discharge in another cell in GPe. This neuron had a small early decrease in discharge that began as early as 140 ms before movement, followed by a large increase in discharge that began up to 60 ms before movement and lasted throughout the movement. The small decrease was maximal for movements toward the body (270°) and the increase was maximal for movements made directly away from the body (90°). A plot of mean maximum and minimum discharge versus target direction (Fig. 7A), shows that the small early decrease (○) was only slightly modulated with movement direction, compared with the dramatic directional modulation of the later increase (■). The randomization test found a slight directionality in the early decrease (0.02 < P < 0.05, preferred direction at 223°), whereas the directionality of the late increase was highly significant (P < 0.0004, preferred direction at 89°). Cosine functions (Fig. 7, solid lines) accounted for 69% of the trial-to-trial variance in this cell’s perimovement increases, but only 6% of the variance in decreases.

Figure 7B illustrates the directionality of mean maximum and minimum perimovement discharge in a third GPe cell in which both increases and decreases in discharge were highly directional (P < 0.0004). For this cell, cosine functions accounted for 55% of the variance in increases and 28% of the variance in decreases.

In the total sample of globus pallidus cells, perimovement increases or decreases in discharge varied significantly with direction in 78% of the cells (57 of 73, randomization test, P < 0.05). Increases in discharge showed directional tuning more commonly (70%, 45 of 64 of neurons with significant increases) than did decreases (60%, 29 of 48 neurons with significant decreases). In 17 of the 39 neurons with both increases and decreases in discharge, both phases were directional.

The incidence of directionality was marginally higher in GPi than in GPe. Nearly all of the GPi cells studied had significant directional variations in discharge (94%, 17 of 18 cells), compared with 73% of the GPe cells (40 of 55 cells), and this difference approached significance ($\chi^2$ test, $P < 0.06$).

Although GPi discharge tended more frequently to be directional, the directional modulations in discharge were, on average, larger in GPe than in GPi. As shown in the population tuning curves for cells in GPe and GPi, this was true for both increases (Fig. 8A) and decreases (Fig. 8B). The mean peak-to-peak directional modulation in movement-related discharge was, on average, 11 spikes/s greater in GPe neurons (36.7 spikes/s in GPe vs. 25.7 spikes/s in GPi, 2-tailed t-test, P < 0.02).

It is evident from Fig. 8 that a large component of the perimovement changes in discharge, whether they were increases or decreases, was present across all directions of movement. This unmodulated component, which appears as an offset from the baseline discharge rate, also was larger for GPe neurons than for those in GPi. For cells with directional decreases in GPe and GPi, there also was a small difference in the mean baseline discharge rates. This difference was small and insignificant, however, and the directionally unmodulated movement-related components were superimposed on it.

Although the average depth of modulation differed for
cells in GPe and GPi, the two sample populations had tuning curves of similar width, as measured by mean angular deviations (147 and 147.9° means for GPe and GPi, respectively). Cosine functions also accounted for similar amounts of the directional variation in discharge rate for cells in GPe and GPi. The characteristics of directional modulations in pallidal discharge also depended on whether a perimovement change in discharge was an increase or decrease from the baseline discharge rate. Increases in discharge usually had larger directional modulations than did decreases (39.1 and 25.7 spikes/s mean peak-to-peak, respectively, t-test, P < 0.001). This difference can be seen by comparing the depth of modulation of the population tuning curves in Fig. 8, A and B.

The preferred directions of directional changes in discharge had a relatively uniform distribution, as illustrated in Fig. 9A. The distributions of preferred directions for increases and decreases in discharge did not differ substantially, and their combined distribution did not differ significantly from a uniform distribution (Komolgorov-Smirnov test, P > 0.1). In the 17 cells with both directional increases and decreases, the preferred directions of the two were usually shifted by nearly 180° (Fig. 9B). An example of this can be seen in Fig. 7B.

**Consistency of direction effects across movement amplitudes and behavioral conditions**

When directional modulations in movement-related discharge were large, they also were consistent across different amplitudes of movement and under different behavioral conditions. Figure 10A shows, for one neuron with a movement-related decrease in activity, the mean minimum discharge during movements to targets in eight directions at 1, 2, and 3 in. from the start position. (Data for 0, 45, and 90° directions are plotted again at 360, 405, and 450° to aid illustration of the directional modulation.) This neuron’s decrease in discharge, maximal during movements toward the monkey and to the right (270°–405°), showed a consistent directionality across the three target distances. The preferred directions (indicated in Fig. 9A by 3°) differed by only 9.9° when the deviation of the three preferred directions from equality was computed as the distance in three dimensions (1 in. vs. 2 in. vs. 3 in.) between the observed preferred directions and the line representing equality (1 in. = 2 in. = 3 in.).
Eight neurons were studied during three amplitudes of movement in at least four different directions under the sensory condition. All of these neurons had both increases and decreases in discharge that were directional. The preferred directions of these movement-related increases and decreases are plotted in three dimensions in Fig. 11A, with one dimension for each movement amplitude. Both increases (filled circles) and decreases (open circles) commonly had similar preferred directions across different movement amplitudes, so that most points in Fig. 11A lie near the line of equality. In 62.5% of cases (10 of 16), the observed preferred directions were within 45° of equality.

The preferred direction of movement-related discharge was also similar for movements made under different behavioral conditions. Figure 10B shows the mean maximum discharge rates of a neuron studied during movements to targets at a 2-in. distance under sensory, precued, and self-timed conditions. Although fewer directions were sampled under precued and self-timed conditions, the overall shape of the directional modulation in discharge was clearly similar under the three conditions, and the preferred directions under the three conditions were very close (3 overlapping near 270°). The perimovement discharge had significant directionality under all three behavioral conditions in 47% of the cases examined (21 of the 45 cases in which all conditions were presented and a directional change in discharge was detected). A plot of the preferred directions of these 21 cases (Fig. 11C) shows that preferred directions were similar under the three conditions.

The preferred direction of a change in discharge was most likely to be similar across different movement amplitudes and behavioral conditions (Fig. 11, B and D, respectively) when the peak-to-peak directional modulation in discharge was large. Conversely, if the angular difference between preferred directions for different amplitudes or conditions was large, >45° (open circles in Fig. 11, B and D, respectively), then the directional modulation in discharge of that change in discharge was typically small.

In summary, movement-related discharge in both segments of the pallidum was commonly and consistently related to the direction of movement. Directional modulations in discharge were typically larger in GPe neurons and they were particularly prominent for movement-related increases in discharge. The preferred direction for movement-related discharge was similar for different movement extents and for movements made under different behavioral conditions, especially when the magnitude of the directional modulation in discharge was large.

**Influence of movement amplitude on perimovement discharge**

There was a significant relation between movement amplitude (or target distance) and perimovement discharge rate in a high proportion of pallidal neurons. Figure 12 illustrates an example of this for a neuron in GPi. Data are plotted for movements made to targets at 1, 2, and 3 in. directly to the left and right of the start position (left and right columns). The average movement trajectories are shown in the middle. During movements to the left, this neuron had an increase in firing rate that began at about the time of M and became smaller in peak magnitude as movement amplitude increased. The discharge remained above control values after movements to the left were completed (during the target hold time), but the magnitude of this sustained discharge was not influenced by the distance of the target from the start position. During movements to targets to the right of the start position, the neuron had a small but consistent decrease in firing rate, but its magnitude was not influenced perceptibly by the amplitude of movement.

Target distance had a significant effect on perimovement discharge in 78% of the neurons tested (32 of 41, target distance vs. maximum or minimum discharge ANOVAs, F test, P < 0.05). Of the 116 target directions (cases) for which these cells’ activity was evaluated, 54 (47%) showed significant effects of target distance on perimovement discharge (ANOVA, P < 0.05). Although target distance effects tended to be more common in GPe neurons than in GPi, this was not significant at the P < 0.05 level (52% and 35% of changes in GPe and GPi neurons, respectively, χ² test). As was the case for target direction, increases in discharge were more often affected by target distance than were decreases (51% of increases and 38% of decreases).

In most cases, target distance effects could be interpreted as a monotonic scaling of discharge rate with movement amplitude or target distance. Figure 13A shows an example from the neural discharge plotted in Fig. 12 of a near linear relation between maximum perimovement discharge and the amplitude of leftward movements. Mean maximum discharge is plotted versus mean movement amplitude for movements to targets at three distances in two opposing movement directions. During movements to the left (180°, ○), the maximum perimovement discharge was inversely related to movement amplitude, and this relation was approximately linear, with a slope of −8.6 spikes·s⁻¹·cm⁻¹ (least-squares linear regression, P < 0.001, R² = 0.42). The neuron’s discharge did not change with movement amplitude, however, when movements of similar amplitude were made to the right (0°, ■).

A cell’s movement-related discharge was commonly scaled with movement amplitude in more than one target direction. Figure 13B shows an approximate linear effect of movement amplitude on the discharge of a GPe neuron for three different target directions. This cell had a decrease in discharge during the perimovement period, and the magnitude of the decrease was influenced significantly by target amplitude.
FIG. 7. Examples of the directional tuning of mean change discharge rates. A: mean maximum and minimum discharge rates from data shown in Fig. 6B. B: mean rates for GPe neuron with significant directional modulations in both mean maximum and minimum discharge rates. Mean maximum (●) and minimum (○) discharge rates for each of 8 target directions. Error bars: means ± SE. Solid curves: best-fit cosine functions. Arrows: preferred directions. Horizontal dotted lines: baseline discharge rates.

distance in six of the eight target directions tested ($F$ test, $P < 0.05$). In all six directions, decreases in discharge were more pronounced with increasing movement amplitudes, and this relation was significantly linear ($P < 0.001$, $R^2 = 0.43$, 0.37, and 0.29 for illustrated directions of 0, 45, and 135°).

The proportion of cells with significant linear amplitude effects increased with the number of target directions tested (Table 2), even when the significance level was adjusted to compensate for the number of directions tested per cell (Bonferroni correction, $P < 0.05$/number of directions tested). When six or more directions were tested, all cells ($n = 5$) had significant discharge rate–amplitude relations for one or more directions of movement.

There were no consistent differences in the degree to which discharge was scaled with movement amplitude (e.g., the slopes of regression lines) between GPe and GPi neurons, between increases and decreases in discharge, or between regressions with positive and negative slopes. Figure 14 illustrates this point with population means for all of the cases with significant positive ($n = 32$, Fig. 14A) or negative ($n = 20$, Fig. 14B) linear relations between movement amplitude and the change in neural discharge. The only measure that differed between these groups was the component of increases in discharge that was unaffected by movement amplitude (i.e., the unmodulated component or $Y$-intercept), which was larger for neurons in GPe than for those in GPi ($2$-tailed $t$-test, $P < 0.02$). This effect was present regardless of whether movement amplitude effects were positive or negative (e.g., filled symbols in Fig. 14A and B, respectively).

The directions in which linear movement amplitude effects were detected also held no consistent relation to a cell’s directional modulation in discharge. Figure 15, A and C, illustrates this finding in plots of the slopes of linear regressions versus the difference between the target direction tested and the cell’s preferred direction. For cells in which a move-
Perimovement discharge was monotonically scaled with the amplitude of movement more frequently than with MT or mean velocity. Significant regressions of discharge rate onto movement amplitude were found in 45% of the cases tested (32 of 116 cases independent of ANOVA results). In contrast, regressions of discharge rate onto MT and mean velocity were significant in only 33% of the cases (38 of 116 cases tested for each). The higher incidence of movement amplitude effects was nearly significant compared with the incidence of MT and mean velocity effects ($\chi^2$ test, $P < 0.06$).

Regressions of discharge onto movement amplitude also typically accounted for more of the trial-to-trial variance in discharge than did regressions onto velocity or MT (Fig. 16). In 88% of cases, coefficients of determination were greater for movement amplitude regressions than for the

![Figure 9](image-url) Angular distribution of preferred directions. A: distribution of preferred directions for increases and decreases in discharge. B: distribution of preferred directions for decreases in discharge relative to the preferred direction for increases in neurons that had significant directional modulations for both increases and decreases in discharge.

ment amplitude effect was noted in at least one target direction, points are plotted for all target directions tested for an amplitude effect. Cases for which the linear regression was significant ($P < 0.05$) are indicated by open symbols. Although in GPi neurons significant linear effects tended to be more common in target directions close to a cell’s preferred direction, the angular distribution of linear effects did not differ significantly from the distribution of all directions tested for either GPe or GPi (Fig. 15, B and D, Komolgorov-Smirnov 2-sample test, $P > 0.5$). These findings were consistent for both increases and decreases in discharge (open circles and triangles, respectively, in Fig. 15, A and C) and for amplitude effects with positive and negative slopes.

The apparent linear relations between pallidal discharge rate and movement amplitude could be due to the covariation of movement amplitude with some other parameter of motor performance to which pallidal discharge was more closely linked. As a partial test of this possibility, maximum and minimum perimovement discharge was also regressed on average velocity and on movement time. These kinematic measures covary to a certain extent with movement amplitude, and previous studies have found that pallidal movement-related discharge is often correlated with one or the other (Anderson and Turner 1991b; Georgopoulos et al. 1983).

![Figure 10](image-url) Examples of similar preferred directions for different movement amplitudes and different behavioral conditions. A: mean minimum discharge rate in 1 neuron for movements to targets at 1 in. (squares), 2 in. (circles), and 3 in. (triangles) from the start position in each of 8 directions. B: mean maximum discharge rate in a different neuron for movements to targets presented in different directions under the sensory (squares, 8 directions), precued (circles, 6 directions), and self-timed (triangles, 3 directions) conditions. Data for directions of 0–45° are repeated at directions of 360–450° to aid depiction of directionality. Horizontal dotted lines: baseline discharge rates. Arrows: preferred directions, 1 for each of the tuning curves.
FIG. 11. Comparison of preferred directions across movement amplitudes and behavioral conditions in the population of pallidal neurons. A and C: preferred directions for each directional change in discharge observed during movements to targets at 3 distances (A), and during movements to the same targets but under 3 behavioral conditions (C). Filled circles: preferred directions for increases in discharge. Open circles: preferred directions for decreases in discharge. Data are included in C only for changes in discharge that were significantly directional under all 3 conditions. B and D: relationship between the magnitude of directional modulation in discharge and the difference between preferred directions (distance from equality in 3 dimensions) across amplitudes (B) and conditions (D). When preferred directions were dissimilar, the directional modulation in discharge tended to be small. Changes in discharge with the largest directional modulations in discharge also had preferred directions that differed by <45° (filled circles).

corresponding average velocity regressions (points below the diagonal line in Fig. 16A). Comparison of movement amplitude and MT regressions led to a similar finding (Fig. 16B) that coefficients of determination were usually larger for movement amplitude than for MT regressions (68% of cases).

Consistency of amplitude effects across behavioral conditions

When there was a strong relation between perimovement discharge and movement amplitude, the effects of movement amplitude were similar under the sensory and precued conditions. Figure 17A shows an example of similar movement amplitude effects under sensory and precued conditions in data from a GPe cell. Maximum perimovement discharge rate on single sensory and precued trials (■ and ○, respectively) is plotted versus amplitude of movement. The slopes of the regression lines plotted for each condition did not differ significantly between the two conditions (6.2 and 5.6 spikes s⁻¹ cm⁻¹ under sensory and precued conditions, respectively; F test, P > 0.5). The regression Y-intercepts were significantly different, however (150.9 and 127.8 spikes/s respectively, F test, P < 0.05), indicative of a larger movement-related change in discharge under the sensory condition that was not influenced by the amplitude of movement.

The effect of movement amplitude on pallidal discharge was studied under both sensory and precued conditions in 10 cases (7 cells, 3 of which were studied in 2 target directions). When linear regressions were performed on minimum and maximum discharge rates versus movement amplitude, significant linear regressions were found under both sensory and precued conditions in 7 of the 20 tests (5 of 7 cells; Fig. 17B, ●). These were the cases in which regression slopes were large (3.35 and 3.33 spikes s⁻¹ cm⁻¹ mean absolute slopes in sensory and precued conditions, respectively), and in most cases the slopes did not differ under the two conditions (71%, 5 of 7 cases). In one case, however, the slopes had opposite signs under the two conditions.

In contrast, the Y-intercepts of the regression lines usually were different under the two conditions. This was true for six of the seven cases with significant regressions under both conditions, and for all eight of the cases with a significant regression under just one of the conditions. Thus behavioral condition often changed the magnitude of the perimove-
ment discharge of pallidal neurons, but it seldom changed the relation between movement amplitude (or target distance) and discharge rate when that relation was strong.

**DISCUSSION**

The current results show that, when the perimovement discharge of pallidal neurons was evaluated during multijoint arm movements made in several different directions, movement-related changes in discharge were directionally modulated. Changes in discharge also varied with movement amplitude or a kinematically related characteristic of the movement. The directional modulation was broadly tuned, and it was consistent for different amplitudes of movement and for movements made under different behavioral conditions. Movement amplitude-related changes in activity were not restricted to a cell’s preferred direction, nor were they distributed across all directions in a manner that would shift the entire directional tuning curve. When movements were made to visible versus remembered target locations, the magnitude of a cell’s movement-related change in discharge was often different. When that movement-related change was scaled strongly with movement amplitude, however, amplitude scaling was similar across different behavioral conditions.

**Form and timing of changes in pallidal discharge**

The current study reveals a higher incidence of initial decreases in the discharge of pallidal neurons than was reported in other studies of limb movement. In the oculomotor-related portion of the substantia nigra, neurons with axons directed to the superior colliculus have a reduction in discharge in association with saccadic eye movements (Hikosaka and Wurtz 1983a). Reduced nigral inhibition is believed to facilitate the saccade-related bursts of discharge in collicular cells (Hikosaka and Wurtz 1983c). In contrast, studies of pallidal activity associated with arm movement always have shown a strong majority of initial increases in discharge (Anderson and Horak 1985; DeLong 1971; Georgopoulos et al. 1983; Mitchell et al. 1987). The incidence ratio of movement-related increases to decreases detected in perimovement pallidal discharge has been reported to be as low as 2.4 (Mink and Thach 1991b) and as high as 4.2 (Georgopoulos et al. 1983). In the current study, increases were only 1.56 times as common as decreases across all movement directions tested in all cells.

The multiple movement directions and/or the multijoint movements used in the current study may have been reason(s) for the higher incidence of decreases in discharge. Although initial increases still occurred more frequently than initial decreases when all cases (i.e., cells × directions...
Increases in pallidal discharge were, however, still predominant in GPi as well as in GPe. This is in contrast to the primary reduction of activity in basal ganglia output cells in the substantia nigra during saccadic eye movements (Hikosaka and Wurtz 1983c). The heavy preponderance of limb movement-related increases in GPi discharge reported in previous studies led to the conclusion that the main action of movement-related GPi discharge is to increase the inhibition of thalamocortical circuits and thereby suppress unwanted or inappropriate muscle excitation or reflexes (Mink and Thach 1991c). Why such phasic suppressive actions would not also be required by the SNr–superior colliculus saccadic control system remains unclear. It is possible that the large and variable loads encountered during limb movements but not in eye movements, which place additional requirements on skeletomotor control systems, give rise to such phasic increases in pallidal discharge.

The population average for GPe neurons showed only an increase in discharge. This occurred not only because increases in discharge were more frequent and of larger magnitude, but also because increases and decreases in the discharge of GPe neurons occurred with similar timing. Although the changes in discharge of pallidal neurons usually began before M, they seldom preceded the initial activity of muscles that were the prime movers for the task. The earliest changes in activity of shoulder muscles (posterior deltoid, pectoralis, and anterior deltoid) that were the prime movers in this task occurred at means of 56, 63, and 68 ms before M, respectively (Turner et al. 1995). The median onset time for decreases in pallidal discharge was 50 ms before movement (55 for GPi alone), and for increases it was 40 ms before movement onset. This near concurrence between the initial change in pallidal and muscle activity was also the case in the studies of Nambu et al. (1990), Anderson and Turner (1991b), and Mink and Thach (1991b). One study of pallidal discharge reported onset times for movement-related pallidal discharge that were 60 ms later than those found here (Georgopoulos et al. 1983). Differences in the behavioral task employed and analysis techniques may account for that difference.

FIG. 13. Examples of the near linear relations between movement amplitude and perimovement changes in discharge. A: mean maximum discharge vs. mean movement amplitudes for movements to the left (○) and right (■) for records shown in Fig. 12. B: mean minimum discharge rates of a GPe neuron for movements of different extent to targets in directions of 0, 45, and 135°. Lines from least-squares regressions are shown for each data set. Error bars: means ± SE.

tested) were considered, it is of interest that for two-thirds of the pallidal cells studied, decreases in discharge were noted for at least one movement direction tested. Furthermore, in GPi neurons, the major source of basal ganglia output to the thalamus, 91% of the decreases detected as the first change in discharge began before M. This provides the possibility that, for most GPi neurons in the area studied, an early decrease in inhibitory output could facilitate activity in thalamocortical neurons before the onset of movements made in specific directions. The population average for the GPi neurons studied (Fig. 4) provides further evidence that a reduction in discharge that begins and peaks early is significant in this population. The current hypothesis for pallidal influences on limb movement (Alexander et al. 1990), as for nigral influences on eye movement, is that this reduction in GPi discharge would facilitate movement.

Despite the fact that the onset of movement-related changes in pallidal discharge occurred rather late to contribute to M, they were temporally related most often to the time of M rather than to E. A close temporal linkage between a change in discharge and a behavioral event implies that there is a functional relationship between the two (Commenges and Seal 1985; Hanes et al. 1995). Such a linkage does not indicate a direct causal relationship (e.g., that the onset of neural discharge contributes to M). It implies strongly, however, that the change in discharge is initiated by processes that are related more closely to development of the movement than to E. The prolonged duration of increases in discharge for larger-amplitude movements, which also usually have longer durations (unpublished observations), does open the possibility that the termination of the movement-related change in discharge is linked, in some way, to E. Because changes in pallidal activity also were seldom linked to T, this implies that they were seldom involved in the early stages of visuomotor transformation.

**Movement direction**

The incidence of significant directionality in the discharge of 78% of the pallidal neurons studied is much higher than
has been reported in other studies, all of which used movements restricted to one dimension and often to one joint. Georgopoulos et al. (1983), who studied the activity of individual pallidal neurons during two directions of movement of a handle that the animal grasped (either push-pull or side-to-side), found directionally different activity in 48% of the cells in GPe and 56% of those in GPi. Mitchell et al. (1987), whose task restricted movements to flexion and extension around the elbow, reported that 30% of the pallidal neurons in both GPe and GPi had direction-dependent changes in firing. Mink and Thach (1991b) and Hamada et al. (1990) both used wrist flexion/extension tasks, and the former study reported directionally different movement-related discharge in 28% of the cells in GPe and 41% in GPi, whereas the latter reported only that movement-related changes in discharge were quite similar for wrist flexions and extensions.

The most likely reason for the higher incidence of directionality in the current study is the larger range of movement directions tested. Movements were made toward targets that were visible in up to eight different directions in the two-dimensional work space, the movements were not constrained by the trajectory of a manipulandum, and they involved displacement at proximal joints, including the shoulder and the elbow. As described previously (Turner et al. 1995), two-joint movements made by the two animals whose pallidal activity is reported here (monkeys F and I) had generally straight trajectories and single-peaked velocity profiles, and EMG activity in muscles acting at the shoulder (anterior and posterior deltoid and pectoralis) had directionally tuned changes in both the magnitude and the time of onset. Both the discharge of pallidal neurons and the EMG tuning curves for shoulder muscles were broad and fit well by a cosine function. Such broad neuronal tuning curves imply that in the one-dimensional tasks used by others, movements in opposite directions could easily be associated with similar neuronal discharge rates.

A second experimental factor that could have affected the relation between discharge rate and target direction is the requirement that the animals actively control the trajectories of multijoint movements. Control of multijoint movements requires the resolution of kinematic and mechanical redundancies that are not present in single-joint movements (Bernstein 1967). There are also demands in multijoint movements for postural stabilization and compensation for dynamic interactions that are not present in single-joint movements (Gordon et al. 1994). It is possible that the discharge of pallidal neurons varies with movement direction because it plays a role in joint stabilization or inertial compensation, both of which change with movement direction.

It is also possible that the incidence of directional sensitivity was enhanced by use of a task that involves proximal movement at both the shoulder and the elbow. Neurons whose activity is reported here were selected because they showed movement-related changes in discharge during performance of the task before testing by manipulation of the arm. As reported previously (Turner et al. 1995), movements in this task are associated with directionally graded changes in both the amplitude and the timing of bursts of muscle activity in anterior deltoid, posterior deltoid, and pectoralis. Smaller EMG bursts in biceps and brachialis, which cross the elbow, showed smaller directional gradation in both amplitude and timing. Previous studies have found that a higher proportion of neurons in the somatomotor portions of the putamen and pallidum responds to manipulation of the proximal (shoulder or elbow) joints than to distal
FIG. 15. Distribution of target directions with amplitude-related modulations in discharge relative to the preferred directions of GPe (A and B) and GPi (C and D) neurons. A and C: relations of target direction tested relative to a cell’s preferred direction (abscissa) and the slope of the regression line (ordinate). Open circles and triangles: increases and decreases in discharge, respectively, that had significant amplitude-related modulations. Dots: cases with nonsignificant regressions. B and D: cumulative angular distributions of target directions in which significant amplitude-related modulations were found relative to a cell’s preferred direction (thick lines). These were not significantly different from the cumulative distributions of all target directions tested (thin lines).

FIG. 16. Comparison of the linear relations between modulations in discharge and movement amplitude, movement velocity, and movement duration. The coefficients of determination (i.e., the proportion of variance accounted for, $R^2$) for linear regressions of discharge onto movement amplitude (abscissas) are plotted vs. those for regressions onto average velocity or movement duration (ordinates in A and B, respectively). Points are plotted for all cases in which either regression was significant. Points below the diagonal dotted lines (which denote equal $R^2$ for both regressions) indicate cases in which a change in discharge was more closely related to movement amplitude.
(wrist or finger) stimulation (Crutcher and DeLong 1984a; DeLong et al. 1985; Hamada et al. 1990). Any pallidal neuron whose discharge is influenced by movement at either the shoulder or the elbow joint, then, might be expected to have a directional variation in movement-related activity.

The incidence of directionality in pallidal discharge could certainly depend on which portion of the nucleus, and thus which basal ganglia circuit, is studied (Hoover and Strick 1993; Nambu et al. 1990). It is reasonable to expect that neurons in the pallidal territory that is influenced by primary motor cortex/primary somatosensory cortex would respond most frequently to passive movement of arm joints and/or muscle palpation (Flaherty and Graybiel 1993). These are the cells that were sought in the current study. Although DeLong and colleagues (Georgopoulos et al. 1983; Hamada et al. 1990; Mitchell et al. 1987) also focused on pallidal neurons that responded to manipulation of the arm, others have studied populations that seldom responded to sensory stimulation of the arm (e.g., Brodtchie et al. 1991a; Mink and Thach 1991a).

The breadth of the directional tuning curves for perimovement discharge rate in pallidal neurons is similar to that described for neurons in cortical areas such as primary motor (Fu et al. 1993; Georgopoulos et al. 1982; Kalaska et al. 1989; Schwartz et al. 1988), premotor (Fu et al. 1993), and posterior parietal cortex (Kalaska et al. 1983, 1990). All of these cortical areas are sources of input to the putamen, and thus to the portions of the globus pallidus in which most of the neurons examined in the current study were located. Although addition of higher harmonics to the regression equation, which allowed the width of peaks and valleys in the turning curve to vary, sometimes improved the fit significantly, the width of the peaks still ranged from 90 to 270° and centered on the 180° width that characterizes a cosine function (unpublished observations).

In the current study, the consistency of preferred directions across different movement extents and behavioral conditions was correlated with the magnitude of the directional modulation in discharge. The margin of error for determining a preferred direction is inversely proportional to the magnitude of the directional modulation in discharge (Fisher 1993). In addition, the fewer the directions sampled, the more inaccurate the determination of a cell’s preferred direction. Thus many of the cases in which preferred directions did not agree across changes in behavioral condition, in this and in other studies, may be accounted for by errors introduced by limited sampling and by relatively small directional modulations in discharge.

In most pallidal cells, a movement-related change in discharge (increase or decrease) was present for all movement directions, but the magnitude of this change was modulated with movement direction. The “baseline” discharge rate of 87 spikes/s in neurons of both GPe and GPi presented the opportunity for substantial increases and decreases in discharge. The average depth of firing rate modulation across different movement directions (36.7 spikes/s in GPe and 25.7 spikes/s in GPi) was a large fraction of this mean control discharge rate. In both GPe and GPi neurons, however, an average of ~40% of a cell’s peak movement-related change in discharge was not modulated with movement di-

<table>
<thead>
<tr>
<th>Directions Tested</th>
<th>Percent Significant</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>14 (1/7)</td>
</tr>
<tr>
<td>2</td>
<td>73 (19/26)</td>
</tr>
<tr>
<td>3</td>
<td>100 (1/1)</td>
</tr>
<tr>
<td>4</td>
<td>50 (1/2)</td>
</tr>
<tr>
<td>6</td>
<td>100 (1/1)</td>
</tr>
<tr>
<td>8</td>
<td>100 (4/4)</td>
</tr>
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</table>

Number in parentheses is number of cells significant over number studied.

Table 2. Frequency of significant amplitude-related effects as a function of the number of target directions studied.
crease and decrease in discharge were generally in reciprocal change in discharge around the baseline discharge rate for opposing movement directions.

Despite the robust character of directional tuning across different movement amplitudes and task conditions, it is unlikely that pallidal activity plays an essential role in determining the direction of a movement. Lesions of the basal ganglia, either reversible (Inase et al. 1996) or permanent (Horak and Anderson 1984a), do not result in changes in the trajectory or accuracy of targeted movements. Likewise, phasic stimulation of the pallidum during reaching movements commonly influences the speed of movement but does not alter movement trajectory (Horak and Anderson 1984b). It is more likely that the discharge of a pallidal cell contributes especially to some other aspect of motor control for movements made in particular directions.

The common relations in the current study between pallidal discharge and the direction of hand displacement relative to the start position could reflect a relationship of pallidal discharge to some task parameter that covaries with movement direction. For instance, previous studies of the somatomotor portion of the pallidum have reported that the discharge of pallidal neurons is associated with specific movements of single joints (DeLong et al. 1985; Filion et al. 1988; Hamada et al. 1990). Therefore the directional modulation in a pallidal neuron’s discharge may have been linked to the direction and extent of rotation of the cell’s specific joint. A recent study of neural discharge in primary motor cortex and parietal and premotor cortices during similar movements with the use of different arm postures suggests that the rotation of specific joints is represented in those areas as well (Scott and Kalaska 1995; Scott et al. 1995). At the other end of the spectrum of possible covariates, some neurons in the somatomotor putamen have task-related discharge that is related to the direction of the target or goal of the movement, independent of the direction of movement (Alexander and Crutcher 1990). Although the percentage of neurons in the putamen that responded in this way was low, at least some of the pallidal neurons in the present study may have had directional modulations in discharge that were related to the direction of the target and not to the direction of movement. In the present study, as well as in nearly all studies of the directionality of movement-related discharge in cortical neurons (Fu et al. 1993; Georgopoulos et al. 1982; Kalaska et al. 1983, 1989, 1990; Schwartz et al. 1988), target direction and movement direction were not dissociated.

More than half of the pallidal neurons studied showed both increases and decreases in discharge during the period of movement, and the preferred directions for the increases and decreases in discharge were generally in reciprocal directions. This implies that increases and decreases in discharge must be particularly important in association with movements in reciprocal directions.

Movement amplitude

Movement-related changes in pallidal discharge commonly varied not only with movement direction but also with movement amplitude. Amplitude-related changes in pallidal discharge during the movement time also were reported for a large percentage of the cells studied by Georgopoulos et al. (1983) (66% of the cells in GPi and 79% of those in GPe). That task involved multijoint push-pull or side-to-side movements of the entire arm, but it only examined amplitude scaling in two directions along one dimension. Although a similar incidence of significant linear amplitude scaling was found in the current study when only two directions were studied, all cells studied during movements in six or more target directions showed significant linear amplitude scaling during movement in at least one direction.

Relations of pallidal discharge with movement extent were reported to be rare and inconsistent in two other studies that differed in several ways from the current study and that of Georgopoulos et al. (1983). Mink and Thach (1991b) and Brotzchie et al. (1991a) both used tasks restricted to flexion/extension of the wrist and both searched for relations of pallidal discharge to movement amplitude that were independent of other aspects of task performance. Mink and Thach (1991b) dissociated the amplitude and velocity of wrist flexion/extension movements by the use of two target distances with two different target sizes. (Movements to small targets were slower than those to large targets at the same distance.) Twenty-one percent (7 of 34) of globus pallidus neurons showed significant correlations between movement amplitude and peak change in discharge. Brotzchie et al. (1991a) used both different amplitudes of wrist flexion or extension movements and similar-amplitude movements that started from different initial positions to test for relations of pallidal discharge to the extent of movement that were independent of the movement start and stop positions. In only 29% of the 92 pallidal neurons studied was the discharge influenced by the amplitude of movement independent of start position, and in only 13% was that relationship linear. Both studies rejected the hypothesis that movement-related changes in pallidal discharge commonly reflect the amplitude of movement independent of other task factors.

It is important to emphasize that movements used in the present study were 1) multijoint, including the shoulder and elbow, and 2) made in up to eight target directions. In light of the fact that both studies in which multijoint movements of the entire arm have been used (the present study and that of Georgopoulos et al. 1983) have found a high proportion of cells with amplitude-related changes in discharge, and that this relation was found in all cells in which six or more movement directions were tested, we suggest that amplitude-related scaling of changes in a pallidal arm neuron’s discharge is especially prevalent during multijoint movements of the arm that are made in particular directions.

Movement-related discharge could signal the combined direction and amplitude of movement in several ways that would result in consistent relationships between a cell’s direction- and amplitude-related modulations in discharge. 1) If amplitude scaling was present for all directions of movement, it could shift the entire directional tuning curve up or down. In this way the magnitude and the direction of movement could be signaled by neural activity in a purely additive manner. 2) If amplitude effects appeared reciprocally at the peak and valley of the directional tuning curve, amplitude scaling could control the peak-to-peak magnitude of the di-
directional modulation in discharge. Such an interaction would arise if movements across the workspace were coded according to a “gain field,” similar to those observed in parietal cortical neurons coding gaze angle (Andersen et al. 1985).

Finally, if amplitude effects occurred only at specific points in a directional tuning curve, they could sharpen or broaden the width of the peaks or valleys in the directional tuning curve. This type of interaction would arise, for instance, if a neuron discharged according to the proximity of a movement’s endpoint to a specific target zone or “movement field” in the workspace (Hikosaka and Wurtz 1983a,b). In the present study and in a study of motor cortices by Fu et al. (1993), the distribution of directions in which amplitude scaling was identified did not exclusively fit any of these models. Although individual neurons might signal the combined amplitude and direction of movement according to any one of the schemes outlined above, the limited number of directions consistently tested for amplitude effects in the current study precludes the categorization of most individual cells’ discharge to one or another of these response types.

Although the movement amplitude relations detected in the present study probably did not reflect an exclusive neural “coding” of movement amplitude, independent of target direction [and perhaps even target location in the workspace; see Brotchie et al. (1991a)], we found that the relation between movement amplitude and peak change in a pallidal neuron’s discharge was frequently consistent across different behavioral conditions. Thus the movement-related discharge of a pallidal neuron is usually influenced by a combination of task factors, but the amplitude of movement or some covarying movement or target parameter is a frequent component of that combination.

Movement variables that may covary with movement amplitude include the velocity of movement and MT (Fitts 1954), the magnitude and duration of the force impulse produced to initiate the movement (Schmidt et al. 1979), the duration of the EMG burst in the agonist muscles (Buneo et al. 1994), the somatosensory consequences of the movement, and the target position (Alexander and Crutcher 1990). In the current study we provide evidence that pallidal discharge was more closely related to movement amplitude than to movement velocity or MT. Mink and Thach (1991b) also found a smaller percentage of pallidal neurons with significant correlations between peak change in discharge and peak movement velocity (6%) than with movement amplitude (22%). Brotchie et al. (1991a) reported that movement amplitude and velocity were not dissociated during the targeted movements, and they did not determine the relation between discharge and movement velocity quantitatively. They did, however, report that there was no relation between the magnitude of neuronal discharge and the velocity of oscillatory movements made at the final hold position.

It is also unlikely that the movement amplitude effects found in the current study were actually reflecting a close relation of pallidal discharge to the pattern of muscle activity. In studies that used static loads to dissociate the direction of movement from the pattern of muscle activity, it was found that directional movement-related activity in both the pallidum and putamen was most often related to the direction of movement independent of the pattern of muscle activity used to perform the movement (Crutcher and Alexander 1990; Crutcher and DeLong 1984b; Mitchell et al. 1987). The discharge of neurons in both putamen and the pallidum was often influenced by task loading conditions (i.e., whether an external load opposes or assists a movement), but the pattern of neural activity is seldom the same as the pattern seen in the activity of muscles used in the task (Crutcher and Alexander 1990; Liles 1985; Mitchell et al. 1987).

Movement-related discharge that is scaled with the extent of arm movements has been described in primary motor cortex and dorsolateral premotor, somatosensory, and parietal cortices (Fu et al. 1993; Riehle et al. 1994). All of these cortical areas project to the somatomotor portion of the putamen and may contribute to the movement amplitude-related modulations in pallidal discharge.

Role(s) of pallidal discharge in motor control

Several roles have been proposed for the basal ganglia, especially with respect to motor function. Hikosaka and Wurtz, who examined the role(s) of the basal ganglia with respect to saccadic eye movements, proposed that the reduction of activity in oculomotor-related cells of SNr facilitated (by disinhibition) the saccade-related burst of discharge in cells of the superior colliculus and resulted in earlier saccades of increased velocity (Hikosaka and Wurtz 1983c). Mink and Thach, who examined the role(s) of the basal ganglia with respect to targeted wrist movements, proposed that perimovement increases in the inhibitory output of the basal ganglia suppressed the maintained activity in muscles that would oppose movement and allowed other mechanisms to generate a volitional limb movement (Mink and Thach 1991c). Although these two models disagreed concerning the sign of the change in discharge that facilitates movement, they both proposed an on-line consequence on movement kinematics of the facilitatory and/or suppressive effects of changes in output from the basal ganglia. Both also reported differences in the magnitude or importance of basal ganglia output in different task conditions.

A model that has gained recent attention proposes that the basal ganglia aid in the activation of behaviorally appropriate frontal cortical subcircuits. In this model, medium spiny striatal neurons would detect a “context” from behaviorally relevant inputs from the cortex and thalamus. The resulting change in the activity of basal ganglia output cells in the pallidum or substantia nigra would facilitate contextually appropriate and suppress contextually inappropriate frontal thalamocortical subcircuits (Houk 1995; Houk and Wise 1995). The functional role of such basal-ganglia-mediated facilitations and suppressions would vary between different basal ganglia/frontal cortical circuits (Alexander et al. 1990). Whereas changes in discharge in pallidal neurons belonging to the prefrontal circuits may modulate response learning, working memory, or other proposed prefrontal cortical functions (Goldman-Rakic 1994; Passingham 1993), similar changes in pallidal neurons belonging to the motor circuit (Hoover and Strick 1993) may produce context-dependent modulations of movement execution.

In a strict interpretation of the model by Houk and Wise (1995), a new context is registered in a binary all-or-nothing
way by self-sustained changes in the activity of corticothalamocortical loops. Such changes in the activity of thalamocortical motor circuits, the consequence of perimovement changes in discharge in basal ganglia output neurons, could bias the motor system to greater or lesser activation. However, they would not necessarily influence the movement in progress in an analog and on-line manner (Houk and Wise 1995).

Several findings from the current study limit the strict application of the Houk and Wise model. The first of these is the timing and form of changes in pallidal discharge during the course of a single movement. The frequent biphasic changes in discharge around the baseline rate (e.g., an initial decrease in GPi discharge followed by an increase) would mean that basal ganglia outflow frequently signals a switch from ‘‘contextually appropriate’’ to ‘‘contextually inappropriate’’ during the course of a single movement. This would result in a transient modulation in the activity of the target thalamocortical loop, not in a sustained change as proposed by the Houk and Wise model. Second, variations in the magnitude of increases and/or decreases in pallidal discharge as movements are made in different directions and with different amplitudes predict that the resulting changes in discharge of the target thalamocortical loop would not simply be binary or dual state.

In addition, the consequences of microstimulation within GPi argue for an influence of changes in pallidal output on an ongoing movement (Anderson and Horak 1985; Horak and Anderson 1984b). Brief stimulus trains applied in the globus pallidus during the RT slowed the ensuing movement only if the train overlapped the time period 100–150 ms before M. Stimulation earlier or later than this critical period did not produce a change in movement time. A perimovement change in the pallidal inhibition of recipient thalamocortical or brain stem circuits must, then, be able to modulate on-line movement execution under at least some behavioral conditions. Although movement-related changes in pallidal activity recorded in this and other studies usually began too late to be involved in M, they did occur sufficiently early to influence the execution of an ongoing movement. These changes in discharge were not so late that they could only influence subsequent movements by a change in motor set, for example.

The directional tuning and amplitude scaling of pallidal discharge observed in the current study could be consistent with either the on-line control model or a context recognition model that was modified to allow graded changes in basal ganglia output. In either model, the requirements for facilitation and suppression in the motor circuit would be expected to vary as a function of target or movement direction and amplitude. Activation of cortical subcircuits to the levels necessary to perform movements of appropriate scale or speed in one direction would require a scaled reduction in discharge in a selected group of GPi neurons. To perform a movement in one direction without the interference of extraneous muscle activations, the activity of other cortical subcircuits presumably must be suppressed, which would require directionally tuned increases in the discharge of a different set of pallidal output neurons. This would result in the robust directional tuning observed in both the increases and decreases in discharge we observed in individual pallidal cells.

Models of basal ganglia function must also account for the consequences of inactivation of basal ganglia output. In a number of studies that used relatively simple movement tasks, the most consistent effects of inactivation of basal ganglia output were positional instability, changes in movement velocity, and, in the limbs, excessive activity of some muscles. Hikosaka and Wurtz (1985) observed, after injection of muscimol into the SNr, that monkeys were unable to maintain constant visual fixation of a target because of ‘‘saccadic jerks.’’ Hore and Vilis (1980), Mink and Thach (1991c), and Inase et al. (1995) all reported that reversible or permanent inactivation of GPi produced a drift of the arm around the joints that were free to move. As shown in the latter study, this was an active drift, accompanied by EMG activity of the agonists. When a cue indicated to the animal that the hand had drifted off the target zone, the EMG activity that contributed to the drift was terminated and the hand was returned to the target zone. This produced an oscillatory movement of the limb, similar to that of a saccadic jerk. Thus one consequence of the normal high level of inhibition of basal ganglia targets by neurons in movement-related portions of the globus pallidus or substantia nigra is positional stability. Concurrent with the period in which positional drift of the arm occurred, the tonic discharge rate of neurons in pallidal-receiving areas of the thalamus was increased (Inase et al. 1995). One might assume that the transient reductions in discharge present in some pallidal neurons under normal conditions would have similar facilitatory effects on their recipient thalamocortical circuits. Thus the facilitation of pallidal reciprocal circuits, either by normal transient reductions in pallidal discharge or by experimental inactivations of pallidal discharge, may promote a positional instability that allows movement to occur.

 Interruption of normal basal ganglia output also leads to changes in movement velocity. When muscimol was injected to inhibit cells in SNr, the peak velocity of saccades made to the contralateral visual field was increased (Hikosaka and Wurtz 1985). In contrast, when neurons in motor regions of the globus pallidus were inhibited or destroyed, the velocity of arm movements was consistently reduced and antagonist muscles in the arm showed a pattern of cocontraction (Inase et al. 1995; Mink and Thach 1991c). It is not clear whether changes in velocity after disruption of basal ganglia output are due to a loss of phasic, movement-related changes in the discharge of pallidal or nigral neurons, and/or due to changes in the tonic activity of basal ganglia receiving circuits (Inase et al. 1995). The apparent conflict between the oculomotor and skeletonmotor studies, however, may be accounted for by the different characteristics and roles of the two circuits. Saccadic eye movements are achieved by a burst of activity in the agonist extraocular muscles that is matched to the mechanical properties of the oculomotor plant, such that a burst of activity in the antagonist muscle is not required to terminate the movement accurately (Robinson 1970). Rapid targeted arm movements, however, are typically achieved by alternating bursts of activity in agonist and antagonist muscle groups (Turner et al. 1995; Wadman et al. 1980). A cocontraction of muscles acting antagonistically around joints also is commonly used to stabilize the
limb against external perturbations. When drift of the limb is induced by injection of muscimol into GPi, the enhanced cocontraction observed in muscles across the joint may be a strategy adopted by the monkey to stabilize the limb and reduce the drift at the cost of slowing intended movement. Such a stabilizing agonist-antagonist cocontraction strategy may not be available in the oculomotor control system. Thus, with GPi inactivations, slowed limb movements could be a consequence of the attempt to maintain a stable position rather than a primary defect in the ability to activate a motor signal or command to produce a rapid movement.

Basal ganglia output neurons have changes in activity related to sensory signals and behavioral condition, as well as to kinematic variables (Brotchie et al. 1991b; Hikosaka and Wurtz 1983b; Mink and Thach 1991a; Mushiake and Strick 1995). Although basal ganglia “function(s)” must thus be understood as the consequence of a basal ganglia output flow that reflects processed combinations of motor, sensory, and contextual information, the present study demonstrates that kinematic information is an important and consistent determinant of the outflow from skeletomotor-related portions of the basal ganglia.

We thank B. Bedell for excellent technical assistance, Dr. Warren Smith for computer programming, and Dr. John Buford for helpful comments. Address for reprint requests: R. S. Turner, Dept. of Neurology, WMRB 6000, Emory University, Atlanta, GA 30322.

Received 2 July 1996; accepted in final form 29 October 1996.

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