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Role of primate basal ganglia and frontal cortex in the internal generation of movements

II. Movement-related activity in the anterior striatum

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Summary. In order to more comprehensively assess the role of the basal ganglia in the internal generation of movements, we studied the activity of neurons in the head of the caudate and in the rostral putamen in relation to the execution of movements. Monkeys performed self-initiated and stimulus-triggered arm reaching movements in separate blocks of trials. With stimulus-triggered movements, 217 striatal neurons increased their activity after the trigger stimulus (127 in caudate, 90 in putamen). Of these, 68 neurons showed time-locked responses to the trigger stimulus, with a median latency of 60 ms, that were independent of visual or auditory stimulus modalities. Three quarters of responses were conditional on a movement being performed. These responses may participate in neuronal processes through which the reception of a stimulus is translated into the execution of a behavioral reaction. Further, 44 neurons increased their activity before the earliest muscle activity without being clearly time-locked to the stimulus (148–324 ms before movement onset), 55 neurons were activated later before the movement, and 50 neurons were activated after movement onset. With self-initiated movements, 106 striatal neurons showed movement-related activity beginning up to 460 ms before movement onset (52 in caudate, 54 in putamen). Comparisons between the two types of movement were made on 53 neurons with premovement activity beginning more than 500 ms before self-initiated movements. Only one fifth of them also showed movement-related activity with stimulus-triggered movements, including trigger responses. Comparisons among 39 neurons with movement-related activity during self-initiated arm movements showed that about half of them also showed movement-related activity with stimulus-triggered movements. These data demonstrate a considerably segregated population of striatal neurons engaged in the internal generation of movements, whereas processes underlying the execution of movements appear to involve overlapping neuronal populations.

Key words: Basal ganglia – Behavior – Stimulus – Movement – Monkey

Introduction

The preceding report described how neurons in the rostral striatum were activated up to a few seconds before self-initiated movements (Schultz and Romo 1992). The timing of this activity would allow these neurons to participate in the internal generation of movements. Only one third of these neurons were also activated during an instruction-induced preparatory period preceding stimulus-guided movements. This indicates that neurons related to the internal generation of movements are largely separated from neurons with instruction-induced preparatory activity, suggesting a preferential relationship of certain striatal neurons to self-initiated movements. A more comprehensive assessment of this potential selectivity would require also investigating processes occurring in closer temporal relation to the execution of the movement.

Movement-related activity in the striatum may occur in several forms. Besides the activity during the execution of movements consistently found in the sensorimotor putamen (Crutcher and DeLong 1984b; Liles 1985; West et al. 1990), previous studies have described responses in the head of the caudate to visual stimuli eliciting immediate arm, mouth, or eye movement reactions (Aldridge et al. 1980; Rolls et al. 1983; Amalric et al. 1984; Hikosaka et al. 1989; for review see Schultz 1989; Montgomery and Buchholz 1991). A recent study separated the activity during movement execution from the time-locked responses to movement-triggering stimuli and showed that these two types of movement-related activity are present in different populations of neurons in the arm area of the

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sensorimotor putamen (Kimura 1990). Tonically discharging neurons as a particular class of striatal cells are also known to respond to movement-triggering stimuli (Kimura et al. 1984; Apicella et al. 1991).

The present experiments extended the investigation of striatal processes involved in internal movement generation to movement-related activity. We addressed two questions. The first involved whether neurons exhibiting premovement activity before self-initiated movements would also show movement-related activity with stimulus-triggered movements. Such activity following a movement-triggering stimulus could be involved in a movement-related initiation process and particularly needs to be taken into account when studying the internal generation of movements. The second question was whether neurons activated during the execution of self-initiated movements would also show movement-related activity with stimulus-triggered movements. To these ends, two periods of neuronal activity in reference to movement onset were distinguished. With self-initiated movements, activity beginning more than 500 ms before movement onset, and thus before earliest movement-related muscle activity, was defined as premovement activity related to internal generation of movement, whereas increases in activity less than 500 ms before a movement or during movement execution were considered to be movement-related. A similar distinction was made with stimulus-triggered movements, with the movement-triggering stimulus separating the preceding preparatory activity from the following movement-related activity.

Materials and methods

The study was performed on the same three *Macaca fascicularis* monkeys of the preceding report, in which all experimental procedures are described in detail (Schultz and Romo 1992). Briefly, the activity of single neurons was recorded with moveable microelectrodes in the left caudate and putamen during contralateral task performance, while monitoring electromyographic (EMG) activity and eye movements. Upon termination of recording, the animals were deeply anesthetized, their brains were perfused with formaldehyde, and microelectrode positions were reconstructed on coronal histological sections.

In addition to the self-initiated movements and the delayed go no-go task described in the preceding report (Schultz and Romo 1992), this study also used a direct go no-go task. Two small food boxes were mounted in front of the animal at 15° and 27° to the right of the midsagittal plane, respectively. Either one of the boxes opened in a given trial. According to the spatial position of the box, the animal either released a resting key and reached into the box to collect a small morsel of apple, cookie, or raisin (go situation; invariably the lateral box), or remained motionless on the resting key for 3 s (unrewarded no-go situation; invariably the medial box). Instruction lights prior to box opening were not used. Thus, opening of a food box door served as trigger stimulus for the arm movement or as stimulus demanding withholding of movement in no-go trials. Box opening was visible (a vertical upward movement of 40 mm in 20-22 ms), produced a sliding noise, and triggered a 1-kHz sound of rectangular waveform, 100 ms duration, and 90–92 dB intensity measured at the animal's head. Besides this composite stimulus, the three sensory components of the door-opening stimulus were also used separately in go trials. The visual component alone was employed by deleting both the 1-kHz sound and abolishing the noise of the sliding door with a masking noise of 91 dB intensity applied close to the animal's head. The sliding noise served as trigger stimulus alone when the 1-kHz sound was omitted and door opening was invisible because of a cover mounted in front of the box. Only the 1-kHz sound component of door opening was used when the cover was mounted and the masking noise applied. During the recording of each neuron, effective masking of door noise was ascertained by the absence of behavioral reactions to door opening when, in addition, the cover was mounted and the 1-kHz sound deleted.

Two periods for evaluating neuronal relationships to task performance were distinguished for each type of movement. Preparatory activity was defined as activity beginning more than 500 ms before self-initiated movements or beginning before the trigger stimulus in the go no-go task. Activity beginning after these time limits was considered to be movement-related. Onset, duration, and significance of increases in neuronal activity were statistically assessed with the sliding window procedure (Schultz and Romo 1992). Step size and time window were 8 ms and 80 ms, respectively, for activity related to execution of movement. In order to obtain finer temporal resolution for the responses to box opening, their latency, duration, and statistical significance were assessed from the inflections of the cumulative frequency distribution against a line representing control activity, followed by a Wilcoxon test over the duration of the activation against a 250- to 500-ms control period prior to box opening (for details, see Ljungberg et al. 1992). Only neurons tested with at least 10 (up to 64) trials in a given task situation are reported. Depressant responses occurred occasionally but were not further investigated because of the low spontaneous activity of the striatal neurons studied.

EMG latencies following box opening and onsets and offsets of saccadic eye movements were determined off line by single-trial analysis using a moveable cursor on a computer screen. The median (50th percentile) was determined as a single numerical value for distributions of neuronal and behavioral data. Differences in distributions were assessed with two-tailed versions of the Mann-Whitney *U*-test for unpaired and the Wilcoxon test for paired data.

Results

Activity was recorded from 1226 slowly discharging neurons in the head of caudate and the rostral putamen (Table 1). Stimulus-triggered movements were tested with 1197 neurons (851 in the delayed go no-go task, 361 in the direct reaction go no-go task, including 15 in both tasks). Data from these two task variations were pooled because of insignificant differences in most parameters. Self-initiated movements were investigated with 683 neurons, of which 654 were studied with both stimulus-triggered and self-initiated movements.

Table 1. Numbers of neurons tested

	Caudate	Putamen	Sum
Delayed go no-go task	497	354	851
Direct reaction go no-go task	215	146	361
Both delay and direct task	10	5	15
Subtotal stimulus-triggered movements	702	495	1197
Self-initiated movements	390	293	683
Both stimulus-triggered and self-initiated movements	375	279	654
Total	717	509	1226

Stimulus-triggered movements

The activity of 217 striatal neurons increased after the trigger stimulus. Of these, 68 neurons showed time-locked responses to the trigger stimulus (41 in the direct reaction, 27 in the delay task). These responses were characterized by their close temporal relationship to stimulus onset and the lack of relation to onset of muscle activity and movement, as judged from visual inspection of individual trials referenced to these different task components. Most of these responses were restricted to go trials (Fig. 1A). Only 17 neurons were also activated in no-go trials in

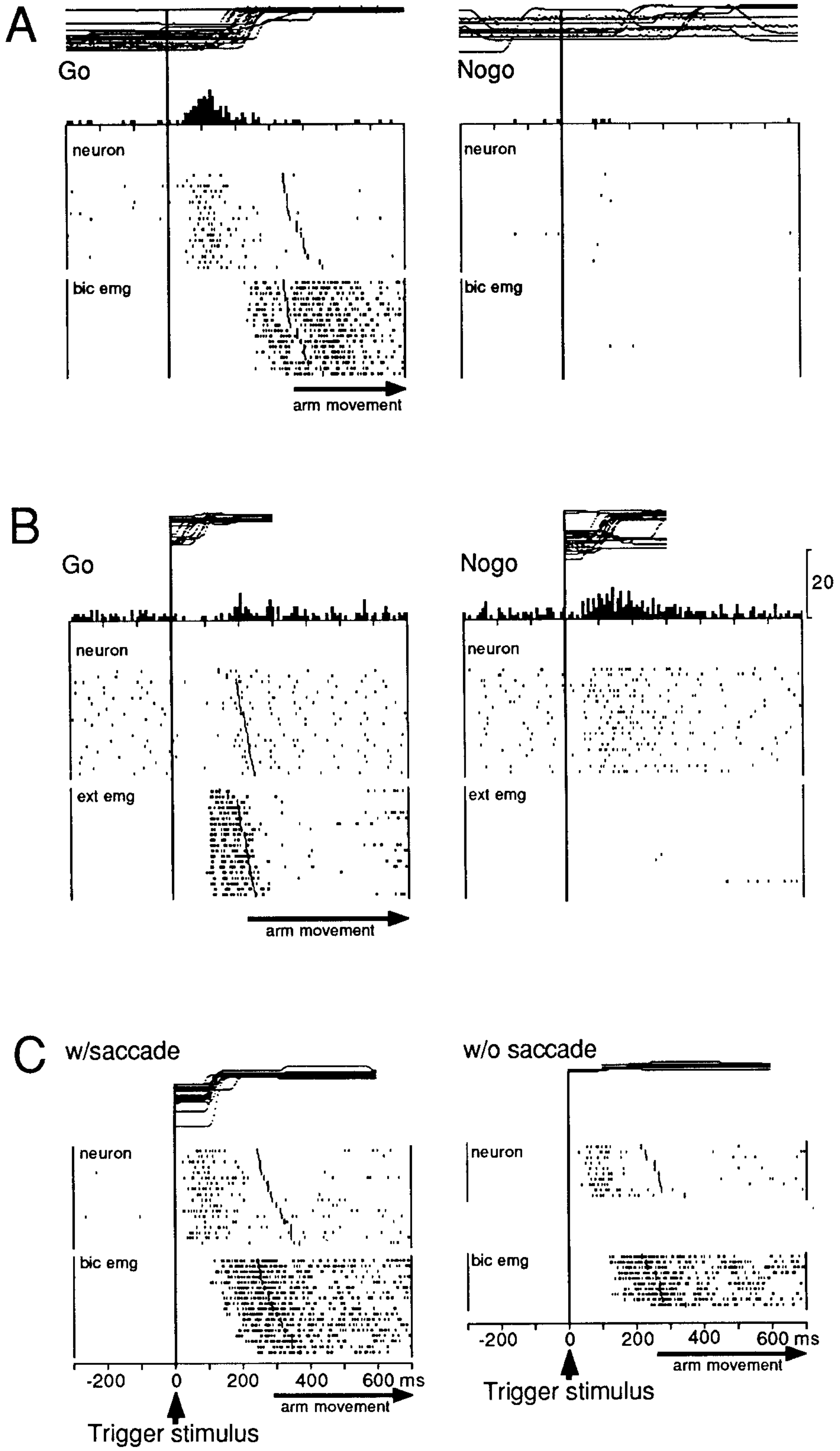

Fig. 1A–C. Responses of three striatal neurons to trigger stimuli. **A** Response to opening of the food box serving as trigger stimulus for arm and eye movements, but lack of response in no-go trials (*Nogo*) without following arm movement (putamen neuron tested in delayed go no-go task). **B** Response of caudate neuron is restricted to no-go trials without following arm movement. There is only a mild depression in go trials with arm movements. **C** Response to trigger stimulus in caudate neuron is unrelated to saccadic eye movements. Eye movements occurred in close association with the reaching movement, unless animals incidentally fixated the stimulus when it came on. Trials were separated for analysis according to the presence (*left*) or absence (*right*) of saccades, and only go trials are shown. Go and no-go trials in **A–C** alternated randomly during the experiment and were separated for analysis. All go trials are ordered according to reaction time (from stimulus to movement onset), both for neuronal and electromyographic (*emg*) rasters, whereas no-go trials are shown in original order downward. Onset of arm movement (key release) is indicated by *short vertical lines* in raster displays, and below the time scale. Individual parts show from the top: horizontal electrooculogram, perievent time histogram (**A, B**) of the neuronal impulses shown in raster display below (*neuron*), rasters from activity of biceps brachii (**A, C**; *bic emg*) or extensor digitorum communis muscles (**B**; *ext emg*) contralateral to neuronal recording. Each dot denotes the time of a neuronal impulse or emg activity exceeding a preset level whose distance to stimulus onset corresponds to the real-time interval. Each raster line shows one trial. Eye movements, neuronal impulses, and emg activity were recorded simultaneously. Vertical calibration is 20 impulses/bin for all histograms

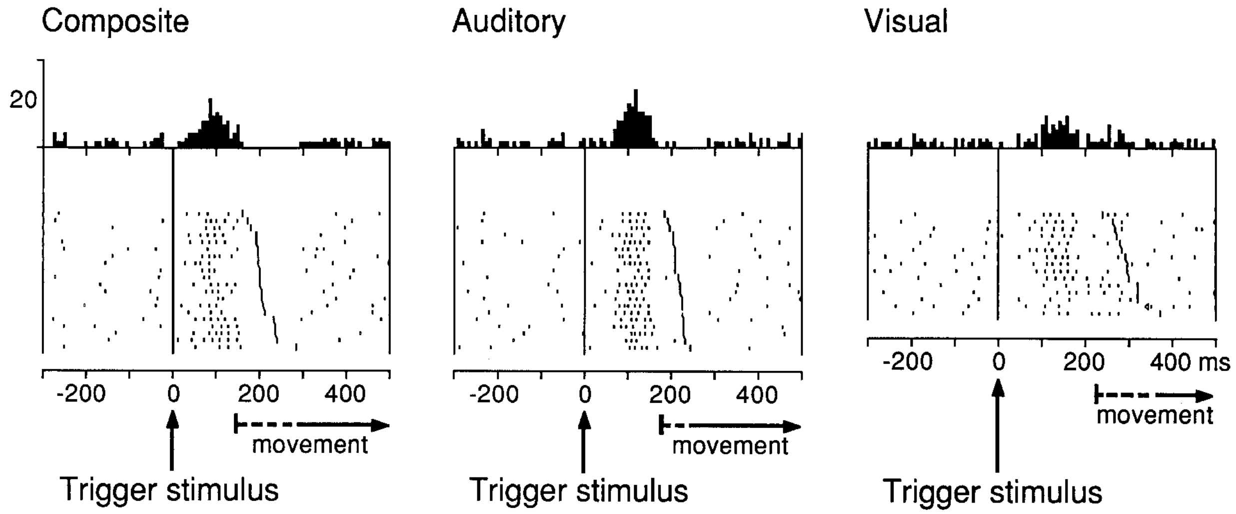

Fig. 2. Polymodal character of response to trigger stimuli. The response of this caudate neuron is maintained when the composite door-opening stimulus is separated into its individual sensory components. *Auditory* refers to the sliding noise component (1 kHz component not tested with this neuron). Only data from go trials are shown

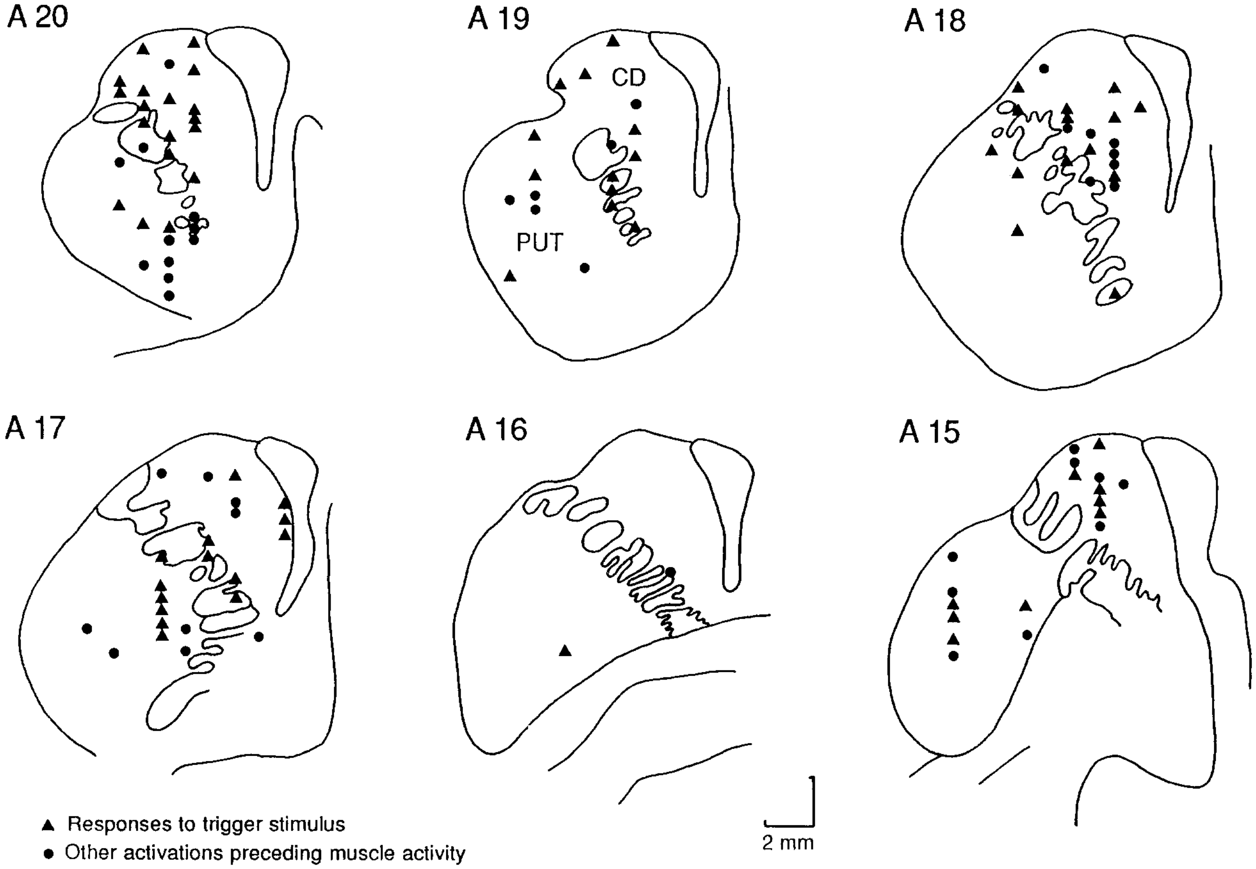

Fig. 3. Recording positions of striatal neurons showing early movement-related activity with stimulus-triggered movements. *Triangles* indicate neurons with time-locked responses to the trigger stimulus ($n = 68$), whereas *circles* refer to activity which began before earliest muscle activity (> 140 ms before movement onset) but was not clearly time-locked to the stimulus ($n = 44$). Positions of neurons from all three monkeys are drawn on the outlines of coronal sections from the left brain of one monkey at approximately corresponding positions. Sections are labeled in anteroposterior stereotaxic planes (*A15–A20*). *CD*, caudate; *PUT*, putamen

which arm movement reactions were absent. An additional 9 neurons responded exclusively in no-go trials (Fig. 1B). All neurons responding in no-go trials lacked responses to the same stimuli outside the task. In all but two neurons, responses were independent of saccadic eye movements (Fig. 1C). Separation of the sensory components of the trigger stimulus revealed that neurons responding to the composite stimulus typically were driven by each of the visual, door noise, and 1-kHz sound components (4, 11, and 11 neurons tested, respectively; Fig. 2). Trigger responses showed latencies of 28–176 ms (median 60 ms) and began 148–360 ms before movement onset (median 276 ms). The responses in 15 neurons lasted beyond movement onset. These parameters differed insignificantly between caudate and putamen ($P > 0.25$, Mann-Whitney test). Responding neurons were distributed over the entire rostral parts of both caudate ($n = 47$) and putamen ($n = 21$; Fig. 3).

Movement-related activity in the remaining 149 neurons began before movement onset without being clearly time-locked to the trigger stimulus (54 neurons in caudate, 45 in putamen) or after movement onset (26 in caudate, 24 in putamen). In 44 of these neurons, increases in activity began before the earliest time of muscle activity observed in any monkey (140 ms), i.e., 148–324 ms before movement onset (median 204 ms; Fig. 4). These neurons were found in rostral parts of both caudate ($n = 23$) and putamen ($n = 21$) where they were intermingled with neurons responding to the trigger stimulus (Fig. 3). Activity in the 50 neurons beginning after movement onset showed a median onset time of 158 ms (range 4–1092 ms) and lasted for 328 ms (range 120–1264 ms). All measures in the 149 neurons differed insignificantly between caudate and putamen ($P > 0.2$).

Self-initiated movements

Neuronal activity increasing less than 500 ms before movement onset or during the movement was considered to be movement-related, rather than representing premovement activity. Activity of this type was found in 106 striatal neurons (52 in caudate, 54 in putamen), many of which were found in the arm area of putamen and in the head of caudate, whereas fewer were located at the rostral pole of striatum (Fig. 5). Quantitative evaluations of the movement-related activity of 47 neurons (28 in caudate, 19 in putamen) showed that their activity increased 12–460 ms before movement onset in 22 neurons, and 12–604 ms after movement onset in the remaining 25 neurons (median 12 ms after movement onset for all 47 neurons; Fig. 6A). These activations lasted 104–3200 ms (median 424 ms). All measures differed insignificantly between caudate and putamen ($P > 0.07$). Movement-related activity occurred in conjunction with premovement activity in eight neurons, either temporally separated

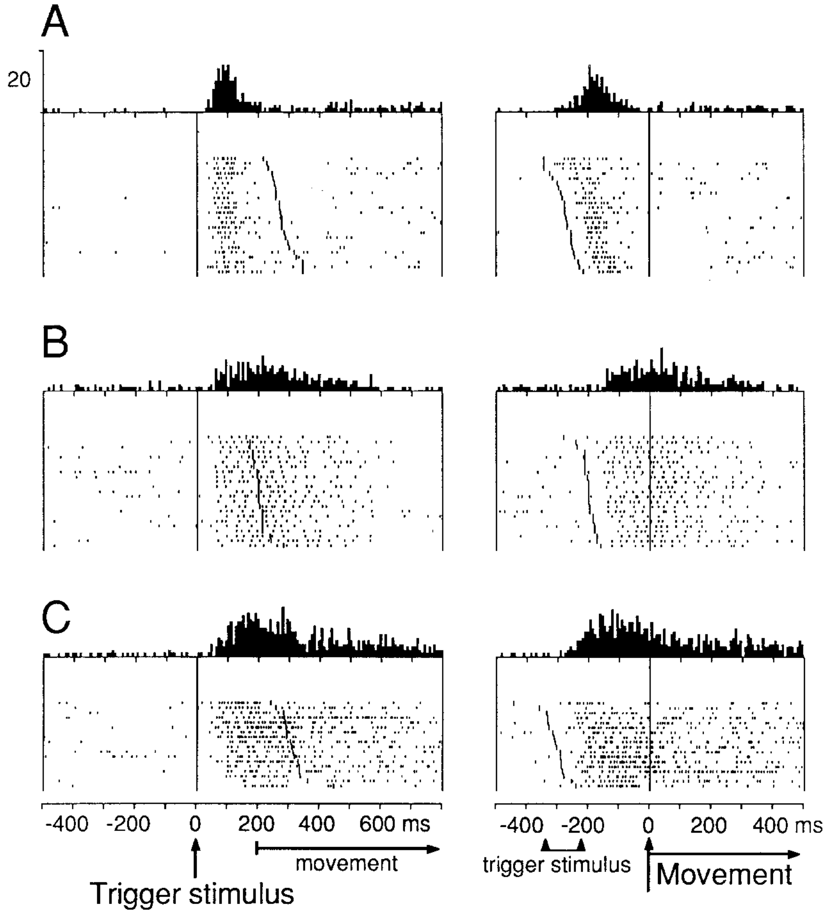

Fig. 4A–C. Different stimulus relationships of movement-related striatal neurons. **A** Response of a putamen neuron whose onset is time-locked to the trigger stimulus (*left*). This relationship is also evident when the same data are referenced to movement onset (*right*). **B, C** Early movement-related activity of two putamen neurons that was not clearly time-locked to the stimulus. Graphs on the *left* and *right* show neuronal data from the same trials referenced to the trigger stimulus and to movement onset, respectively. Trials are ordered according to reaction time

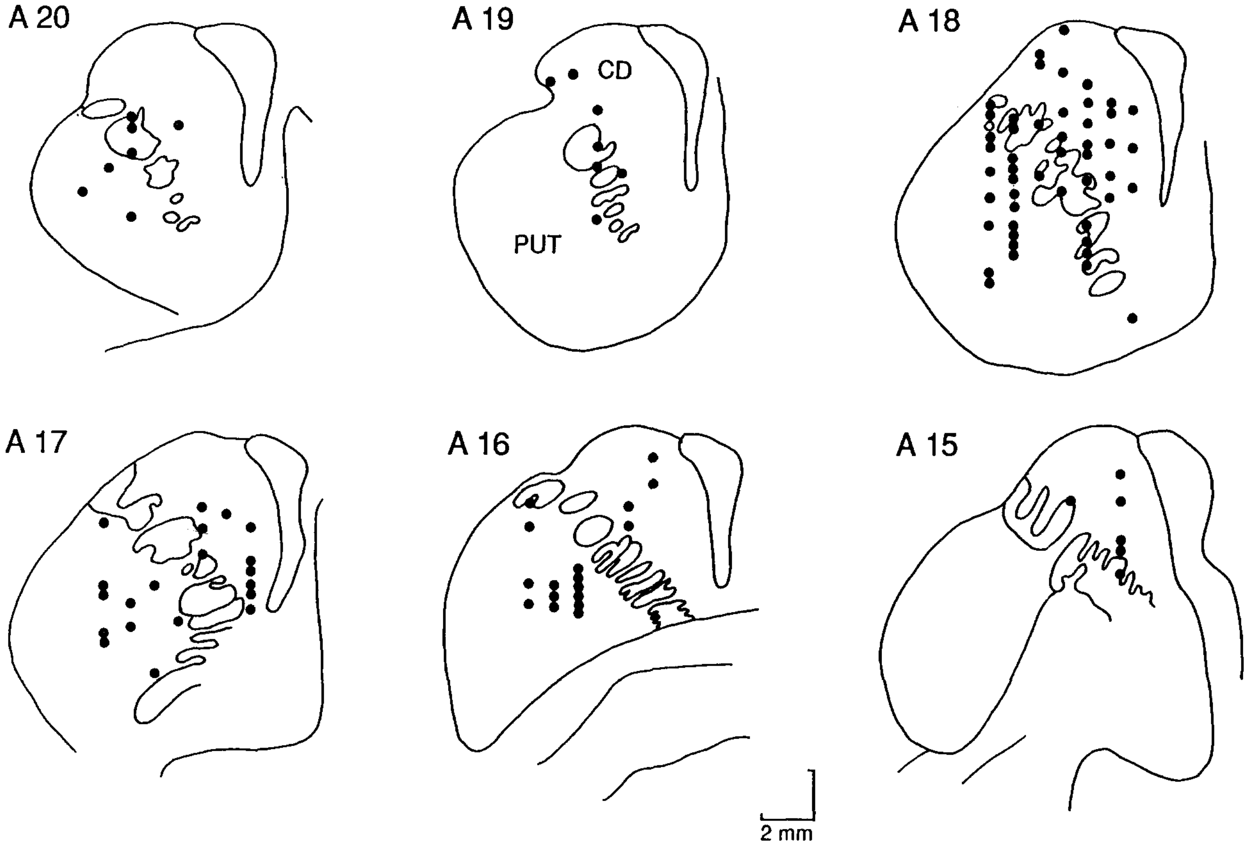

Fig. 5. Recording positions of striatal neurons with movement-related activity during self-initiated movements (*dots*). Positions of neurons from all three monkeys are drawn on coronal sections (*A15–A20*) from the left hemisphere of one monkey. *CD*, caudate; *PUT*, putamen

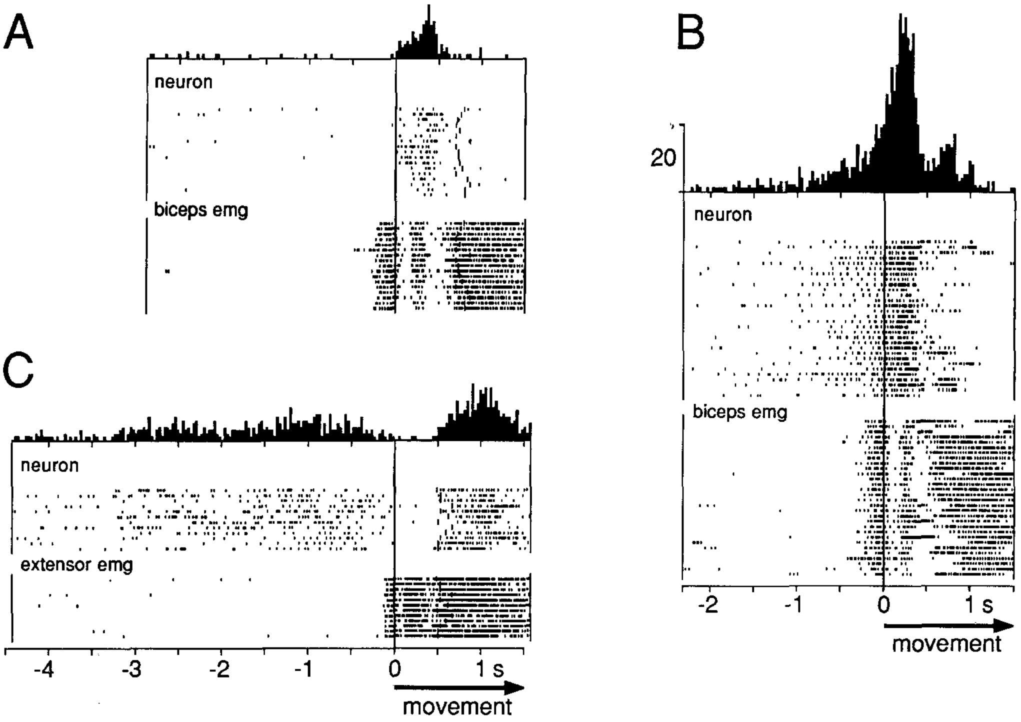

Fig. 6A–C. Movement-related activity during self-initiated movements. **A** Activity of a putamen neuron during the movement. **B** Activity of a movement-related putamen neuron showing, also, modest premovement activity. **C** Activity during the movement temporally separated from premovement activity from premovement activity (Fig. 6C) or superimposed on comparatively modest premovement activity (Fig. 6B).

Comparison between self-initiated and stimulus-triggered movements

A total of 53 neurons with premovement activity before self-initiated movements were also studied with stimulus-triggered movements (25 in caudate, 28 in putamen). Of these, 11 neurons (21%) showed movement-related activity with stimulus-triggered movements (7 in caudate, 4 in putamen), including 4 neurons with time-locked responses to the trigger stimulus (Fig. 7). Six of the 11 neurons also showed sustained or transient preparatory activity in the delay task. Together with the results from the companion report (Schultz and Romo 1992), these data allow us to calculate the final number of neurons that showed exclusively premovement activity preceding self-initiated movements in the present tasks. Of the 53 neurons activated more than 500 ms before self-initiated movements that were tested in the delayed go no-go task, 18 neurons showed sustained and an additional 4 transient activations during the delay. Together with an additional 5 neurons showing movement-related activity with stimulus-triggered movements, this results in a total of 27 of the 53 neurons showing some activations in both tasks. Thus, 26 of the 53 neurons (49%) activated more than 500 ms before self-initiated movements lacked any activations in a stimulus-guided task (10 neurons in caudate, 16 in putamen).

A total of 39 neurons with movement-related activity during self-initiated arm movements were also tested with stimulus-triggered movements (23 in caudate, 16 in putamen). Of these, 22 neurons showed movement-related activity with stimulus-triggered movements (13 in caudate, 9 in putamen; Fig. 8), of which 5 neurons had time-locked responses to the trigger stimulus and 8 neurons also showed sustained or transient preparatory activity in the delay task. An additional 7 of the 39 neurons were activated separately during the preparatory period of the delay task or responded transiently to the instruction light. With a total of 29 neurons being activated in both tasks, only 10 of the 39 neurons (26%) with movement-related activity during self-initiated movements lacked any activations in a stimulus-guided task (7 neurons in caudate, 3 in putamen).

Discussion

The present study resulted in three principal findings: (1) Neurons with time-locked responses to trigger stimuli, as

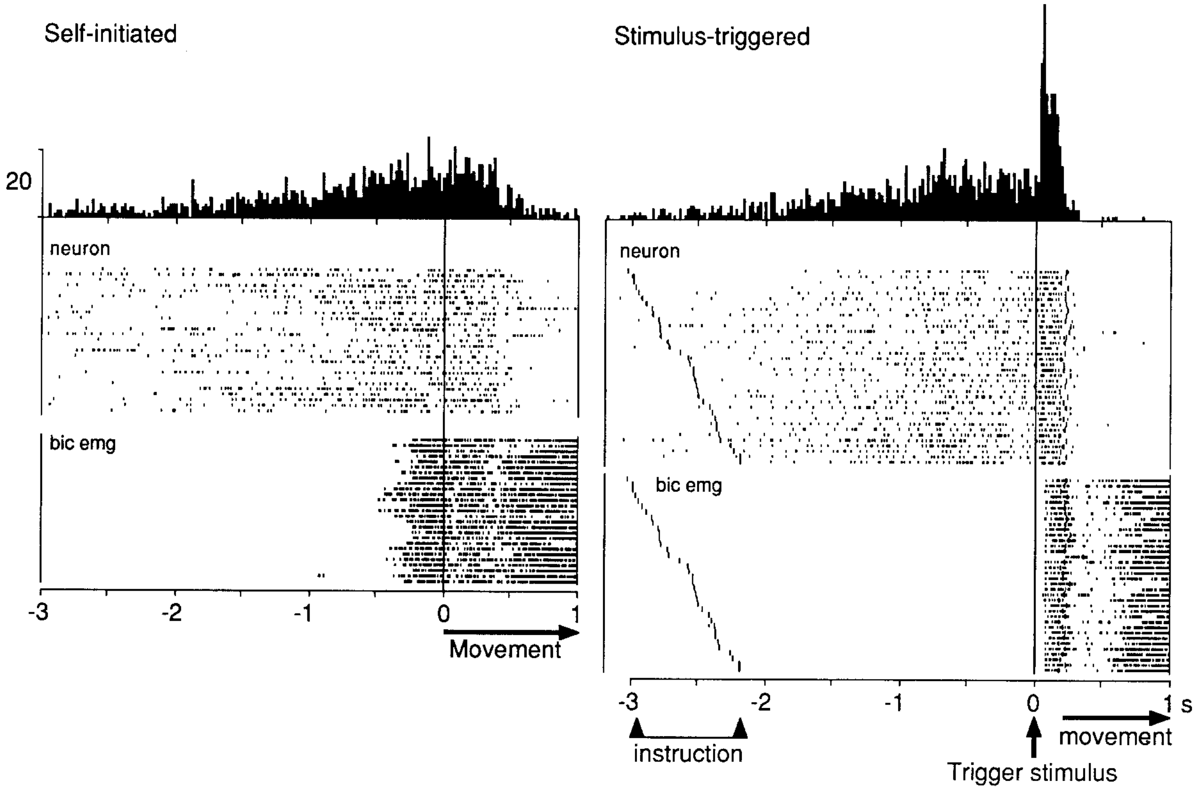

Fig. 7. Conjoint task-related activity in a putamen neuron with different types of movement. The neuron shows premovement activity preceding self-initiated movements (*left*). With stimulus-triggered movements, the same neuron displays movement-related activity and separate instruction-induced preparatory activity preceding the movement (*right*). Trials on the *left* and *right* were collected in separate blocks. Impulses on the *left* are referenced to the time of movement onset (key release) and on the *right* to onset of the trigger stimulus. *Vertical bars* in the raster to the *left* and *right* of the trigger stimulus indicate onsets of the instruction and arm movement, respectively. Trials with stimulus-triggered movements are ordered according to instruction-trigger intervals. *bic emg*, biceps electromyographic activity

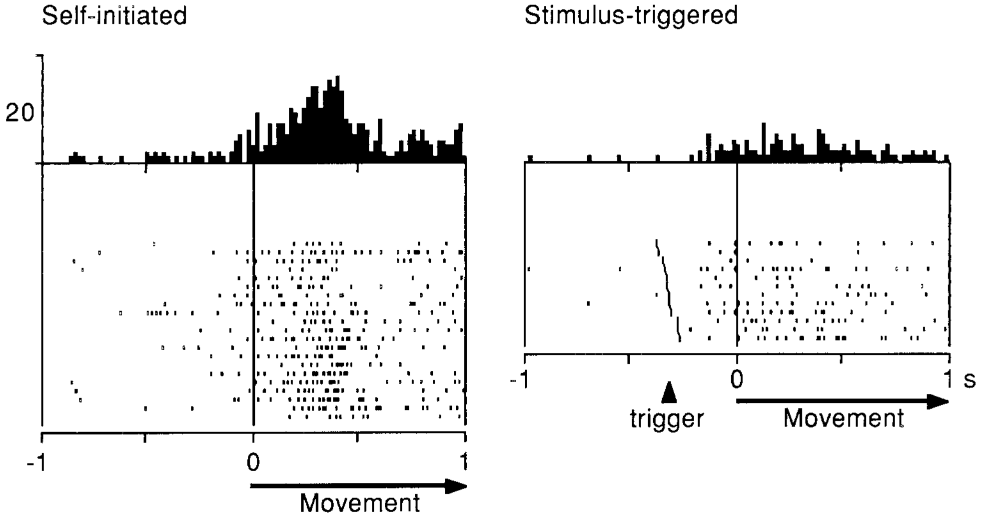

Fig. 8. Conjoint movement-related activity in a putamen neuron with different types of movement. This neuron shows an activation during both self-initiated (*left*) and stimulus-triggered movements (*right*). Trials shown to the *left* and *right* were collected in separate blocks. Trials to the *right* are ordered according to reaction time

well as a limited number of other striatal neurons, increased their activity before the earliest muscle activity. These neurons may participate in the generation of movements in response to external stimuli. (2) Only one fifth of striatal neurons with premovement activity preceding self-initiated movements showed movement-related activity with stimulus-triggered movements. This strengthens the suggestion that striatal activity related to the internal generation of movements is largely segregated on the level of individual neurons from that participating in stimulus-triggered movements. (3) Slightly more than one half of striatal neurons which exhibited movement-related activity during self-initiated movements also showed movement-related activity with stimulus-triggered movements. Thus, striatal activity related to the execution of self-initiated movements was less specific for that particular mode of movement generation than premovement activity.

Some responses of striatal neurons to the trigger stimulus were stimulus locked, were independent of the visual and auditory modality, and occurred before earliest movement-related muscle activity. The responses in most neurons were conditional on the movement being actually performed and were absent in no-go trials. These results are in general agreement with earlier findings on striatal responses to movement-triggering stimuli (Aldridge et al. 1980; Rolls et al. 1983; Amalric et al. 1984; Hikosaka et al. 1989; Montgomery and Buchholz 1991). The finding of time-locked responses to the trigger stimulus in both the caudate and putamen extends previous similar results on putamen neurons and corroborates the notion that these neurons adhere to a separate category of striatal movement-related neurons than those whose activity is more closely related to the time of movement execution (Kimura 1990). In these respects, striatal responses to movement-triggering stimuli differ from activity in the motor cortex and in some neurons of the cerebellar dentate nucleus that show a close temporal relationship to the following arm movement but are not time-locked to the teleceptive trigger stimulus (Evarts 1966; Lamarre et al. 1983; Chapman et al. 1986). Thus, striatal neurons activated before earliest muscle activity and in close temporal relation to the trigger stimulus may be involved in the stimulus-induced initiation of movement by which the reception of a movement-triggering signal is transferred into the generation and initiation of an ensuing behavioral reaction. Striatal neurons with this activity would be functionally situated closer to the trigger signal and further 'upstream' from the final contraction of individual muscles, as compared to motor cortical or certain dentate neurons. However, recent experiments showed that some putamen neurons lost the initial stimulus-locked response component when an instruction cue preceded the stimulus (Kimura 1990), suggesting that these neurons may not be unconditionally involved in movement initiation. Activity in some neurons of the globus pallidus and pars reticulata of the substantia nigra slightly precedes earliest muscle activity (Georgopoulos et al. 1983; Schultz 1986; Nambu et al. 1990; Mink and Thach 1991b), suggesting that activity related to the initiation of stimulus-triggered movements arrives at the principal output stations of the striatum and may leave the basal ganglia.

The observed responses may enter the striatum through cortical inputs. Neurons responding specifically to movement-triggering stimuli are found in several areas of the frontal cortex, such as the premotor and supplementary motor cortex (Tanji and Kurata 1982; Kurata and Tanji 1985; Romo and Schultz 1987; 1992), dorsolateral prefrontal cortex (Sakai 1974; Kojima 1980; Boch and Goldberg 1989), and orbitofrontal cortex (Thorpe et al. 1983). Prefrontal neurons responding in a visual reaction time task are found in layer V, which is a major source of corticostriatal projections (Sawaguchi et al. 1989). Some of these responses have similar latencies to those observed here (50–200 ms, Sakai 1974; 40–200 ms, Tanji and Kurata 1982; 50–100 ms, Sawaguchi 1987). Responses in the parietal association cortex resemble the present trigger responses to a certain extent. For example, some neurons of area 5 respond to deep somatosensory input only when an arm movement follows (Chapman et al. 1984), and neurons of area 7 show enhanced visual responses when the stimulus becomes a target for saccadic eye movements (Yin and Mountcastle 1977; Robinson et al. 1978). Although behavioral relationships of posterior parietal neurons differ in other respects from those in the striatum, the cited responses may contribute to the activation of striatal neurons. The widespread and interdigitating projections of the frontal and parietal cortical areas to the caudate and putamen (Selemon and Goldman-Rakic 1985) may give rise to the responses presently observed in several parts of the striatum. By contrast, the input from dopamine neurons does not appear to drive the majority of observed responses in the striatum, since dopamine neurons respond to trigger stimuli independent of movement or no-movement reactions (Schultz and Romo 1990).

Dopamine neurons of the substantia nigra show specific responses that provide a neurophysiological basis for the involvement of dopamine systems in behavioral reactivity (Schultz and Romo 1990). Although the nature of the present striatal responses suggest a circumscript movement-related function rather than a more basic motivational mechanism, the short response latencies of some striatal neurons were comparable to those of dopamine neurons (50–90 ms). Similar to most dopamine cells, a quarter of striatal neurons were activated by trigger stimuli in both go and no-go trials and lacked responses outside the task. Striatal activations may participate in driving dopamine neurons via an excitatory, substance P-ergic projection from striatal striosomes to the pars compacta of the substantia nigra (Davies and Dray 1976; Walker et al. 1976; Mroz et al. 1977; Graybiel et al. 1981; Gerfen 1984). The extent to which these striatal influences could participate in inducing the specificity of responses in dopamine neurons remains to be elucidated, in particular as the functions of other inputs to the substantia nigra are not yet well understood.

Activity closely related to the time of execution of stimulus-triggered or self-initiated arm movements occurred in both the caudate and putamen and was not restricted to the arm area of the posterolateral putamen in which activity during movements is frequently found (Crutcher and DeLong 1984a; Liles 1985; Kimura 1990). Because of the design of the present task, it is unknown to what extent this activity encodes particular movement parameters. Activity during the execution of stimulus-triggered movements is frequently found in frontal cortical areas rostral to primary motor cortex, which project heavily to the regions presently explored in the caudate and putamen. A considerable fraction of neurons in the premotor and supplementary motor cortex are activated during movements or isometric contractions, such as during the precision grip (Smith 1979), wrist movements (Kubota and Hamada 1978; Tanji and Kurata 1982), key pressing (Weinrich and Wise 1982; Kurata and Tanji 1985, 1986; Kurata 1989) , and arm reaching (Godschalk et al. 1981; Romo and Schultz 1987; 1992). Movement-related activity in the prefrontal cortex occurs during the performance of delayed response tasks (Niki 1974; Watanabe 1986), reaction time tasks (Sakai 1974; Kojima 1980; Ito 1982; Sawaguchi 1987; Sawaguchi et al. 1989), and wrist tracking movements (Funahashi 1983). This may suggest that some of this striatal activity is driven by frontal cortex input related to more general aspects of task execution and may not encode specific parameters of muscle activity or movement.

Relatively few of the striatal neurons exhibiting premovement activity preceding self-initiated movements also showed movement-related activity with stimulus-triggered movements (21%). A subset of these neurons responded to trigger stimuli. The companion report demonstrates that only about one third of the neurons activated before self-initiated movements also showed sustained or transient activity during the preparatory period preceding stimulus-guided movements (Schultz and Romo 1992). When these results are combined, and a certain overlap of activations in the stimulus-guided task is taken into account, about one half of striatal neurons with premovement activity preceding self-initiated movements did not show other modulations in any other task employed. This demonstrates a considerable specificity of certain striatal neurons for the internal generation of movements and suggests that largely different modes of neuronal processing are operational during the generation of the two types of movement. Striatal neurons may be selectively activated during the generation of movement according to the type of movement, such that neurons activated before self-initiated movements participate in the internal movement generation process, whereas neurons activated during the instruction-induced preparatory period or responding to the trigger stimulus are involved in neuronal processes through which the reception of a stimulus is translated into the execution of a movement. These considerations suggest that the striatum may not play a preferential role in the generation of one particular type of movement, as some pathophysiological findings may suggest. Rather, the different modes of neuronal processes during the generation of movements appear to engage separate striatal circuits subserving the various types of movements.

In contrast to this partial selectivity for premovement activity, slightly more than one half of striatal neurons activated during the execution of self-initiated movements did also covary with stimulus-triggered movements. Together with the preparatory activity preceding stimulus-guided movements, only one quarter of neurons with activity related to the execution of self-initiated movements lacked any activation with stimulus-guided movements. This suggests a lack of relationship of movement-related activity to the particular movement generation mode. A partial overlap of activity during the execution of self-paced and stimulus-triggered movements was also found in neurons of the globus pallidus (Mink and Thach 1991a), suggesting that this feature might be common to different nuclei of the basal ganglia.

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