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Somatosensory-Motor Neuronal Activity in the Superior Colliculus of the Primate

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Summary

The superior colliculus (SC) in primates plays an important role in orienting gaze and arms toward novel stimuli. Here we ask whether neurons in the intermediate and deep layers of the SC are also involved in the interaction with objects. In two trained monkeys we found a large number of SC units that were specifically activated when the monkeys contacted and pushed a target that had been reached with either hand. These neurons, however, were silent when the monkeys simply looked at or reached for the target but did not touch it. The activity related to interacting with objects was spatially tuned and increased with push strength. Neurons in the SC with this type of activity may be involved in a somatosensory-motor feedback loop that monitors the force of the active muscles together with the spatial position of the limb required for proper interaction with an object.

Introduction

The superior colliculus (SC) is a multilayered, multimodal sensorimotor structure of the mammalian midbrain, and a presumed homolog of the optic tectum plus subtectal and tegmental regions of other vertebrate groups, containing topographical maps of the visual, auditory, and somatosensory world (Updyke, 1977; Meredith and Stein, 1986; Jay and Sparks, 1987b). It plays an important role in visually guided behavior, and due to the integration of multimodal sensory information, the SC is involved in orienting responses toward an object of interest of any modality (Wurtz and Albano, 1980; Jay and Sparks, 1987a, 1987b; Schiller and Tehovnik, 2001; Stein et al., 2001). The SC guides oculomotor processes, i.e., the initiation and control of saccadic eye movements (for a review see Sparks and Hartwich-Young, 1989), and contributes to skeletomotor functions. The activity of SC neurons is linked to movements of the head (Roucoux et al., 1980; Cowie and Robinson, 1994; Pare et al., 1994; Freedman et al., 1996), neck (Grantyn and Berthoz, 1985), and front leg (Abrahams and Rose, 1975; Cowie and Robinson, 1994; Werner, 1993; Werner et al., 1997a, 1997b). Neurons with arm movement-related activity that code the arm trajectory in two different reference frames (gaze dependent or gaze independent) were described in the SC earlier (Stuphorn et al., 1999; Lünenburger et al., 2000, 2001). Also, if the colliculus is involved in skeletomotor functions, one might expect that it receives cutaneous or proprioceptive feedback similar to other skeletomotor areas (Martin et al., 1993; Arts and Cools, 2000).

Despite the well-described function of the SC in reaching movements, we have no information whether the SC plays a role in grasping, holding, or pushing the reached targets. In most manipulations, we use our fingertips to apply time-varying forces to the target object in controlled directions. The posterior parietal cortex (PPC), which is also involved in reaching and is intimately linked to the SC, clearly contributes to encoding the direction of fingertip forces for grasp stability during manipulation (Birznieks et al., 2001; Ehrsson et al., 2003). Does the SC play a similar role?

To answer these questions, we aimed to investigate whether we could find SC units that were active during contact with and pushing of a button that had been reached for. Our results led to the description of a functional neuronal type in the SC of the primate brain, denominated by us as the "somatosensory-motor neuron."

Results

Identifying Somatosensory-Motor Neurons

We recorded single neurons in the monkey SC that exhibited significant modulation of their discharge rate during specific phases of visually guided reaches (Figure 1). A surprisingly high proportion of the SC units that modulated during the reach tasks were significantly distinct from previously described reach neurons (Werner, 1993; Werner et al., 1997a, 1997b; Stuphorn et al., 1999; Lünenburger et al., 2001) in that they responded vigorously when the monkey made contact with or pushed against the central and/or peripheral targets on the working panel. They were inactive or only slightly active during the reach (arm-moving) phases. These neurons were also not sensitive to visual stimuli and were inactive or only weakly activated by fixation or saccades. Because the activity of these neurons showed no relationship to visual stimuli or saccades, but instead required self-accomplished physical contact with the target, we denominated them or their activity as somatosensory-motor. In reach paradigm *A*, 12 SC cells were recorded, all of which exhibited their highest activity during contact with the target (Figure 2). In order to investigate the nature and the coding properties of this activity, we modified the task in reach paradigm *B* by implementing push buttons requiring different push forces in five different spatial positions; we then recorded another 118 neurons.

The typical activity profile of a somatosensory-motor neuron in reach paradigm *B* is shown in Figure 3. The neuron was not active before contact with the target, in the fixation phase, or in the first hand-moving phase. The first sharp increase in discharge rate occurred 50 to 100 ms after contact with the central target and continued until the end of the push phase. With the beginning

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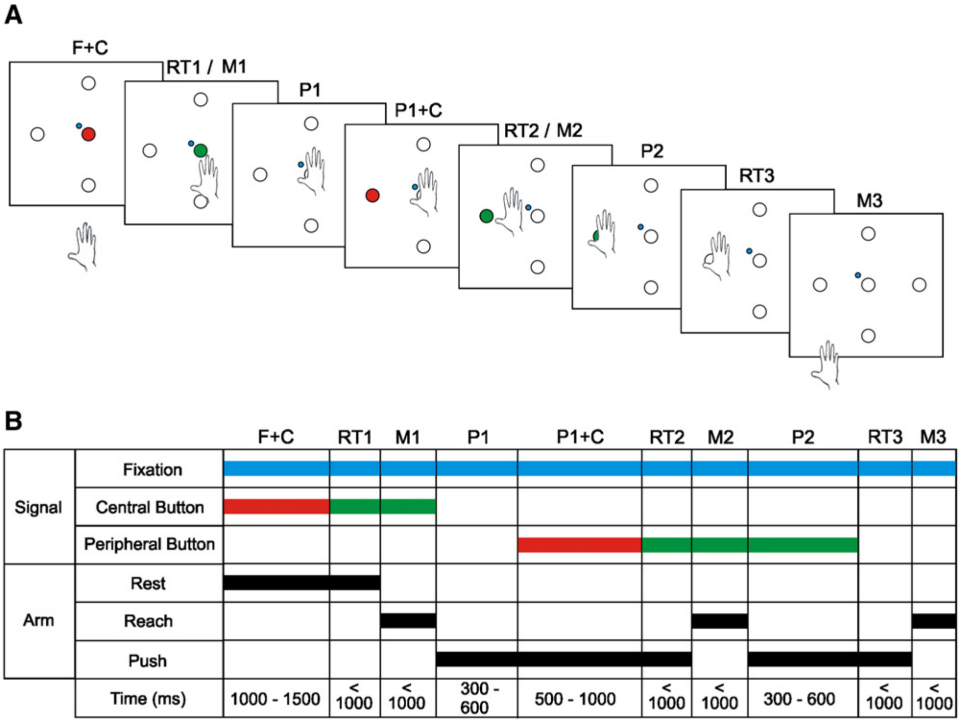

Figure 1. Schematic Drawing of the Visually Guided Reach Paradigm *B* Performed by the Monkey

(A) Spatial arrangement of the reach task. The typical sequence in the reach paradigm was as follows: (1) Fixation + Cue phase (F+C): the animal placed his hand at the start position and fixated on a blue spot on the screen. The central target for the hand turned red immediately. (2) Reaction time 1 (RT1): the central push button changed to green. The time between the appearance of the green go signal to the start of the arm movement is the reaction time 1. (3) Move phase 1 (M1): first arm movement to the central push button. (4) Push phase 1 (P1): the animal pushed the central button without getting a new target signal. (5) Push 1 + Cue phase (P1+C): one of the 4 peripheral push buttons turned red. (6) Reaction time 2 (RT2): the red peripheral push button changed to green. The time between the appearance of the green go signal to the start of the arm movement is the reaction time 2. (7) Move phase 2 (M2): the monkey performed the second arm movement to the green peripheral push button. (8) Push phase 2 (P2): the animal had to press the peripheral button until the green signal turned off. (9) Reaction time 3 (RT3): this phase extends from the extinction of the green hold signal to the beginning of the movement back to the start position. (10) Move phase 3 (M3): the monkey placed his hand back to the start position.

(B) The temporal arrangement of the paradigm. The visual signals that guide the paradigm have the same color codes as those in Figure 1A. The thick black lines denote the arm actions.

of the second arm movement, the activity was strongly attenuated and reappeared with the second push phase at the peripheral target. The activity was attenuated again in the third arm movement phase back to the start position, and low spontaneous or no activity prevailed until the first push phase of the next trial.

The time course of somatosensory-motor neuron activity coincided with the monkey maintaining a fixed reach (hold), making contact with the button, and pressing of the button. We therefore investigated in paradigm *C* whether the somatosensory-motor neurons were also active when the monkey actively held his arm up by the target without contacting or pressing it. We found consistently higher neuronal activity during the push phase than during the hold phase. Two types of somatosensory-motor neurons could be distinguished by their neuronal activity in the hold phase (Figure 4A). The large majority of the cells (13 out of 16) exhibited vigorous responses during the push phase, but were not or only very weakly active during the hold phase (analysis of variance [ANOVA], $p < 0.05$ comparing push and hold phase). The minority of the neurons (3 out of 16) were moderately activated during the hold as well as the push phase. Even here the elevation of the somatosensory-motor activity was higher during the push (though not significantly; ANOVA, $p > 0.05$) than during the hold phase.

All of the 130 somatosensory-motor neurons (12 in paradigm *A*, 102 in paradigm *B*, and 16 in paradigms *B* and *C*) investigated in the two monkeys were located in the intermediate and deep layers of the SC, between 1.2–4 mm under the collicular surface (median = 3.1 mm); i.e., in the same depths as the reach neurons (median = 2.8 mm, range: 1.4–4 mm).

Control for Cutaneous and Proprioceptive Responses

In these investigations we searched for cutaneous fields on the arm, hand, or finger surface by light touches and strokes. We also looked for proprioceptive influences similar to those occurring during the active push by moving the arm of the animal passively or by pushing against the shoulder to stretch the neck, shoulder, or trunk muscles. We could record the activity of 54 out of the 130 somatosensory-motor units during these manipulations. Only two of these neurons were responsive to somatosensory stimulation of the body surface, specifically at the palms and the fingers of the monkey. However,

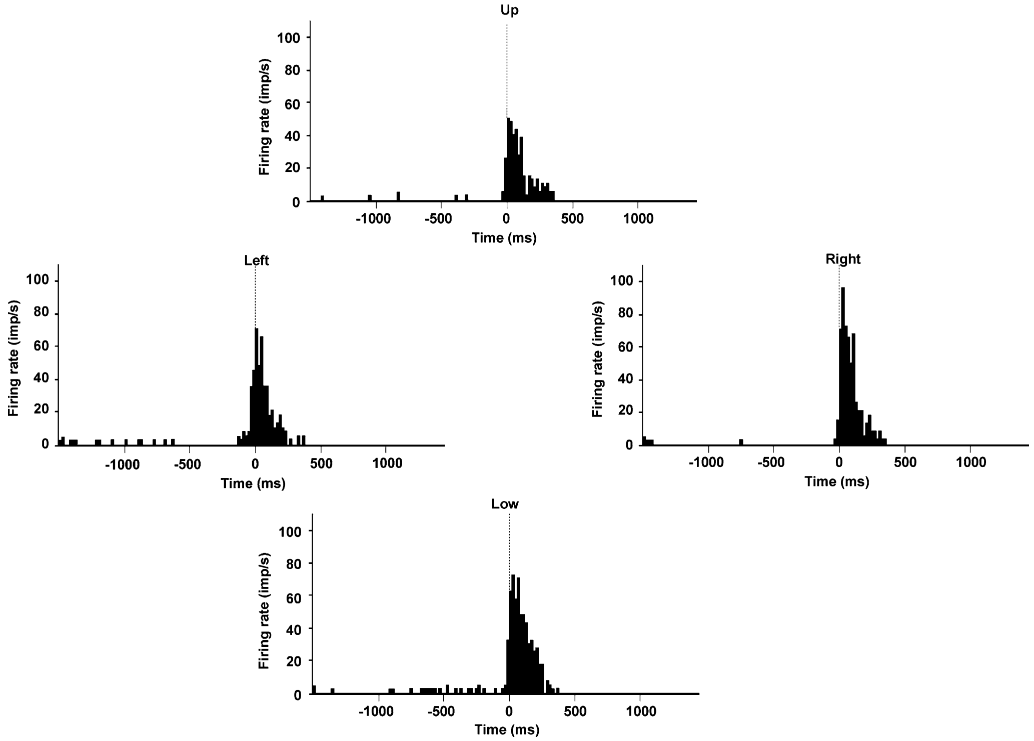

Figure 2. Neuronal Activity in a Primate's Superior Colliculus when His Hand Contacts a Target

Peristimulus time histograms (PSTH, 20 ms bins) of activity of a single somatosensory-motor neuron in paradigm *A*. The abscissa represents the time relation of the neuronal activities (ms), while the ordinate represents the firing rate (imp/s) of the unit. The data are aligned to time t = 0 ms, when the monkey's hand made contact with the target. Note that the activity of this neuron is restricted to the contact phases. Moreover, this neuron showed a significant difference between its activity levels for different target locations, with a preference for the right target.

about half of the 54 neurons were activated when the experimenter moved the arm of the monkey passively (22 out of 38) or pushed strongly against the shoulder (5 out of 16, Figure 4B). We subjectively estimated that the higher the monkey's arm was passively lifted or the stronger the push against the shoulder, the more increased the activity in these 27 neurons. This passive stretch response to lifting the arm or pushing against the shoulder was much weaker than the neuronal response during the active push and did not correlate with the spatial tuning during the active push; i.e., a neuron could be most active when the monkey pressed the lower target, but only started to discharge when the arm was passively lifted up well above the preferred target.

Somatosensory-Motor Responses Occur after Contact

The spontaneous activity of the 130 somatosensory-motor neurons measured during the fixation phase was very low, with a median firing rate of 2 spike/s (127 cells with a range of 0–10 spikes/s and 3 cells which fired 14, 18, and 20 spikes/s, respectively). In contrast, the responses during the contact and push phases at the preferred position of each unit were moderate to vigorous, with a median firing rate of 31 spikes/s (range: 6–135 spikes/s). The responses appeared with some delay after target contact, when the animal was already pressing the button with a minor force of 1.5 N to close the contact of the sensor. The median response onset delay of the activity during the press of the central button was 50 ms (n = 34, range: 15–135 ms); at the upper target, it was 72 ms (n = 29, range: 30–130 ms); at the left target, it was 60 ms (n = 28, range: 20–110 ms); at the right target, it was 50 ms (n = 29, range: 30–100 ms); and at the lower target, it was 65 ms (n = 26, range: 30–155 ms). There was no significant difference in the delay periods during the presses of the different targets (ANOVA, $p = 0.39$).

Somatosensory-Motor Neurons in the Colliculus Are Bimanual

We recorded somatosensory-motor activity in 12 neurons from the left and 3 neurons from the right SC while the monkey performed the task first with his contralateral arm and then with his ipsilateral arm (Figure 3). All of these units were bimanual, and the spatial tuning of the somatosensory-motor responses of 13 units remained clearly similar irrespective of whether the ipsilateral or contralateral arm was used. However, 6 of these 15 neurons showed arm specificity (ANOVA, $p < 0.05$). Four of them were significantly more active when the ipsilateral arm was used, while two of them elicited significantly higher activity during the button press with the contralateral arm (Figure 5). The median activity of these 15 units during the press with the contralateral arm (median = 23 spikes/s, range: 6–55 spikes/s) or the ipsilateral arm (median = 24 spikes/s, range: 11–52 spikes/s) was not significantly different (Wilcoxon test for correlated samples, $p = 0.35$). Furthermore, we recorded somatosensory-motor activity from 6 units in the right (ipsilateral) SC during the push with the right arm and

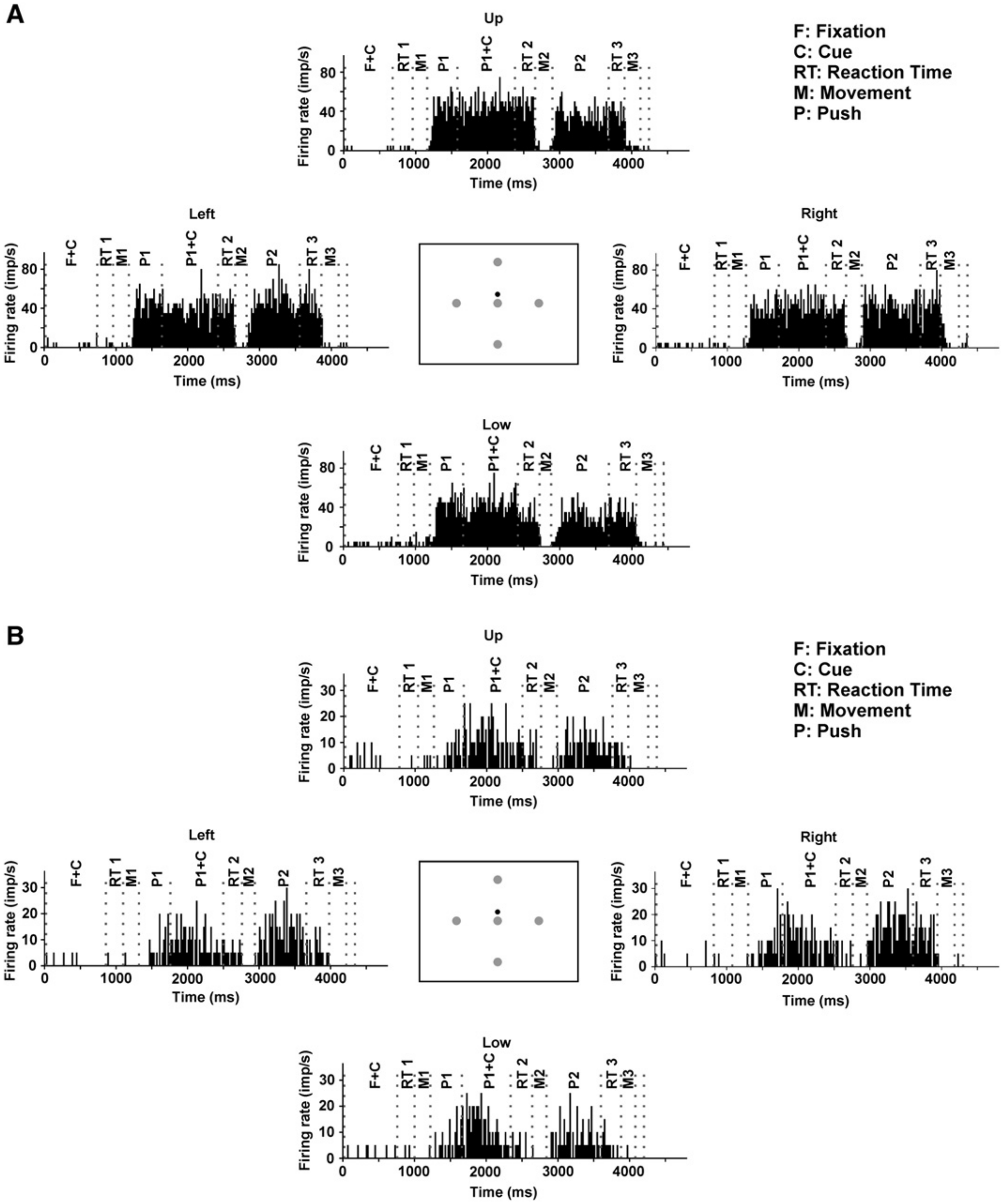

Figure 3. Neuronal Activity in a Primate's Superior Colliculus when His Hand Presses a Target

Relative time histograms (RTHs) of activity of a somatosensory-motor superior colliculus unit in paradigm *B* during use of the contralateral arm (A) followed by the ipsilateral arm (B). Note that this neuron displays a strong arm specificity, activity during the use of the contralateral arm being significantly higher. The sequences in the reach paradigm were the same as described in Figure 1. Vertical broken lines delineate the phases. Note that this neuron was inactive in the reach phases and highly active in the push phases. The abscissa represents the time relation of the neuronal activities (ms), while the ordinate represents the firing rate (imp/s) of the units. In the central part of each panel is the schematic drawing of the reach paradigm. The rectangle represents the panel with the push buttons that was placed 28.6 cm in front of the animal. The five gray spots show the arrangement of the five push buttons. The black spot represents the position of the fixation point during the whole task.

compared it with activity from 16 neurons recorded in the left (contralateral) SC. The population activity profiles of the units in the SC ipsilateral and contralateral to the right arm were identical, with no difference in either response amplitude or tuning.

Coding of Push Strength and Spatial Location

Irregardless of whether the somatosensory-motor activity is efferent or reafferent, it should vary with push strength. Therefore, we tested this activity in 18 units during button pressing with stronger force (6 N) intermingled with the pushes with lighter force (1.5 N). Pressing with stronger forces elicited significantly higher discharge rates in 8 neurons than pressing with weaker forces (ANOVA, $p < 0.05$) (Figure 6). The median activity of these 18 units caused by a stronger push (median = 20 spikes/s, range: 4–38 spikes/s) was significantly higher than that caused by a lighter push (median = 16 spikes/s, range: 2–38 spikes/s; Wilcoxon test for correlated samples, $p < 0.01$).

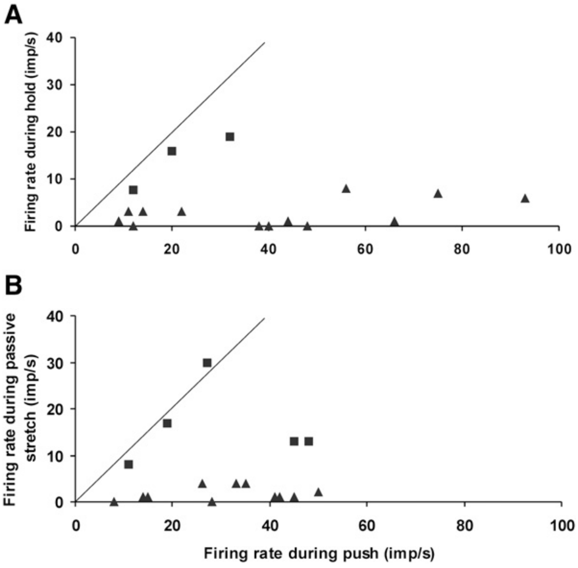

Figure 4. Activity of Somatosensory-Motor Neurons during Hold and during Passive Stretch

Activity of somatosensory-motor neurons when the monkey holds his arm near the target (A) or during passive stretch (B) of the trunk and the chest in comparison to the monkey actively pressing the buttons. Each point in the scatter plot demonstrates the relationship between the median responses of a single neuron during a button press (abscissa in A and B) and during a period when the monkey holds his arm aloft without contact to the same button (ordinate in A) or during the period when the experimenter pushes the chest of the fixed monkey backward in order to stretch the trunk and chest muscles (ordinate in B). The solid line corresponds to unity slope. Note the consistently higher neuronal activity during the monkey's button push. The squares indicate the somatosensory-motor neurons that either elicited significant hold activity (A) or were activated significantly above spontaneous activity levels during passive stretch (B), while the triangles represent the units with significantly elevated activity only during target pushing. Axes are scaled in impulses per second (imp/s).

We analyzed the activity of somatosensory-motor neurons while the monkey made contact with targets in different spatial locations. Thirty-three of the sixty-one units tested (54%) were selective for the location, i.e., at one of the five different target locations the discharge rate of a neuron was significantly higher than the mean of the discharge rates at the other positions ($p < 0.05$). Within this population of these 61 neurons, the target location that elicited the maximal neuronal discharge rate was distributed almost evenly. Sixteen units were most active during contact with and pushing the central target, nineteen with the right target, nine with the upper target, seven with the left target, and ten with the lower target. We sorted the 61 SC neurons into five subpopulations according to the target site eliciting maximal activity and analyzed the tuning of these groups. In each neuronal subpopulation the spatial tuning of the responses was clearly recognizable. The subpopulation that was most active during the press of the right target exhibited the sharpest spatial response tuning. (Figure 7).

The averaged somatosensory-motor responses to different target locations summed over all 61 neurons were very similar. The median firing rate in the contact and push phase at the central target was 17 spikes/s (range: 0–135 spikes/s); at the upper target, it was 16 spikes/s (range: 0–110 spikes/s); at the left target, it was 16 spikes/s (range: 0–103 spikes/s); at the right target, it was 19 spikes/s (range: 1–123 spikes/s); and at the lower target, it was 16 spikes/s (range: 0–115 spikes/s). There was no significant difference ($p = 0.48$) among these values in a one-way ANOVA.

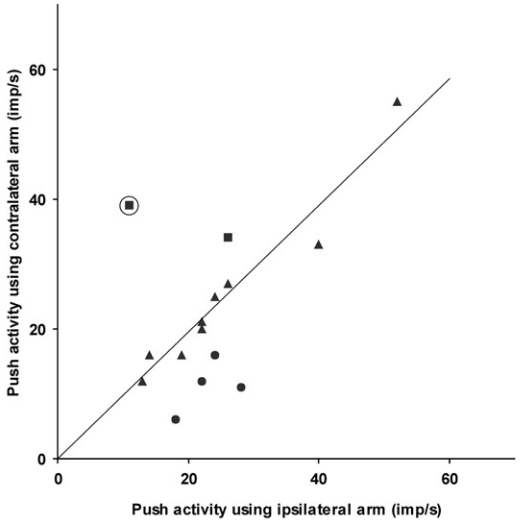

Figure 5. Bimanual Responses of 15 Somatosensory-Motor Neurons

Each point of the correlogram demonstrates the relationship between the median responses of a single neuron during button pressing with the ipsilateral (abscissa) arm and the contralateral (ordinate) arm. The solid line corresponds to unity slope. The triangles show the SC units that were similarly active using both arms, the squares represent the units that exhibited significantly higher activity during the button press with the contralateral arm, and circles show the neurons that were significantly more active during the button press with the ipsilateral arm. Note that the activity of the majority of the units was not different whether the ipsilateral arm or the contralateral arm was used. The RTHs of the circled neuron are presented in Figure 3. Axes are scaled in impulses per second (imp/s).

Discussion

We recorded neuronal activity from the SC of the macaque brain in visually guided reach paradigms and determined the SC population activated during this task. These neurons exhibited vigorous responses during contact with the reached for target and/or during the press of the target. These neurons were inactive or only slightly active during the reach phases of the task. Thus, these neurons played no significant role in the control of the trajectory of the arm, but instead were highly active during the interaction with the reached object. The results detailed above seem to reveal yet another functional role of neurons in the primate's SC, in addition to their well-described contribution to changing or holding gaze (see for review: Guitton et al., 2003) and direction of the front leg or arm to a target (Courjon et al., 2004; Werner et al., 1997a, 1997b). These results do not clearly discriminate whether the activity of these somatosensory-motor neurons is efferent or reafferent.

The somatosensory-motor neurons, similar to the reach neurons, spread through the intermediate and

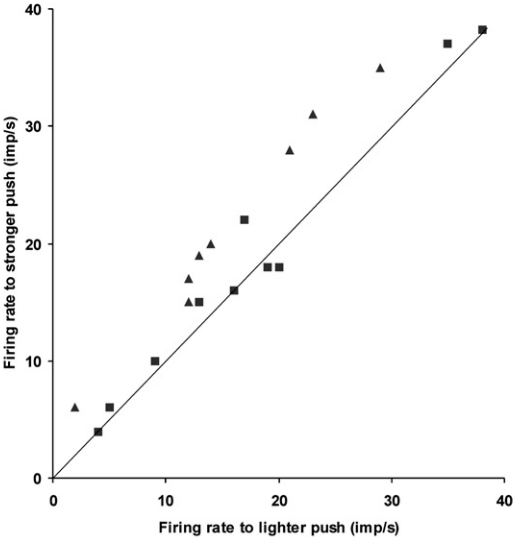

Figure 6. Activity of 18 Somatosensory-Motor Neurons during Pushes with Different Forces

Each point of the correlogram demonstrates the relationship between the median responses of a single neuron during a lighter (1.5 N) and a stronger (6 N) push. The abscissa represents the neuronal push activity (imp/s) associated with a lighter push, while the ordinate shows the neuronal push activity (imp/s) associated with a stronger push. The solid line corresponds to unity slope. The squares demonstrate the SC units that were similarly active during both a stronger and a lighter push, while the triangles represent the units that were significantly more active during a stronger push. Axes are scaled in impulses per second (imp/s).

deep layers of the SC (Stuphorn et al., 2000; Werner et al., 1997b) and are intermingled with other cell types. The spontaneous activity of somatosensory-motor neurons in the SC is very low, lower than in previously described reach units (Werner et al., 1997b). In addition to their low or absent spontaneous activity, these units are inactive during the reaction, delay, and arm movement phases of the task, which makes them unrecognizable in a reach task without a lasting contact or push phase. Also, the large majority of the somatosensory-motor neurons were inactive or only weakly active when the monkey held its arm up beside the target without actually touching or pressing it. These properties are probably the main reasons why these neurons have evaded description so far. Once identified, they were recorded very frequently during our paradigm *B*, outnumbering the reach neurons by far. This specific activity during paradigm *B* suggests a strong connection between somatosensory-motor neuron activity and both contact with or interaction with the target. The activity of some of these neurons covaried with the force that had to be exerted to close the contact of the button. Another important parameter modulating the discharge rate was the spatial location of the target in the working space; i.e., the responses of the majority of the neurons were significantly different during target presses in different spatial positions. The target location eliciting maximal responses varied among the cells recorded, but the averaged responses summed over all neurons were very similar at the five different target locations. Another surprising property of the somatosensory-motor neurons was their bimanual responses. In more than half of these neurons, spatial tuning remains similar when either the ipsilateral or the contralateral arm is used.

The SC is a prominent subcortical projection zone of the PPC (Fries, 1984; Pare and Wurtz, 1997; Glickstein, 2003; Lock et al., 2003), which is the part of the primate cortex strongly involved in the preparation and execution of oculomotor and skeletomotor processes (Mountcastle et al., 1975; Ferraina et al., 1997a, 1997b; Snyder et al., 1997, 1998, 2000; Battaglia-Mayer et al., 2003). Several lines of evidence point to the important role played by PPC in carrying out sensorimotor transformations that underlie visually guided reaching (Battaglia-Mayer and Caminiti, 2002; Buneo et al., 2002; Jackson et al., 2005). In their original influential paper on the parietal cortex, Mountcastle et al. (1975) described that about two thirds of the neurons in area 5 are activated by proprioceptive stimulation and that a large proportion of these neurons were relatively insensitive to passive joint rotation, but were driven to high rates of discharge when the same joint was rotated by active movement of the animal. Georgopoulos et al. (1984) and Kalaska and Hyde (1985) described neuronal activity in parietal area 5 during the active maintenance of the arm in specific positions. Our results for somatosensory-motor neurons in the SC were very similar. These findings suggested a strong functional relationship of the PPC with the SC, not only in reaching, but also in holding and pushing that's directed toward the reached target. The activity of these SC neurons "highlights" spatial information about target location, arm position, and required force while the animal is contacting and pressing the target.

Activity in the PPC can also be clearly evoked by passive somatosensory stimulation (Breveglieri et al., 2006). Hand movement-related neurons have been found in the anterior intraparietal area during manipulation of various types of switches: push button, pull lever, pull knob, and pull knob in a groove (Taira et al., 1990; Sakata et al., 1995, 1997; Fattori et al., 2004). Furthermore, the excitatory and inhibitory responses of individual PPC neurons coincided with specific components of the hand kinematics or signaled interactions between the hand and the object (Gardner et al., 1999; Roy et al., 2000; Debowy et al., 2001). These neurons were clearly active during the delay and premovement periods, which suggests their role in the motor aspects of the target manipulations. Push motor activity has been further described in the arm area of the primary motor cortex, in the supplementary motor area, in the premotor cortex, and in the claustrum (Mushiake et al., 1991; Halsband et al., 1994; Shima et al., 1996). Here we see more differences than similarities to the somatosensory-motor neurons in the SC, especially in the timing of activity onset before contact with the object in cortical neurons and after contact in collicular neurons.

The fundamental question is whether the somatosensory-motor units in the SC are reafferent neurons, providing information about the stretch or force of the adequate muscles during interaction with the target, or whether they are outflow neurons that control the muscle activity that is necessary to push the targets. The somatosensory-motor neurons in the SC, in contrast to cortical neurons described above, never responded

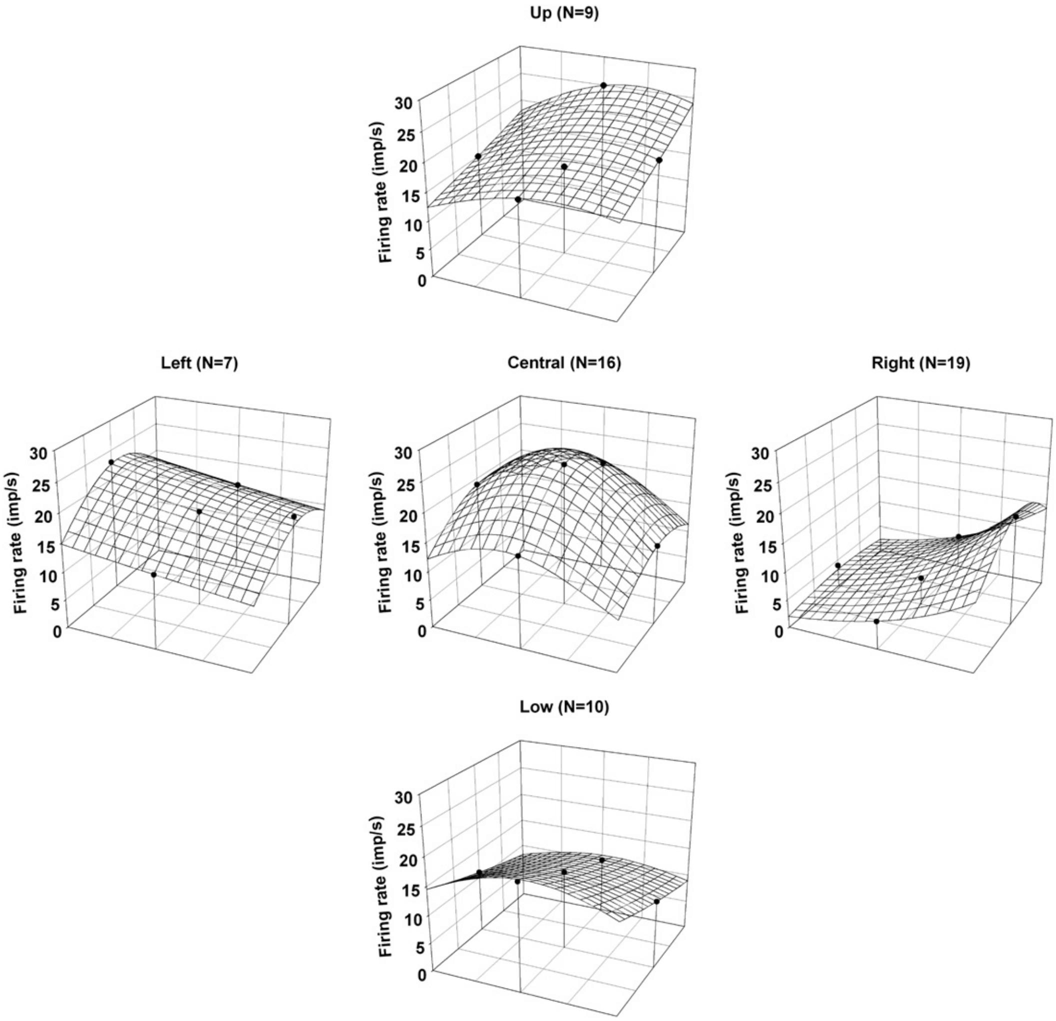

Figure 7. Spatial Tuning of Somatosensory-Motor Activity

Each panel represents a neuronal population clustered upon the target site of their maximal activity (central, right, up, left, low). The numbers above each graph demonstrate the number of cells that exhibited their maximal discharge rate during a push of a button in that target location. The five drop lines in each panel demonstrate the median activity of the SC populations during the push of each of the five different targets. Each surface was fitted to the five median values. Axes are scaled in impulses per second (imp/s).

substantially before contact with the target. Thus, it seems unlikely that these neurons are involved in preparing the muscles involved for push motor actions. The activity in the SC most probably represents feedback about the force of the active muscles during interaction with the target. This view is supported by our finding that push strength correlates with the discharge rate of some of the neurons. It is well known that the SC in primates receives somatosensory projections at least from the spinal cord (spinotectal) and from the somatosensory areas of the parietal cortex (Wiberg et al., 1987; Glickstein, 2003). So far, only receptive fields to passive cutaneous stimulation have been reported in the colliculus (Clemo and Stein, 1991; Wallace and Stein, 1996). Interestingly, in our study of behaving monkeys, a significantly higher number of neurons were activated by possibly proprioceptive inputs (passively lifting the arm) than by cutaneous inputs (mechanical stimulation of the body surface, the palms and the fingers). But most importantly, even more neurons in the behaving monkey were active during self-generated proprioceptive stimulation. Moreover, the activity profile of the somatosensory-motor SC neurons demonstrates high similarity to that of the Golgi tendon organ, the muscle receptor that may provide information on the stretch of the active muscles to the SC somatosensory-motor neurons. The Golgi tendon organ is silent during natural physiological extension of the muscles and can be activated with external passive stretch or during active muscle contractions. This receptor characteristically discharges more vigorously during active muscle contraction than during passive stretch (Houk and Henneman, 1967; Hunt, 1974). This is exactly what we describe above for the somatosensory-motor neurons in the SC.

Can we see any similarity with the well-known eye movement-related neurons in the SC? Clearly, high discharge during active fixation and absent or weak discharge during movement is very reminiscent of the so-called fixation neurons, which are tonically active during visual fixation of a target and pause during saccades (Munoz and Wurtz, 1993; Bergeron and Guitton, 2002; Choi and Guitton, 2006). Is this as far as the similarity goes? If one considers, as an alternative explanation of the fixation neurons, that they can encode small position errors around the fovea, the function of the eye movement-related neurons may not be such a dramatic departure from the function of the somatosensory-motor neurons. In particular the range of position errors for fixation cells can extend into the ipsilateral visual field, and cells with fixation-related activity can be found at more caudal sites as well as at the rostral pole of the SC. Our experiments show, however, that using skeletomotor, in addition to the widely applied oculomotor, paradigms reveals additional functional loops incorporating the SC. Somatosensory-motor neurons in SC are most active during interaction with the target; their discharge rate is modulated by the spatial position of the target as well as the force that is exerted. These neurons can have preferred target location, even far in the visual field ipsilateral to the recorded SC. The somatosensory-motor neurons can be found over the entire extent of the SC. In these respects they are very similar to skeletomotor reach neurons in the SC of primates described by Werner et al. (1997a, 1997b).

Experimental Procedures

Single-cell recordings were performed in the left and right superior colliculus of two awake, behaving monkeys (*Macaca mulatta*) in visually guided reach paradigms. All procedures were carried out in a way that minimized discomfort and pain of the animal and followed the European Communities Council Directive of 24 November 1986 (S6 609 EEC) and the National Institutes of Health guidelines for care and use of animals for experimental procedures.

Behavioral Paradigms

Paradigm A

The monkey was seated in a primate chair with his head fixed straight ahead, facing a tangential, translucent screen at a distance of 20 cm (screen size 80° × 80°). The nonworking arm was loosely restrained. During the task the monkey had to perform an arm movement to touch a target located on the screen. These targets were positioned at the central fixation light and at up to eight locations on a circle with a 5.4 cm radius (15° eccentricity) centered on the fixation point. A single trial of the visually guided reach task consisted of five phases. (1) Fixation phase: a single trial started when the monkey used his hand to touch a metal bar (contralateral to the recorded SC) positioned close to the hip. This resulted in the onset of a red fixation light (diameter <1°) back-projected onto the center of the screen, located at the monkey's eye level. (2) Fixation + Cue phase: during fixation, a peripheral reach target light was turned on. After the reach target was illuminated, the animal had to maintain his eye as well as his arm in the original position for a pseudorandomly determined delay period (0.5–2.2 s). (3) Saccade phase: when the central fixation light extinguished, the animal performed a saccade to the peripheral reach target. (4) Reach phase: after another variable delay, an auditory signal instructed the monkey to start the reach movement to touch the foveated reach target. The release of the touch bar (i.e., movement onset) as well as the contact with the target (i.e., end of movement) caused a transistor-transistor logic (TTL) pulse, which was used as a behavioral trigger event. (5) Contact phase: the monkey had achieved the target and held the contact with the target for up to 600 ms.

After discovering neurons in the SC that were active during the contact phase, the experimental procedure was slightly changed such that the animal not only had to hold the arm at the target, but also had to press the target with variable forces for a variable amount of time.

Paradigm B

In this visually guided arm movement task, the monkey had to reach first to a central target, followed, after some delay, by one of up to four (up, left, right, or low) peripheral targets (Figure 1). The targets for hand movements were push buttons that required a force of either 1.5 N or 6 N to close the contact. Each contained a red and a green light emitting diode (LED). The five push buttons were integrated in a translucent acrylic plate that was fixed in the vertical plane 28.6 cm from the eyes of the monkey. The distance of each peripheral button from the central button was 9 cm. During all phases of the visually guided arm movement task, the monkey had to fixate on a stationary blue spot (diameter = 1.6°). To exclude the influence of eye movements on neuronal activities, the trial was aborted immediately if the animal broke fixation. A single trial of the visually guided reach task consisted of ten phases. (1) Fixation + Cue phase: the animal placed its hand at the start position close to the hip and fixated on a blue spot on the screen. Then the central target turned red immediately to cue the upcoming arm movement (duration 1000–1500 ms). (2) Reaction time 1: the central push button changed to green to signal the monkey to perform a hand movement to the central button. The time between the appearance of the green go signal and the start of the arm movement is the reaction time 1 (<1000 ms). (3) Move phase 1: the monkey performed the first arm movement to the central push button (<1000 ms). (4) Push phase 1: the animal pushed the central button without getting a new target signal (300–600 ms). (5) Push 1 + Cue phase: one of the four peripheral push buttons turned red (500–1000 ms). (6) Reaction time 2: the red peripheral push button changed to green to signal the monkey to perform a hand movement to the green peripheral button. The time between the appearance of the green go signal and the start of the arm movement is the reaction time 2 (<1000 ms). (7) Move phase 2: the monkey performed the second arm movement to the green peripheral push button (<1000 ms). (8) Push phase 2: the animal had to press the peripheral button until the green signal turned off (300–600 ms). (9) Reaction time 3: this period ran from the extinction of the green hold signal to the beginning of the movement back to the start position (<1000 ms). (10) Move phase 3: the monkey placed his hand back to its start position (<1000 ms). After successful completion of a trial, the animal got a drop of liquid reward. The computer-controlled trials were presented in a pseudorandom order. The monkey had to perform at least ten trials toward each peripheral target.

Paradigm C

In this paradigm the monkey was conditioned to lift his arm between the right and upper push buttons without touching them. After a lasting hold phase of 500–1400 ms, the monkey got a piece of fruit as a reward. This arm hold test was applied in alternation with paradigm *B*, in which the monkey had to push the buttons. The arm position and the neuronal activity during the arm hold test were recorded on a video recorder. Action potentials were subsequently counted off line and used to calculate the neuronal activity, and the length of the holding phase was estimated by counting the video frames in which the arm was held aloft.

Animal Preparation

After training for the fixation and arm movement task, the monkeys were surgically prepared for chronic neurophysiological recordings. Each monkey was treated preoperatively with atropine (0.1%) and initially anesthetized with ketamine hydrochloride (10 mg/kg i.m.). Under general anesthesia (sodium pentobarbital 25 mg/kg i.v.) the monkeys were implanted with a device for holding the head. For monitoring the eye position, a scleral search coil was implanted according to the method published by Judge et al. (1980) and connected to a plug on the top of the scull. A recording chamber (19 mm in diameter) was implanted over a craniotomy. The chamber was centered on the midline over the occipital pole, tilted 45° backward from the vertical to allow penetrations perpendicular to the surface of the SC in a parasagittal plane. In the second monkey, the placement of the cylinder was guided by nuclear magnetic resonance images, which were taken from the animal before the first surgery. Analgesics and antibiotics were applied postoperatively for 7 days.

Recording

Extracellular electrophysiological recordings of single neurons from the intermediate and deep layers of the SC were carried out using tungsten microelectrodes (impedance 2–4 MΩ) positioned either by a hydraulic single-electrode manipulator (Narishige) or by a multielectrode manipulator (Thomas Recording, Giessen, Germany). The discrimination of individual action potentials was achieved in real time with help of a computer-controlled multichannel spike sorter (Plexon Inc., Dallas, TX). Time stamps for detected spikes were stored at 10 μs resolution by the same computer which was controlling the behavior of the animal.

Data Analysis

The neuronal activity recorded in the fixation phase was considered as spontaneous activity. We defined a neuron as either a reach or a somatosensory-motor unit if the neuronal firing rates during the reach or the contact/push phases of the task were significantly higher ($p < 0.05$) than those during the fixation phase (paired t test). We compared, for each unit, whether its discharge rate during contact with or push against one of the five different targets was significantly higher than the mean of the other targets (one-way ANOVA; $p < 0.05$). The target location with the highest contact/push activity was defined as the preferred location.

The neuronal activities in the reach paradigm *A* were stored as peristimulus time histograms (PSTH, bin width 20 ms). To eliminate the trial-by-trial variation in the duration of different behavioral phases, in paradigm *B* we divided each epoch into a fixed number of bins that remained the same in each trial. The number of bins for each epoch was chosen in such a way that one bin accounted on average for ~20 ms. (For example, the epoch of the first movement, with a mean duration of 258 ms, was divided into 13 bins). The actual time represented by such a bin could vary with the duration of the respective epoch in each trial. We call the resulting histograms "relative time histograms" (RTH) (Stuphorn et al., 2000) (Figure 3). In the RTHs, the temporal relationship of the neuronal activity to the various behavioral epochs becomes more evident than in the peristimulus time histograms, which are aligned to only one of the different phases of the task. The activities denote the firing rates in impulses/second (imp/s).

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