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Neurophysiology of Prehension. III. Representation of Object Features in Posterior Parietal Cortex of the Macaque Monkey

E. P. Gardner, K. S. Babu, S. Ghosh, A. Sherwood and J. Chen
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Neurophysiology of Prehension. II. Response Diversity in Primary Somatosensory (S-I) and Motor (M-I) Cortices

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Gardner EP, Ro JY, Babu KS, Ghosh S. Neurophysiology of prehension. II. Response diversity in primary somatosensory (S-I) and motor (M-I) cortices. *J Neurophysiol* 97: 1656–1670, 2007. First published November 8, 2006; doi:10.1152/jn.01031.2006. Prehension responses of 76 neurons in primary somatosensory (S-I) and motor (M-I) cortices were analyzed in three macaques during performance of a grasp and lift task. Digital video recordings of hand kinematics synchronized to neuronal spike trains were compared with responses in posterior parietal areas 5 and AIP/7b (PPC) of the same monkeys during seven task stages: 1) approach, 2) contact, 3) grasp, 4) lift, 5) hold, 6) lower, and 7) relax. S-I and M-I firing patterns signaled particular hand actions, rather than overall task goals. S-I responses were more diverse than those in PPC, occurred later in time, and focused primarily on grasping. Sixty-three percent of S-I neurons fired at peak rates during contact and/or grasping. Lift, hold, and lowering excited fewer S-I cells. Only 8% of S-I cells fired at peak rates before contact, compared with 27% in PPC. M-I responses were also diverse, forming functional groups for hand reshaping, object acquisition, and grip force application. M-I activity began ≤ 500 ms before contact, coinciding with the earliest activity in PPC. Activation of specific muscle groups in the hand was paralleled by matching patterns of somatosensory feedback from S-I needed for efficient performance. These findings support hypotheses that predictive and planning components of prehension are represented in PPC and premotor cortex, whereas performance and feedback circuits dominate activity in M-I and S-I. Somatosensory feedback from the hand to S-I enables real-time adjustments of grasping by connections to M-I and updates future prehension plans through projections to PPC.

INTRODUCTION

In an earlier report, we analyzed the role of hand manipulation neurons in areas 5 and 7b/AIP of posterior parietal cortex (PPC) as monkeys performed a trained prehension task (Gardner et al. 2007). The data obtained suggested that these neurons participate in a sensorimotor network involved in grasp planning, prediction of sensory stimulation, and monitoring of appropriate execution of the desired actions. Firing patterns of PPC neurons were postulated to reflect the internal motor commands needed to accomplish task goals and the sensory events resulting from self-generated movements. In this model, likely sources of the central motor commands are the primary motor cortex (M-I) and premotor cortex (PMd for arm movements and PMv for hand movements). Somatosensory feedback could be transmitted from the primary somatosensory (S-I) cortex, particularly area 2, that is the source of strong anatomical connections to area 5 (Jones and Powell 1969, 1970; Pearson and Powell 1985).

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The experiments described herein provide a direct test of these models. During our earlier studies of PPC neurons, we also recorded spike trains of neurons in adjacent regions of S-I and M-I cortex of all three monkeys, using the same behavioral task and data analysis protocols. Digital video recordings of hand kinematics were used to correlate neuronal spike trains to specific actions performed by the hand as the animals grasped and lifted a variety of objects. The data obtained indicate that neuronal activity of hand manipulation neurons in the PPC precedes that in S-I, but overlaps the onset of activity in the hand representation of M-I. Firing patterns of S-I and M-I neurons tend to be focused on particular hand actions during prehension, rather than the overall task goals. In this manner, activation of specific muscle groups in the hand is paralleled by matching patterns of tactile and proprioceptive feedback needed for efficient task performance.

METHODS

Neurophysiological and behavioral data were obtained from three adult rhesus monkeys (*Macaca mulatta*, two male and one female, weight 8–16 kg), trained to perform a prehension task; these animals were also used in companion studies of PPC neurons (Gardner et al. 2007). Both studies used the same experimental procedures, including the prehension task and electrophysiological data-acquisition and analysis techniques; these are summarized briefly below. Experimental protocols were reviewed and approved by the New York University Medical Center Institutional Animal Care and Use Committee (IACUC) and are in accordance with the guiding principles for the care and use of experimental animals approved by the Councils of the American Physiological Society, the National Research Council, and the Society for Neuroscience.

Prehension task

The monkeys were trained in a grasp-and-lift task to manipulate objects placed at defined locations in the workspace. The objects were a set of four knobs mounted on a box placed 22–24 cm in front of the animal as shown in Fig. 1. The animals could view the workspace and used visual guidance to position their hand on the objects. The knobs required a whole-hand power grasp between fingers and palm to lift them. The animal was directed on each trial toward the rewarded object by positional cues displayed on a computer monitor. The animal had to reach to the specified knob, grasp, and lift it until an upper stop was contacted. If the correct object was lifted and held in place, the animal received a juice reward; if the animal chose the wrong object, there was no reward on that trial. Although the visual cues directed the animal's attention to a specific object on each trial, the animal selected the particular grasp postures used to accomplish

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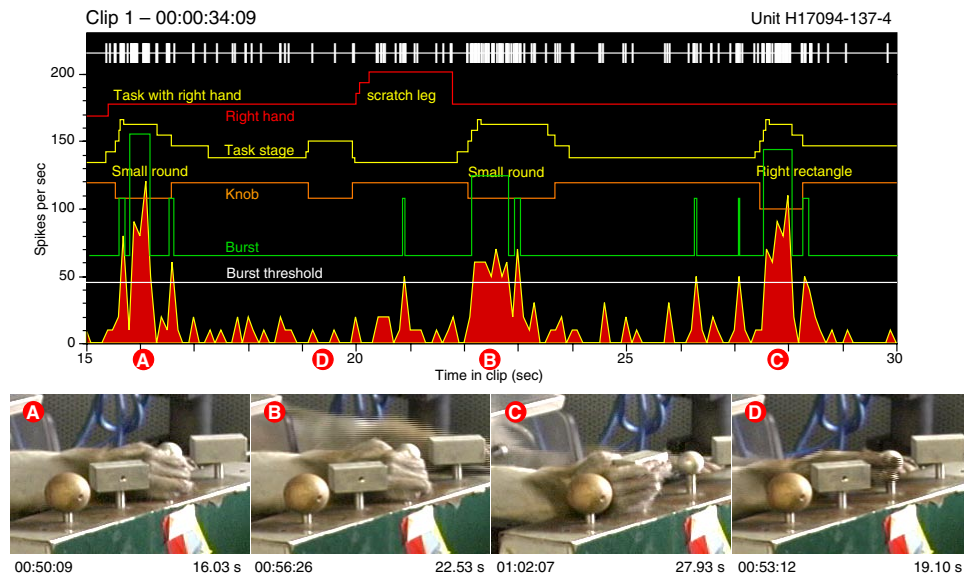


FIG. 1. Burst analysis graphs of continuous neural and behavioral activity recorded in area 2 of Monkey H17094 during a 15-s period. Spike train was binned in 100-ms intervals (red graph) to compute continuous firing rates. *Yellow task stage trace*: each stepped yellow pyramid marks a single trial. Upward deflections denote the start of stages 1–4 (approach through lift); downward deflections mark the onset of stages 5–8 (hold through release). Three complete trials (A, B, C) and one incomplete trial (D) occurred during this interval. *Orange knob trace*: downward pulses that span the contact through lower stages indicate the knob location on the shape box and the duration of hand contact. Pulse amplitude is proportional to the knob distance from the left edge of the box. *White burst threshold trace*: firing rate set 1 SD above the mean rate during the entire 2.5-min video clip. *Green burst trace*: upward pulses mark periods when continuous firing rates exceeded the burst threshold; the burst pulse amplitude indicates the mean firing rate during this interval. Burst trace has been displaced by 65 spikes/s to improve readability. Images in the *bottom* of this figure were captured at the peak of bursts A–C, and in the time interval marked D. Neuron responded most vigorously during lift on each trial. Unit H17094-137-4; tactile receptive field on the thumb, shaft of digit 2, and the web between these digits.

the task goals. Each animal developed an individual grasp strategy that was natural, comfortable, and fluid and was used repeatedly during the period of study.

The task consisted of a succession of stages characterized by 1) a specific goal for each action, 2) a unique pattern of underlying muscle activity expressed as kinematic behavior, and 3) a transient mechanical event signaling goal completion and transition to the next stage. We divided the task into 8 stages: 1—Approach; 2—Contact; 3—Grasp; 4—Lift; 5—Hold; 6—Lower; 7—Relax; 8—Release. Stages 1–3 were required for object acquisition, stages 4 and 5 for manipulation, and stages 6–8 for release of the object.

We monitored hand kinematics during the task using digital video (DV) recordings of the animal's behavior synchronized to neuronal spike trains, as previously described (Debowy et al. 2001, 2002; Gardner et al. 1999, 2002, 2007; Ro et al. 1998). A set of up to three DV camcorders provided lateral, frontal, and overhead images of the monkey and the workspace at 29.97 frames/s. The onset of each task stage was measured from the time code of the matching video frame by visual observation and/or by tracings of the hand posture in successive video images. Event time codes were stored in spreadsheets and were subsequently used as markers for display in burst analyses, alignment of neural responses in rasters and peristimulus time histograms (PSTHs), and for bracketing task stages in statistical analyses of firing rates.

Recording and data analysis techniques

Extracellular single-unit recordings from S-I and M-I were made in the left hemisphere of the three animals studied as described in Gardner et al. (2007); the specific recording locations are illustrated in Fig. 3 of that report. S-I recordings spanned the cortex between representations of the wrist and face; M-I sites were located immediately rostral to the S-I hand representation. Spike trains were digitized at 16-bit resolution, 48 kHz, or 12-bit resolution, 32 kHz by the DV camcorders, and stored as an audio trace together with video records of the hand actions. Video clips of the animal's behavior and the

digitized spike trains were downloaded to the lab computers, and stored as both QuickTime files and in audio-interchange file format (AIFF) for quantitative analyses of firing patterns. Because video and spike trains were simultaneously recorded and digitized, both data sets spanned the same time interval. Thus knowledge of the time code of each video frame in the clip provided a precise way to locate the matching firing patterns. Similarly, measurements of the timing of spikes with respect to the onset of the audio data sample placed each spike in a precisely designated video frame.

The spike trains of each neuron were analyzed with standard methods to measure instantaneous and mean firing rates during specific task stages and to quantify response amplitude and time course as functions of the hand kinematics. Burst analysis graphs (Fig. 1) provided a continuous record of neural and behavioral events within a video clip and were used to screen neural responses in the task. Spike trains were represented as rasters and continuous binned firing rates together with markers of actions performed by the monkey and/or experimenter during the clip. Reverse correlation of periods of high firing (green "burst" trace) with the matching video images of the monkey's behavior was used to highlight the behaviors to which the neuron was most responsive. Spike rasters and PSTHs, aligned to the frame onset times of hand contact with the knob, were used to measure the consistency and reliability of neural responses during the task (Fig. 2).

Average firing rate profiles were compiled from measurements of mean firing rates per stage on each trial (Fig. 3) and used for statistical analyses and for objective classification of firing patterns within the population. Neurons were grouped by the stage(s) that evoked maximum firing and subdivided into classes tuned to single actions, two successive actions, or broadly tuned classes by statistical comparison of mean rates during sequential task stages. A repeated-measures ANOVA model (StatView, SAS Institute) analyzed whether there was significant modulation of firing rates across the task stages and the pretrial interval (F-test, $P < 0.05$); nearly all task-related neurons yielded $P < 0.001$ on F-tests. In addition, task-related neurons were

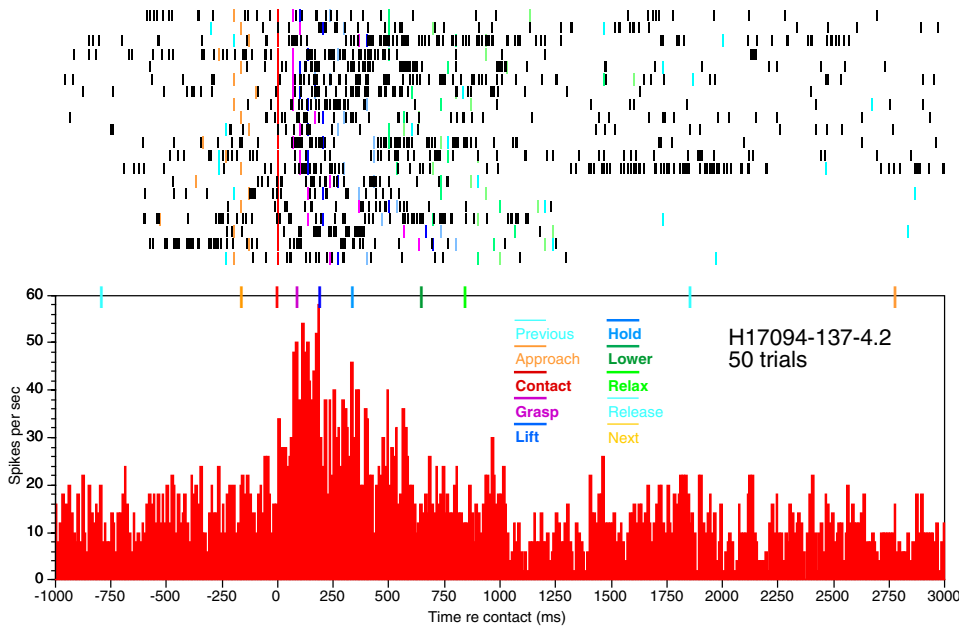


FIG. 2. Rasters of the first 20 approach trials and peristimulus time histogram (PSTH) aligned to contact for the area 2 neuron shown in Fig. 1. Colored bars on the rasters and markers above the PSTH indicate the task stage timing relative to contact. Firing increased as the objects were grasped and lifted; they remained at elevated rates through holding.

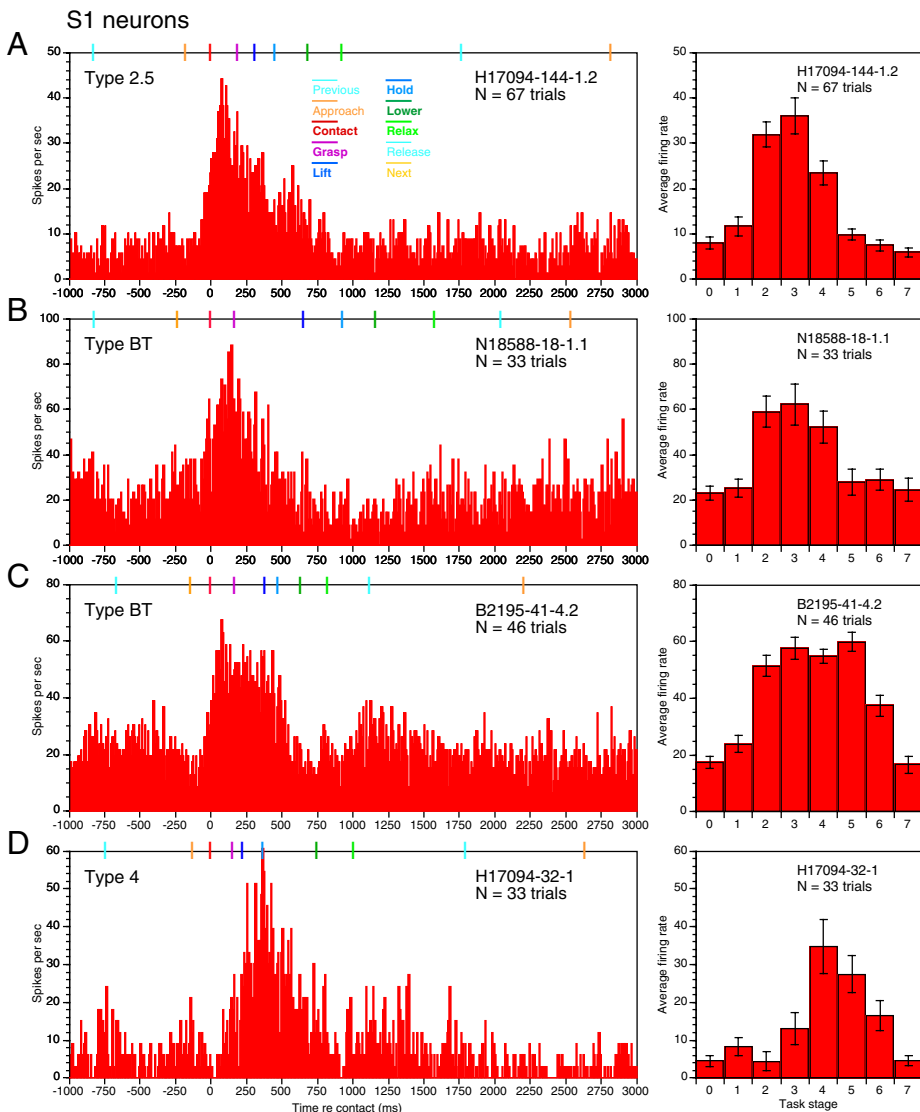


FIG. 3. PSTHs (left) and average firing rate graphs (right) for the major response classes recorded in area 2. Bar graphs show average firing rates per task stage (\pm SE); stage 0 indicates the pretrial interval. Neural responses were categorized by the stage(s) in which peak firing occurred. A: contact–grasp neurons (Type 2.5) fired at highest rates during stages 2 or 3 (contact or grasp); mean rates did not differ significantly during these stages. Unit H17094-144-1.2; receptive field on the glabrous tips of digits 1, 2, and 3. B and C: broadly tuned neurons (Type BT) fired at high rates during ≥ 3 successive stages. B: Unit N18588-18-1.1 fired at highest rates in stages 2–4 (contact through lift); receptive field on the glabrous tips of digits 2 and 3. C: Unit B2195-41-4.2 fired at highest rates in stages 2–5 (contact through hold); receptive field on the interdigital palm pads below digits 2 and 3. D: lift tuned (Type 4) neurons fired at highest rates in stage 4. Unit H17094-32-1 responded to passive flexion of the wrist and elbow.

required to show significantly increased or decreased firing rates during at least one task stage compared with the pretrial rate in paired means comparisons ($P < 0.05$).

RESULTS

This report describes the responses of 60 task-sensitive neurons recorded in the hand representation of S-I cortex (area 3b/1, $n = 10$; area 2, $n = 50$) and 16 neurons in primary motor cortex (M-I, area 4) of the same three monkeys used in our earlier studies of posterior parietal cortex (Gardner et al. 2007). The S-I population includes data previously reported from one of these animals (monkey B2195) tested with a rectangular knob (Debowy et al. 2001; Gardner et al. 1999; Ro et al. 2000). Responses analyzed from the other two animals pooled trials of the round and rectangular knobs because the evoked spike trains had similar temporal profiles.

S-I neurons respond to hand-object interactions

Figure 1 shows continuous spike trains recorded from an area 2 neuron in burst analysis format, together with markers of the hand actions. The yellow task stage trace marks the time course of three complete trials (A–C) plus an incomplete trial in which the knob was touched but not grasped (D). As in our earlier study of PPC neurons, the approach, contact, grasp, and lift stages (first four upward deflections) were relatively brief and occurred in rapid succession. The hold, lower, and relax stages (subsequent downward deflections) were longer and more variable in duration. The neural response on each trial began as the knob was contacted and grasped and ended late in the hold stage before lowering the knob back to the rest position. Unlike most neurons in PPC, there was little or no response of this S-I neuron during approach when the hand was preshaped for grasp.

Reverse correlation of periods of high firing, denoted by the green “burst” trace, with the matching video images showed that the neuron was particularly sensitive to grasping objects regardless of their shape. Peak firing during each of the large bursts coincided with grasp and lift actions of the hand (images A–C). Simply touching the knob without grasping it (image D) failed to excite the neuron. Although the hand postures used by this animal were nearly identical to those illustrated in our studies of PPC neurons, the neuron fired later in the task and required direct interaction between the hand and object. As indicated by the orange knob trace, high firing rates spanned the period of hand-object contact. The neuron also responded weakly to relaxation of grasp as the palm and fingers were displaced away from the knob.

The sensitivity of this neuron to grasping can also be seen in rasters and PSTHs compiled from the entire set of trials. Figure 2 shows raster displays of the first 20 trials aligned to hand contact with the knob, together with the matching PSTH. Unlike neurons in area 5 or AIP/7b, there was almost no change in firing after the onset of approach (gold marker) and even immediately after contact (red). High firing coincided with the onset of static grasp (magenta) when hand movement over the object ceased and the grip force rose. High firing was sustained through the grasp stage and during lift (dark blue), then declined in rate in the hold stage (light blue). Firing returned toward baseline rates as the knob was lowered (dark

green), but the cell often fired a brief late burst as the grip was relaxed (light green).

The neuron’s responses to prehension were consistent with the receptive field location on the hand. The neuron responded to touch and pressure on the thumb and in the web between the thumb and index finger. These regions were contacted directly by the knobs as they were grasped, lifted, and held by the hand. One can see in Fig. 1, A and B that the small round knob was enclosed between the thumb and proximal digits 2 and 3. Similarly, the short end of the rectangular knob was pressed against the webbing joining the thumb to the palm, whereas the thumb and digit shafts were placed on opposite faces of the object (Fig. 1C). These regions were also stimulated by motion of the hand off of the knob as grasp was relaxed. Contact by the tips of digits 2 and 3 on the surface of the small round knob did not stimulate the most effective portions of the receptive field (Fig. 1D).

Responses of S-I neurons to the prehension task were linked to stimulation of their somatosensory receptive fields on the hand by the test objects. The influence of receptive field location can be seen in the PSTHs recorded in area 2 of the three animals illustrated in Fig. 3. The neurons in Fig. 3, A and B had tactile receptive fields on the glabrous surface of digits 2 and 3; the neuron in A also included the thumb. These neurons responded strongly to hand motion over the objects. Contact produced a sharp rise in firing that peaked as the hand moved over the object surface and grasped it securely. Firing rates decayed during lift as the hand and object moved together as a functional unit and returned to baseline during holding. The neuron in Fig. 3C had a proximal receptive field on the interdigital palm pads and displayed more sustained responses that ended as the knob was lowered and grasp relaxed. This animal grasped the top of the knob in an overhand posture and pushed the knob upward with the heel of the hand. In this manner the knob was pushed firmly against the receptive field from the start of grasp until it was lowered. The neuron in Fig. 3D had a deep receptive field that responded weakly to pressure and/or movement of the wrist and elbow joints; it was recorded on the most medial track in the same animal as the cell in Figs. 1 and 2. This neuron did not respond during the earlier stages; instead, its firing rate paralleled proximal joint movement, rising sharply at the onset of lift. Thus individual neurons in S-I tracked specific hand actions that stimulated their receptive fields during the various task stages.

The importance of tactile stimulation in the hand area of S-I can be appreciated by examination of firing patterns during the approach stage. Although we previously demonstrated strong responses in PPC during approach, there was little evidence of strong precontact excitation in S-I. Although some of the neurons illustrated in Fig. 3 showed a slight rise in firing rates before contact, the mean onset latency was ≤ 100 ms and firing rates were lower than those in later task stages.

We further quantified neural responses by computing average firing rates per stage across all trial blocks (Fig. 3, right). Three of the neurons illustrated increased their firing rate in stage 2, subsequent to hand contact with the object, but they exhibited different patterns of peak firing. The neurons in Fig. 3, A and B fired at peak rates in stage 3 as grasp was secured (magenta); their activity declined during lift. Other S-I neurons fired at the highest rates at contact (not shown), or in later epochs, during the transition from static grasp to lift, as the

applied load force exceeded the object weight (Figs. 1 and 2). Still other S-I neurons, located more medially, fired maximally during lift (Fig. 3D), or were broadly tuned, firing at high rates throughout the entire period of grip force application (Fig. 3C). In this manner, the transition between task stages was signaled by the relative rise and fall in firing rates among the population of neurons.

Response profiles were classified according to the stage(s) of peak firing and subdivided into groups tuned to single stages, to two sequential stages, or three or more successive actions (Table 1). Response types within S-I fell along a continuum as peak activity shifted between neuronal subpopulations when the object was acquired and lifted. The spike trains of these neurons bridged the various stages of the prehension task, marking their sequential performance. Similar response patterns were recorded from all three animals regardless of the particular hand postures adopted by each of them to perform the task.

Hand contact and grasp were the most effective stimuli for 63% (38/60) of task-responsive neurons in S-I. Contact–grasp neurons (Type 2.5) were the most common type observed, particularly in area 2; they formed 20% of the S-I population. Their mean firing rates did not differ significantly during stages 2 and 3, but were higher than those in the preceding or subsequent stages (Fig. 3A). PSTHs of contact–grasp neurons typically peaked late in the contact stage as the object was secured in the hand. The contact and grasp stages also evoked peak firing in the broadly tuned class (Type BT), but high firing rates persisted in these cells through lift (Fig. 3B). BT neurons constituted 17% of the S-I population (Table 1).

In addition to neurons bridging both the contact and grasp stages, we also recorded neurons whose firing rates were significantly higher in stage 2 or 3 than during other hand actions in the task. Contact-tuned neurons (Type 2) were more prevalent in areas 3b and 1 than in area 2; they fired at significantly higher rates during the contact stage than during static grasp, signaling motion of the hand over the object before grasp was secured. Many of these neurons were inhibited during subsequent task stages, particularly in the hold stage. Unlike contact-tuned neurons recorded in PPC, Type 2 neurons in S-I did not show significant increases in firing rates during approach. Neurons tuned to grasping (Type 3) were less common than contact–grasp cells, in part because static grasp

was the shortest duration stage. Instead, hand movements transitioned rapidly and smoothly from contact through grasp to lift (Gardner et al. 2007).

The later task stages evoked much weaker responses in the S-I hand area. Firing rates were reduced in 43 of 60 S-I neurons during lifting and only three neurons were classified as lift-tuned (Type 4, Fig. 3D). Neural activity dropped still further in the population during holding. Only 14 of 60 neurons fired at higher rates during stage 5 than in stage 4 and none of the cells tested fired maximally during the hold stage. Only five of 60 cells were classified as lower-tuned or relax-tuned, firing at the highest rates as the hold stage ended and the object was discarded from the hand.

Neurons tuned to hand actions before contact were relatively rare in S-I. Only two of 60 neurons fired at significantly higher rates during approach than at contact (Type 1, approach-tuned). Firing rates were higher in the contact stage in 41 of 60 S-I neurons; the difference was statistically significant ($P < 0.05$) in 29 of these cells.

A small group of S-I neurons, called grasp-inhibited (Type GI) cells, showed a sharp drop in firing rates during the initial task stages as the object was first acquired (Ro et al. 2000). Some of these cells subsequently increased their firing rates above background as the grip was relaxed (Type 7, relax-tuned; not shown).

M-I responses bridged actions from approach through lift

We made only a limited number of recordings in the hand representation of primary motor cortex (M-I), so our survey of the responses in this region was not as comprehensive as that in S-I and PPC, possibly posing some sampling biases with respect to the population representation of specific hand actions in M-I. Nevertheless, we were able to attain a general sense of the predominant responses to prehension found in this cortical region, and these parallel the characteristics of M-I responses reported in earlier studies of precision grasp (Baker et al. 2001; Cadoret and Smith 1996; Maier et al. 1993; Picard and Smith 1992a,b).

M-I responses in the hand area often began as early as those in PPC, sometimes before reaching movements were visible in the video records. For example, firing rates of the neuron shown in Fig. 4 rose about 500 ms before contact, at or slightly before the onset of approach (gold). Activity peaked at contact

TABLE 1. *Distribution of response classes in the cortical population analyzed*

Response Class	Label	SI Cortex		MI Cortex		PPC Cortex	
		Total cells %	Total	Total cells %	Total	Total cells %	Total
Broadly tuned	BT	10	16.7	3	18.8	54	42.2
Approach tuned	1	2	3.3	1	6.3	13	10.2
Approach-contact	1.5	7	11.7	3	18.8	12	9.4
Contact tuned	2	7	11.7	3	18.8	21	16.4
Contact-grasp	2.5	12	20.0	3	18.8	8	6.3
Grasp tuned	3	5	8.3	3	18.8	4	3.1
Grasp-and-lift	3.5	4	6.7	0	0.0	2	1.6
Lift tuned	4	3	5.0	0	0.0	1	1.6
Hold tuned	5	0	0.0	0	0.0	0	0.0
Lower tuned	6	2	3.3	0	0.0	3	2.3
Relax tuned	7	3	5.0	0	0.0	1	0.8
Grasp inhibited	GI	5	8.3	0	0.0	9	7.0
Total		60	100.0	16	100.0	128	100.0

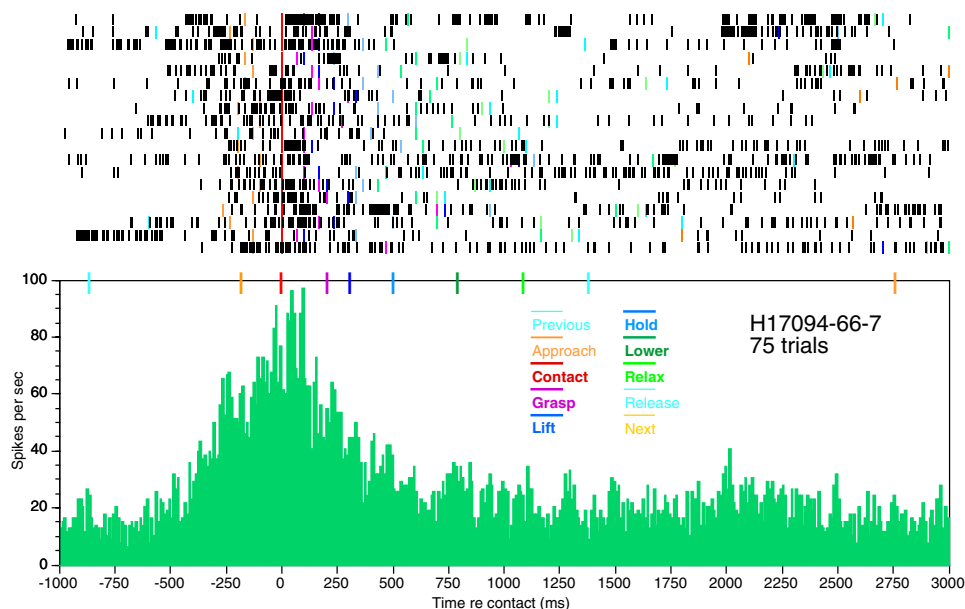


FIG. 4. Rasters of the first 20 approach trials and PSTH aligned to contact from an area 4 neuron recorded in Monkey H17094; same format as that in Fig. 2. This cell began firing before the onset of the approach stage (gold trace), fired at peak rates during approach and contact (stages 1 and 2), and decreased firing during lift. Unit H17094-66-7; deep receptive field at metacarpophalanges (MCP) of digits 4 and 5.

(red) and declined after grasp was secured (magenta). This spike train resembled the acquisition responses we observed in PPC, in that increased firing rates coincided with the planning and initial stages of object acquisition, and persisted through lift. Responses were weaker on trials when the same knob was regripped without a distinct reach.

Other neurons in M-I were more narrowly focused on specific components of the prehension task. An example of an M-I neuron whose firing rates were correlated with hand preshaping during approach is presented in Fig. 5. In this 16-s excerpt from a longer video clip, each of the prominent bursts began at the onset of approach and ended at contact. The images below the burst analysis traces were captured at the peak of bursts A–D. Maximum firing occurred midway through the reach on each trial, as the hand was preshaped to grasp an object. Firing rates were high regardless of whether the target object was the rectangle knob (A), the large round (B, D), or small round knob (C). Similarly, high firing appeared to be

independent of the direction or trajectory of reach. Burst A began as the hand moved downward from the upper plates of the chair. Bursts B and D were evoked during lateral reaches to the right and burst C during medial reach to the left. Instead, high firing rates coincided with the opening of the hand as the fingers extended for efficient grasping. The bursts were succeeded by a period of inhibition in which firing rates dropped to low levels as the knob was enclosed in the hand during grasping. Note that there was little change in firing rates after trial D when the animal lifted the same knob again without relaxing the grasp (T = 14 s).

The sensitivity of this neuron to hand preshaping during approach was replicated when the entire response history was examined. PSTHs compiled from all 30 trials indicated that firing rates rose before the start of reach, often coincident with release of a knob from the hand and extension of the fingers (Fig. 6A). Activity was highest midway through approach and decreased during deceleration as the hand

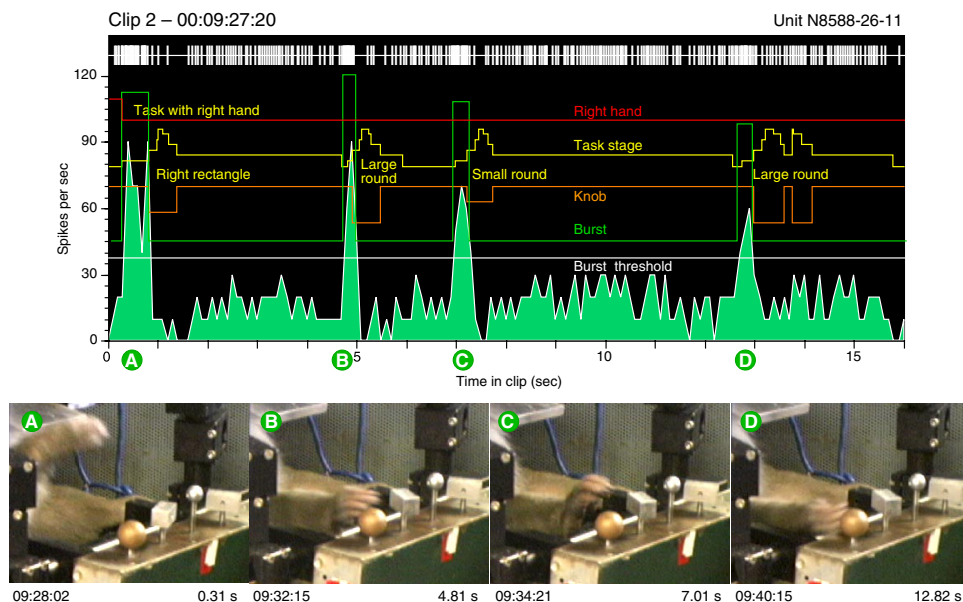


FIG. 5. Burst analysis graphs of continuous neural and behavioral activity recorded in area 4 of Monkey N18588 during a 16-s period. Same format as that in Fig. 1. Firing began at or before the start of approach, peaked during hand preshaping, and declined at contact. Grasp and lift actions appeared to inhibit the firing rate of this neuron. Images below the burst analysis graph were captured at the peak of bursts A–D. A: forward reach from above the workspace. B–D: lateral reach between knobs. Note the preshaped posture of the hand in each image.

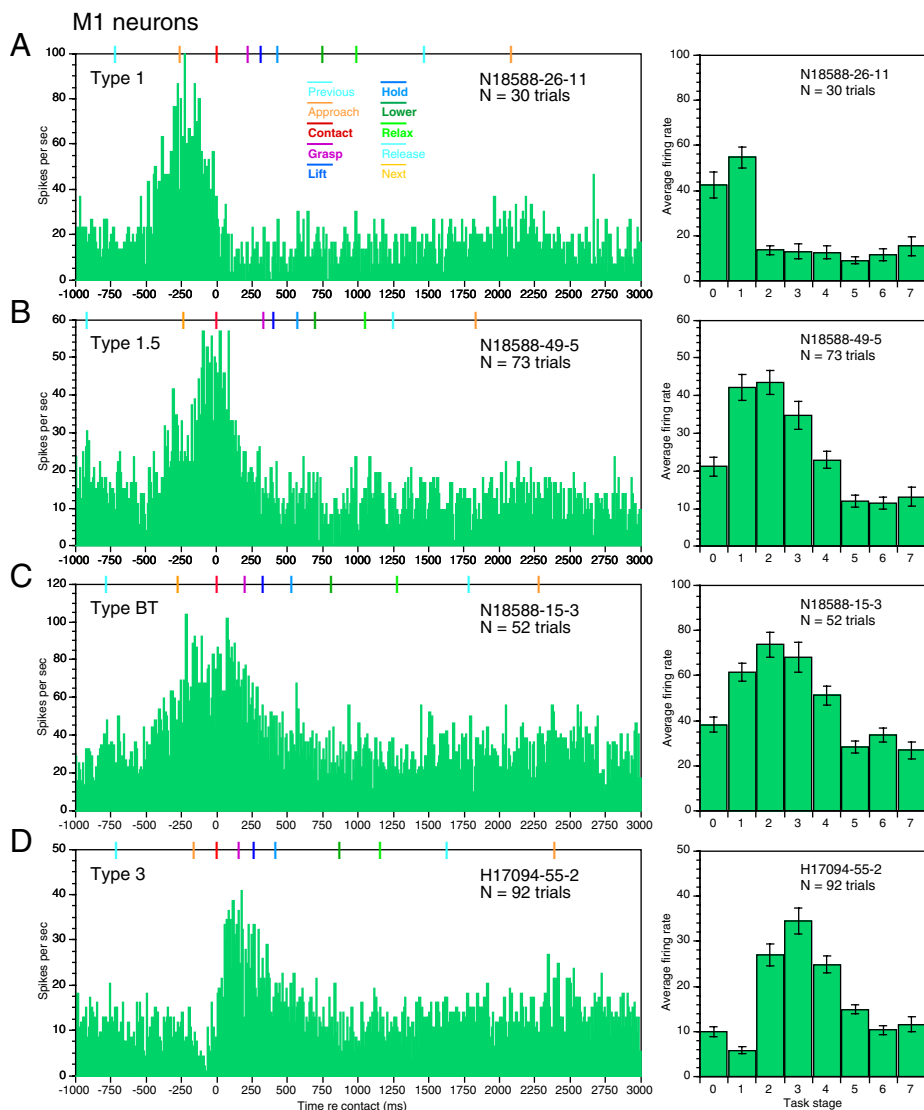


FIG. 6. PSTHs (left) and average firing rate graphs (right) for neurons recorded in area 4 of M17094 and M18588. Same format as that in Fig. 3. *A*: approach-tuned (Type 1) response. Unit N18588-26-11; deep receptive field at MCP of digits 2–5. *B*: approach-contact (Type 1.5) response. Unit N18588-49-5; receptive field on the glabrous skin of digits 3, 4, and 5 and the glabrous/hairy skin of the ulnar side of the hand. *C*: broadly tuned (BT) responses. Unit N18588-15-3; receptive field on glabrous skin of digits 2–5 and the palm. *D*: grasp tuned (Type 3) response. Unit H17094-55-2; receptive field on the hairy dorsum of the hand and arm, from digit 1 to the distal forearm.

velocity slowed before contact. Firing rates remained low during the remainder of the task and then rose slightly after grasp was relaxed.

The rise in firing during approach was observed in M-I neurons in all three animals studied, although the timing of peak activity differed among individual neurons. PSTHs and average firing rate graphs of the major types observed in M-I are illustrated in Fig. 6. Responses to prehension in the hand area of M-I were focused on object acquisition and grasping, but there was no preference in response class in the small population analyzed (Table 1), nor did we observe significant differences in response time course between animals. It is likely that the diverse response patterns reflected the various muscle groups innervated by each of the M-I neurons analyzed. Some neurons were most active as the hand was preshaped during approach (Type 1, Fig. 6A). Others bridged the approach and contact stages as the hand was positioned for grasping (Type 1.5, Figs. 5 and 6B), or were broadly tuned, firing at peak rates at contact (Type BT, Fig. 6C). Another group of M-I neurons was most sensitive to grasping (Type 3, Fig. 6D); their firing rates paralleled previously described patterns of grip and load force application during prehension in

monkeys (Brochier et al. 2004; Cadoret and Smith 1996; Maier and Hepp-Raymond 1995; Maier et al. 1993).

Population activity in S-I, M-I, and PPC during prehension

To compare neural responses to prehension in the cortical populations studied, we examined three characteristics of average firing rate profiles: 1) the stages of peak firing, 2) mean normalized firing rates, and 3) the proportion of the population showing significant excitation and inhibition during each task stage. For comparative purposes we included population data obtained in areas 5 and 7b/AIP in these same animals.

To determine the actions most strongly represented in each cortical area, we grouped neural responses as a function of the task stage in which maximum firing occurred. The population data, shown as stacked bar graphs in Fig. 7, were subdivided by animal tested (*left panels*) and response classes as defined in Table 1 (*right panels*). Hand actions required for object acquisition evoked the greatest responses in S-I, M-I, and PPC. The initial hand contact with the object in stage 2 evoked the strongest firing rates, ranging from 37% of S-I neurons (22/60), 38% of PPC cells (49/128), to 44% in M-I (7/16). However,

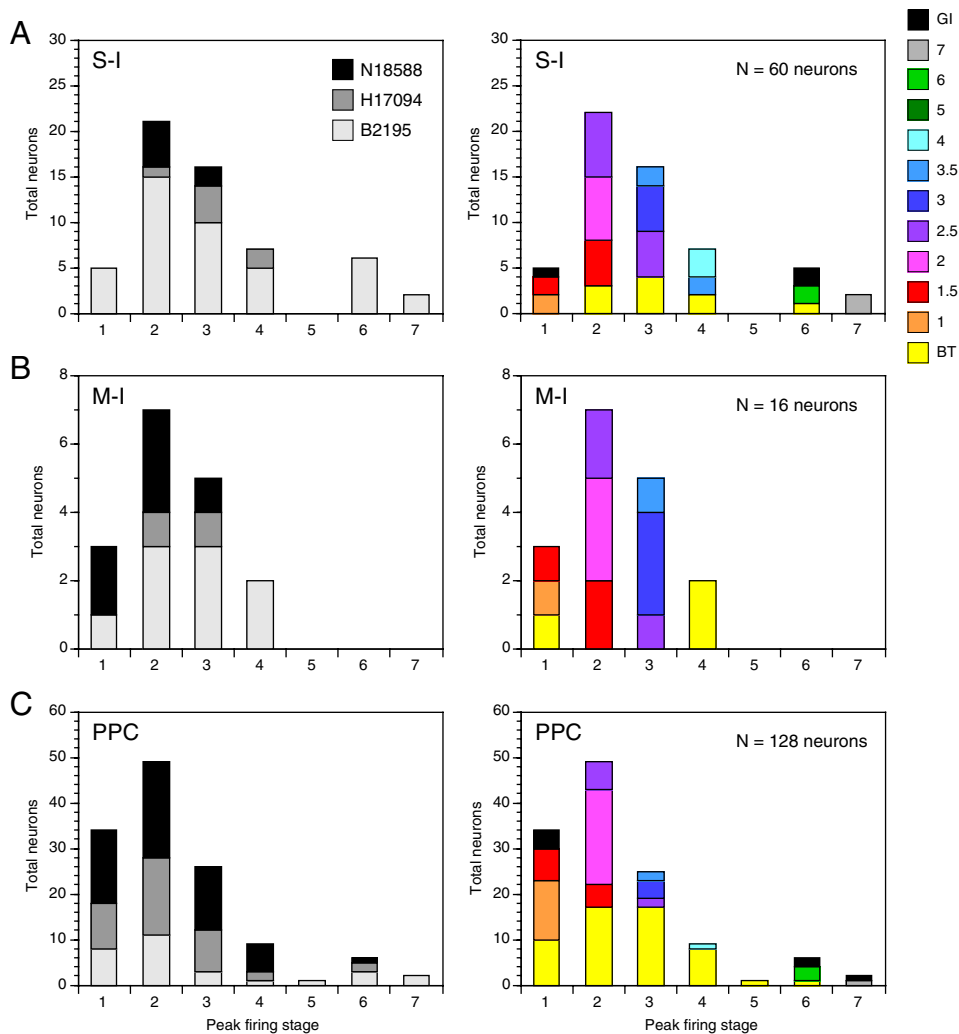


FIG. 7. Stacked bar graphs of the number of primary somatosensory (S-I) cortex, primary motor (M-I) cortex, and posterior parietal cortex (PPC) neurons (A–C) showing peak firing during each task stage; data from areas 5 and AIP/7b have been pooled in C. *Left:* gray scale indicates the total neurons recorded in each of the 3 animals studied. *Right:* color scale indicates the response class of each neuron as defined in Table 1. Object acquisition in stages 1–3 evoked stronger responses than manipulation (stages 4 and 5) or discarding the object (stages 6 and 7). Neurons in all 3 cortical areas, and in each animal, were most likely to fire at peak rates at contact (stage 2). Approach (stage 1) was the second most common period of peak activity in PPC, but was poorly represented in S-I. Grasping (stage 3) evoked stronger responses in S-I and M-I than in PPC. Holding (stage 5) evoked peak firing in only one neuron in PPC and none in the other areas studied.

only 32% of S-I neurons (7/22), 41% of PPC cells (20/49), and 43% in M-I (3/7) were contact-tuned (Type 2); the majority of neurons in each area also showed strong excitation during one or more neighboring stages that did not differ significantly from that in the preferred contact stage.

Grasping was also strongly favored by neurons in S-I and M-I, constituting the preferred action of roughly 25% of neurons in these areas, but grasp-tuned (Type 3) responses were in the minority. Grasping was less strongly represented in PPC, where only 20% (25/128) fired at peak rates in stage 3, 68% (17/25) were broadly tuned, and 16% (4/25) were grasp-tuned.

The approach stage was the second most favored action in PPC, where 27% of neurons (34/128) fired at highest rates before the hand touched the object. In contrast, only 8% of S-I neurons (5/60) responded at the highest rates during approach. The least favored action in all three areas was holding; only one of the 204 task-related neurons fired maximally in stage 5 and this cell was broadly tuned.

Although each of the monkeys contributed different numbers of neurons to the populations recorded in each area and used individualized hand postures to grasp the objects, the same response preferences were observed in all three animals studied (Fig. 7, *left*). Contact in stage 2 was the preferred action of each animal and in each cortical area. Grasping was the

second most preferred action in S-I of all three monkeys and approach was preferred in PPC. The total sample from M-I was too small to draw definite conclusions concerning the relative preference for approach and grasp in these animals.

These same trends emerged when population mean firing rate graphs were analyzed. The average firing rate graph of each task-related neuron was normalized as a function of the firing rate during the peak stage and multiplied by 100. Population firing rate profiles were compiled by averaging the normalized responses of all neurons recorded in each region and are displayed in Fig. 8. Although there was considerable overlap between the spike trains in all four areas, the population averages clearly indicate that PPC neurons as a group were activated earlier than those in S-I and fired at higher rates before contact. Hand actions during approach were ineffective in driving S-I neurons because the population mean firing rate in stage 1 barely exceeded the background rate in stage 0 and was significantly lower than that in later task stages. M-I neurons fired at intermediate rates during approach, whereas firing rates of PPC neurons in this epoch nearly matched those evoked by contact and exceeded activity during grasping.

Because contact was the most likely behavior to evoke maximum activity, it is not surprising that firing rates were highest during stage 2 in all four areas. However, the strong representation of grasping in both S-I and M-I resulted in firing

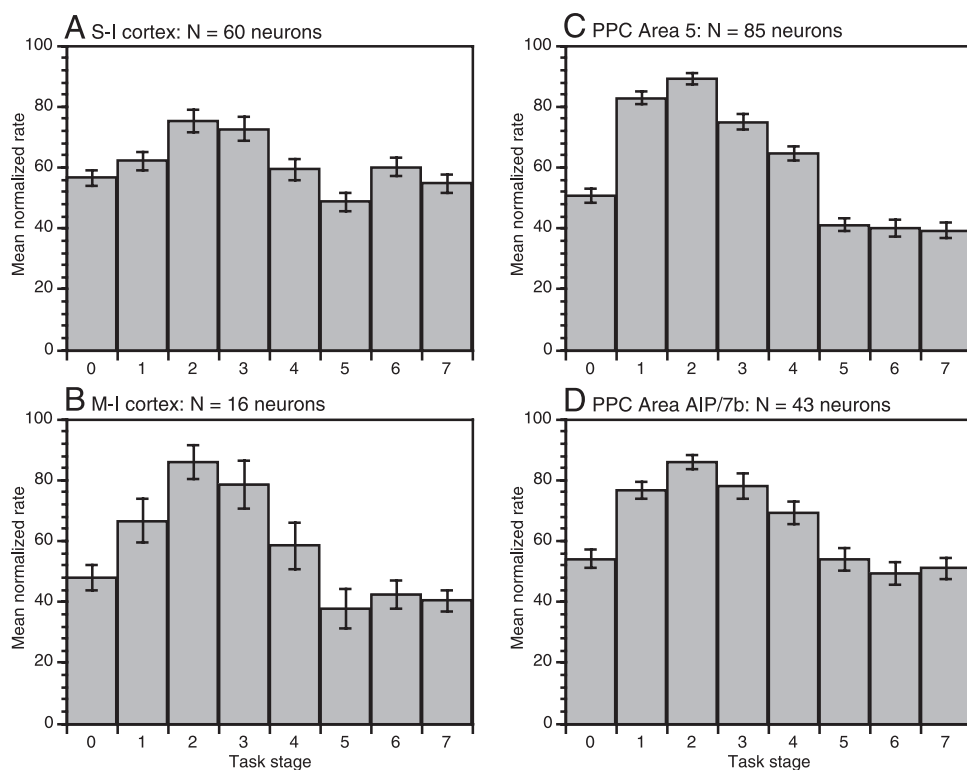


FIG. 8. Population normalized mean firing rates (\pm SE) averaged across the entire set of neurons analyzed in S-I (A), M-I (B), PPC area 5 (C), and PPC area AIP/7b (D). Population mean normalized rate was highest in stage 2 in all 4 areas. Mean firing rates were significantly higher than baseline (stage 0) during stages 1–4 in PPC and in M-I, but only in stages 2 and 3 in S-I.

rates in stage 3 that did not differ significantly from those evoked in stage 2. Grasping was less effective in activating neurons in area 5 than hand preshaping during approach, but still provided strong excitation to a large fraction of the PPC population.

Object manipulation was less effective when the hand and the object moved as a functional unit. Lifting evoked weaker responses than grasping in the S-I hand area because the average firing rates in stage 4 did not exceed background. The low mean response to lifting appeared to reflect differing sensitivities to this behavior within the S-I population, in that some neurons were excited and others inhibited during this stage. Lifting also evoked weaker responses than grasping in the hand representations of M-I and PPC, but the population mean firing rate still exceeded pretrial values.

Activity during holding in stage 5 dropped below baseline in all four areas, reflecting both weak excitation and strong inhibition during maintained grasp. A secondary weak rise in firing rates occurred in S-I during stage 6 as the knob was lowered and the grip relaxed. Responses were suppressed in the other areas analyzed.

A final measure of population activity is illustrated in Fig. 9, which shows the percentage of task-related neurons in S-I, M-I, and PPC that were significantly excited or inhibited during each of the task stages ($P < 0.05$). These measurements were made by statistical comparison of firing rates evoked by each action to the pretrial baseline rate in stage 0. As with the other population metrics, the greatest difference between cortical regions occurred in stage 1. Approach and hand preshaping before contact was the most effective driving force in PPC, producing significant excitation in 83% of area 5 neurons and 72% in area AIP/7b. In contrast, only 28% of S-I neurons showed a significant rise in firing rate during approach and these cells fired at higher rates later in the task. Excitation in

S-I began later in time than in M-I or PPC, typically preceding contact by ≤ 100 ms. M-I neurons occupied an intermediate position in this temporal hierarchy. Forty-four percent of M-I neurons showed significant excitation in stage 1 and they had the longest lead times, ranging ≤ 500 ms before contact.

Behaviors involved in object acquisition were very effective stimuli in all four cortical areas. Hand contact with the knob excited the greatest number of neurons in both S-I and M-I cortices and was nearly as effective as approach in activating PPC cells. Between 65 and 80% of these neurons showed significant excitation during stage 2. Surprisingly, S-I had the lowest percentage of excited neurons during stage 2, in part because neurons with proximal receptive fields on the palm were not stimulated until the knob was fully grasped in the hand. Grasping also provided strong excitation, activating 60% of neurons in both S-I and PPC and 75% of neurons tested in M-I.

Significant excitation decreased in S-I and M-I as hand actions progressed from acquisition to manipulation. Only about one third of S-I and M-I neurons fired at rates above baseline during lift, whereas excitation was maintained at high rates in roughly 60% of area 5 and AIP/7b neurons. This suggests that somatosensory information from the hand and arm may have converged on PPC neurons or persisted longer in PPC than in primary somatosensory or motor cortical areas. Furthermore, inhibition emerged as an important component of neuronal activity in these areas as lift began.

Suppression of firing below baseline was most prominent during holding, when 25–40% of cortical neurons were inhibited. The percentage of inhibited neurons equaled or exceeded those excited in stage 5 by maintained grip and load forces on the object.

Lowering of the knob in stage 6 produced a second wave of excitation in S-I, where 27% of neurons responded. In contrast,

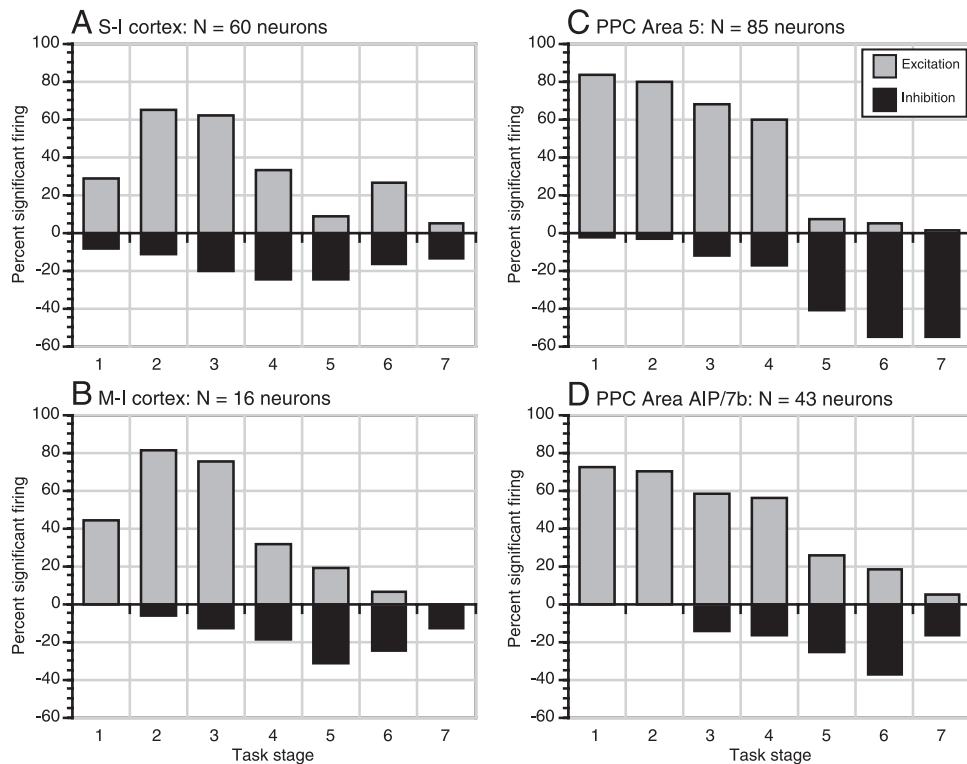


FIG. 9. Bar graphs showing the percentage of neurons exhibiting significant excitation (gray bars) and inhibition (black bars) during the 7 task stages ($P < 0.05$). Excitation occurred most frequently during stages 2 and 3 in S-I and M-I and during stages 1 and 2 in PPC. Excitation started earlier and was sustained longer in PPC than in S-I and M-I. Inhibition was strongest during the late task stages in PPC.

excitation diminished in M-I and PPC as inhibition continued to grow in strength. This change in excitability set the stage for the end of the trial and subsequent acquisition of other objects.

DISCUSSION

Our studies of the neural correlates of prehension in primary somatosensory cortex, primary motor cortex, and posterior parietal cortex are the first to examine multiple stages of information processing from the hand in the same individual animals engaged in a trained prehension task. The main finding from the current study is that the timing of firing differed significantly between these cortical areas. In this report, we demonstrated that task-related activity began and peaked earlier in M-I and in PPC than in S-I. The specific temporal patterns of activity during successive task stages suggest distinctive functional roles for each of these cortical areas.

Somatosensory inputs to S-I cortex during prehension

The important features of prehension encoded by S-I neurons appeared to be the tactile stimulation at contact as the hand was positioned to grasp and the grip and load forces applied by the hand to the object. In all, 63% of task-related neurons responded at peak rates in the contact or grasp stages and another 20% highlighted lift or lowering. The remainder of the population were divided between selectivity for approach or relaxation of grasp; these cells were typically inhibited during prehension. In this manner, the transition between task stages was signaled by the relative rise and fall in firing rates among overlapping populations of S-I neurons.

Each of the three monkeys tested used a distinctive hand posture for object acquisition and manipulation (Gardner et al. 2007). One of the animals (B2195) placed the hand on the top

of the knob and pushed it upward, another grasped the side of the object lifting it by wrist movements (H17094), and the third placed the fingers under the knob scooping it upward (N18588). Nevertheless, the response profiles of all three animals were similar in time course, strengthening findings reported in our earlier studies of prehension (Debowy et al. 2001; Gardner et al. 1999, 2002).

Similar sensitivity of S-I neurons to grasping was previously reported by Wannier et al. (1986, 1991) and by Salimi et al. (1999) using a precision grip task. Both groups found that nearly 60% of S-I neurons representing the thumb and/or index finger showed phasic or phasic-tonic increases in firing rates in parallel with the application of grip force by these fingers. Another nearly 25% of S-I neurons displayed tonic responses to grasp and holding; the remainder were inhibited during grasping. However, neither of these studies analyzed responses to reach or hand positioning on the object before grasp. Instead, the animal simply pinched the manipulandum between the thumb and index finger. The wider range of hand movements required in our task emphasized the importance of S-I responses in monitoring the actual grasping actions during prehension tasks.

The modulation of S-I firing rates during prehension appears to parallel the time course of responses recorded in cutaneous afferents during similar tasks (Johansson and Westling 1984, 1987; Westling and Johansson 1984, 1987). Firing rates of RA, SAI, and SAI receptors rise sharply when an object is first touched and increase still further during grasping, signaling the rate and amplitude of grip and load forces applied by the hand. SAI and SAI receptors remain active at the onset of lift, but firing rates decline somewhat during holding and return to baseline levels when the grasp is relaxed. RA afferents cease firing as lift begins, when the grip and load forces stabilize.

They usually fire a second, weak burst as the grip is relaxed and contact with the object is broken. PC afferents signal transient mechanical perturbations of the object at contact, lift-off, return to rest, and release of grasp. In this manner, the strongest afferent signals from the glabrous skin occur at contact and at grasp, paralleling the stages in which S-I neurons were most active in our task. In addition, tactile information from the object detected by receptors in glabrous skin may be enhanced by afferent signals from the hand dorsum as the skin is stretched during flexion movements (Edin 1992, 2004; Edin and Abbs 1991; Edin and Johansson 1995). Neural activity in the afferent population is likewise reduced during holding as RAs are silenced and may be extinguished during the late stages when SA responses cease. The brief activation of RA and/or PC afferents in response to hand movement off of the object is paralleled by weak responses observed in some S-I neurons during the lower and relax stages.

Tactile signals from the hand concerning object properties are important factors governing force application during grasping. Local anesthesia of the glabrous skin results in delayed load force application after contact and unusually high grip forces (Jenmalm and Johansson 1997; Johansson et al. 1993; Monzee et al. 2003). Furthermore, Johansson and colleagues recently demonstrated that information about surface texture, object shape, and the angle of finger contact may be conveyed to the motor cortex by S-I at the very onset of touch, by the specific populations of cutaneous afferents activated in each fingertip (Birznieks et al. 2001; Jenmalm et al. 2003; Johansson and Birznieks 2004). More natural modes of prehension, such as those used in our paradigm, include reach toward the object, with subsequent positioning of the hand after contact. The tactile information provided by sliding the fingers over the surface of the object may supplement the features conveyed by the initial spikes, further refining the motor programs for grasp.

Precontact activity was observed in roughly 27% of S-I neurons, but it was weaker and less common than that in PPC and occurred closer to the moment of contact. Responses evoked in S-I before tactile stimulation were also previously reported in other studies of active hand movements (Nelson 1987; Soso and Fetz 1980; Wannier et al. 1991). These early responses in S-I were attributed to efference copy of the motor commands transmitted from M-I to spinal motoneurons or intention-related input from PPC neurons. Either type of reafference would help to shape somesthetic expectations related to hand-object interactions. This early S-I activity is not observed during passive stimulation of the hand, highlighting an important difference between active and passive somatosensory processing.

M-I responses in the prehension task

Corticomotoneurons in the hand area of M-I cortex provide the principal cortical output pathway to motoneurons involved in precision grasp tasks (Baker et al. 2001; Buys et al. 1986; Lemon 1993; Maier and Hepp-Reymond 1995; Maier et al. 1993; Picard and Smith 1992a,b; Shimazu et al. 2004). Although we evaluated a relatively small population of neurons in the M-I hand representation, we found a variety of response classes correlated to specific stages of the task. These included neurons activated by 1) hand preshaping during approach, 2)

positioning of the fingers at appropriate grasp sites on the object, or 3) application of grip and load forces on the object.

M-I neurons were active earlier in the task than those in S-I. Nearly 45% of M-I cells increased their firing rates significantly as the animal reached toward an object, preshaping the hand for efficient acquisition; 19% of these cells fired at peak rates during approach and were inhibited during grasping. Thirty-seven percent of M-I neurons responded most vigorously at contact and another 27% were most sensitive to grasping actions, with firing rates that paralleled the application of grip and load forces needed to lift the object. These responses to whole hand grasp resembled activity previously described by others using precision grip tasks (Cadoret and Smith 1996; Lemon et al. 1995; Maier and Hepp-Reymond 1995; Maier et al. 1993; Muir and Lemon 1983; Picard and Smith 1992a,b; Wannier et al. 1991).

The segregation of M-I neurons in distinct functional groups appears to reflect the different muscle synergies needed to accomplish actions required in each stage. Recent electromyographic studies in monkeys by Brochier et al. (2004) demonstrated that different muscle groups in the hand are activated during preshaping, grasping, and manipulation of objects. A similar fractionation of hand muscle groups and corticospinal pathways was demonstrated in humans using transcranial magnetic stimulation applied over the hand area of motor cortex during a prehension task similar to ours (Johansson et al. 1994; Lemon et al. 1995).

In contrast, we previously reported that activity of PPC neurons in these same animals spanned the period of activation of both M-I and S-I neurons (Gardner et al. 2007). Eighty percent of PPC neurons showed a significant rise in firing during approach and the high firing rates were sustained in >60% of the population through lift. Firing rates in PPC declined sharply during hold and the pattern of spiking changed from excitation to inhibition. The differences in temporal response profiles have important functional implications for neural control of prehension by cortical circuits.

Neural network models of prehension

Johansson and colleagues proposed that prehension involves both feedforward and feedback neural networks that plan and implement the various motor programs needed to accomplish the task goals (Johansson 1996; Johansson and Cole 1992; Johansson and Edin 1993). Prehension is initiated using feedforward networks in which visual information about the object's size, shape, and location in the workspace and somatosensory inputs about the hand posture are combined with sensorimotor memories, to construct internal models of the hand shape and grip forces needed for grasping. This process of *anticipatory parameter control* allows rapid movement execution by relying on experience to control the timing of muscle activation in the hand. It is efficient because long-loop feedback to the cortex after contact is unnecessary for initiating grasp. Subjects predict what an object should feel like in the hand as it is viewed and formulate a grasp program. Vision and experience set the context in which ascending tactile information is interpreted after the object is touched.

Prediction operates at several key time points in prehension tasks. During approach, prediction governs the opening of the hand and orientation of the wrist to allow efficient acquisition.

The grip aperture is usually proportional to object size and is widest during deceleration as the hand approaches the target in both humans and monkeys (Chieffi and Gentilucci 1993; Jeannerod et al. 1995; Lemon et al. 1995; Roy et al. 2000, 2002). Prediction also aids selection of appropriate contact points on the object that promote grasp stability and efficient manipulation after grasp (Jenmalm and Johansson 1997; Jenmalm et al. 2000; Johansson et al. 2001). Specific hand postures and grasp sites are better suited to lifting than to pushing, pulling, or rotational actions.

A third important prediction involves the coordinated application of grip and load forces on the object once the desired hand position has been achieved (Flanagan and Wing 1997; Gordon et al. 1993; Jenmalm et al. 2006; Johansson and Westling 1988; Schmitz et al. 2005; Westling and Johansson 1984). Stability of the object in the hand during manipulation requires that sufficient grip force be applied to prevent slippage from the hand, but excessive force is avoided to prevent damage to the object as the result of crush, injury of the hand from breakage, or fatigue of hand muscles. Similarly, load forces should be applied at rates appropriate to the manipulatory goals after acquisition.

Prediction interacts with direct sensory feedback from the hand during performance of prehension tasks as contact is made with the object, grasp is secured, and manipulation begins. Johansson and colleagues describe the sensory information that signals completion of one task stage to allow rapid transition to the next planned action as *discrete event, sensory-driven control*. This process includes error signals of a mismatch between expectation and performance of the task, requiring corrective responses. Somatosensory and visual feedback may guide implementation of the original plan or may modify the expected movement. As such, the sensory signals serve to strengthen grasp motor programs when they are successful or to initiate corrective actions if errors such as slippage occur.

The data presented in this report and in the companion study of PPC (Gardner et al. 2007) support the notion that the predictive and planning aspects of prehension are strongly represented in PPC and its projection targets in premotor cortex, whereas the performance and feedback circuitry appear to dominate activity in M-I and S-I (Fogassi and Luppino 2005; Jeannerod et al. 1995; Rizzolatti and Luppino 2001). Our findings are summarized in Fig. 10, which provides a simplified diagram of the principal inputs and outputs of the brain areas studied with our prehension task. All of the cortical areas outlined in this figure are activated in functional imaging studies of prehension in humans (Binkowski et al. 1998, 1999; Culham et al. 2003; Ehrsson et al. 2000, 2001, 2003; Frey et al. 2005; Jenmalm et al. 2006; Schmitz et al. 2005). However, the relative timing of responses in these regions was derived primarily from single-unit studies in monkeys.

In our task, a trial began with a visual cue presented on a computer monitor signaling the location of a rewarded object. Vision provided two essential components for guiding object selection: 1) precise localization in space by gaze fixation to direct the arm to the target (Johansson et al. 2001) and 2) detailed representation of intrinsic object features (size, shape, texture) needed to preshape the hand and define the initial grasp posture. The visual information is communicated through multiple synaptic relays to area AIP where visuomotor

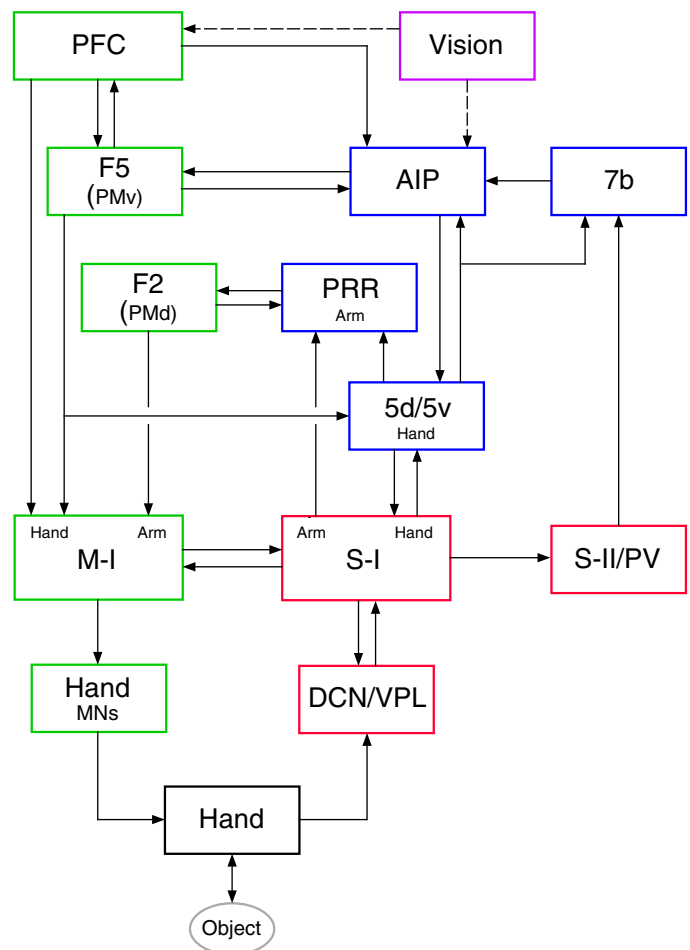


FIG. 10. Simplified schematic block diagram of the input and output connections of cortical areas studied with our prehension task. Somatosensory areas (red): DCN/VPL (dorsal column nuclei and ventral posterolateral nucleus of the thalamus), S-I (primary somatosensory cortex, areas 3a, 3b, 1, and 2), and S-II/PV (secondary somatosensory and parietal ventral cortex). Posterior parietal areas (blue): 5d/5v (rostral end of superior parietal lobule), PRR (parietal reach region, caudal end of superior parietal lobule), AIP (anterior intraparietal area of inferior parietal lobule), and 7b (lateral convexity of the inferior parietal lobule). Frontal motor areas (green): PFC (prefrontal cortex), F5 (ventral premotor cortex), F2 (dorsal premotor cortex), and M-I (primary motor cortex). Other important frontal motor areas that project to M-I, such as the supplementary motor area (SMA) and cingulate motor area (CMA), are not shown, nor are the corticomotor pathways to spinal interneurons from M-I and F5. Visual areas (violet): for simplicity, the visual pathways from the retina to area AIP and PFC have been compressed into a single box that includes important visuomotor centers of PPC such as areas LIP, CIP, 7a, and V6A; the dashed arrows denote polysynaptic pathways. Spinal, brain stem, and thalamic areas are color-coded by their major cortical input or output targets. See text for further description.

neurons respond to viewing and grasping objects (Fogassi and Luppino 2005; Jeannerod et al. 1995; Murata et al. 2000; Sakata et al. 1995; Selzer and Pandya 1980; Taira et al. 1990). Proprioceptive information from the hand is likewise communicated to area AIP and to neighboring regions of area 7b from area 5 (Neal et al. 1986). Stored representations of objects in prefrontal cortex (PFC) can substitute for direct vision when such tasks are performed in the dark or when view of the object is blocked.

Sensorimotor representations of the object are communicated from area AIP to ventral premotor cortex (area F5) where objects have been shown to be represented in terms of the

actions needed to grasp them (Jeannerod et al. 1995; Luppino et al. 1999; Murata et al. 1997; Raos et al. 2006; Rizzolatti and Luppino 2001). Motor signals from F5 are then communicated to the M-I cortex and to area 5 in PPC (Cavada and Goldman-Rakic 1989; Cerri et al. 2003; Ghosh and Gattera 1995; Ghosh et al. 1987; Godschalk et al. 1984; Matelli et al. 1986; Shimazu et al. 2004), as well as to spinal motoneurons and interneurons controlling hand movements (not shown in Fig. 10).

The timing of neural activity in area AIP, area 5, and in M-I documented in this report and in our earlier study of PPC (Gardner et al. 2007) suggests that these areas play an important role in hand preshaping during approach. This is supported by lesion studies in humans (reviewed in Milner and Goodale 1995) and by muscimol injections into areas AIP and F5 (Fogassi et al. 2001; Gallese et al. 1994) in which hand preshaping is impaired.

The accuracy of the projected hand posture is tested when the hand contacts the object and is positioned to grasp it. We demonstrated in this report that strong tactile and proprioceptive signals from the hand are relayed back to the S-I cortex, particularly during the initial period of object acquisition. Sensory feedback to S-I is crucial for skilled hand behaviors of various types. Grasping and manipulation are severely impaired in monkeys by muscimol injections into S-I (Brochier et al. 1999; Hikosawa et al. 1985), by surgical lesions to the dorsal columns (Glendenning et al. 1992; Leonard et al. 1992), and in humans by damage to the postcentral gyrus (Binkowski et al. 2001; Freund 2001; Pause et al. 1989; Scholle et al. 1998).

S-I activation plays a critical role in adjustment of grasp and load forces in normal subjects when the predictions of planned actions turn out to be incorrect. In a recent functional MRI study of prehension, Jenmalm et al. (2006) reported selective activation of contralateral S-I and M-I in humans when object weight was heavier than predicted. The subjects responded by slow increases in applied grip and load forces until the object was successfully lifted. On subsequent trials, the subjects lifted the heavy weight rapidly and smoothly, having made the appropriate adjustments to the planned action, and S-I and M-I activity returned to their previous levels. Interestingly, these cortical areas were not activated selectively when the object was lighter than predicted; rather cessation of the predicted motor program activated cerebellar circuits.

The anatomical projections from S-I cortex to other regions of the cerebral cortex suggest that the feedback projections from the hand serve a dual purpose. Direct, short-loop projections from S-I to M-I cortex (Darian-Smith et al. 1993; Jones et al. 1978) provide circuits for immediate adjustment of the grasp program needed to increase the force produced by hand motoneurons. In addition, the long-loop projections from S-I to area 5 (Jones and Powell 1969, 1970; Pearson and Powell 1985) and from PPC to frontal motor areas may serve to update future motor programs for grasping. In this manner, somatosensory feedback from the hand may reinforce its actions when they are successful and modify them when the task conditions are unexpectedly altered. The need for continuous sensory monitoring of prehension is demonstrated by the excessive force production observed when tactile feedback is interrupted by local anesthesia (Jenmalm and Johansson 1997; Johansson et al. 1993; Monzee et al. 2003).

Prehension tasks are but one example of self-generated skilled hand behaviors. Wolpert and colleagues distinguished active and passive touch by the notion of motor prediction (Bays et al. 2005; Blakemore et al. 1999; Flanagan et al. 2003; Wolpert and Flanagan 2001). During active touch, the motor system controls information flow through somatosensory pathways so that the subject can predict when feedback information should arrive in the S-I cortex. Internal representations of the expected inflow are implemented by corollary discharge from the motor system. Convergence of central and peripheral signals allows neurons in the parietal cortex to compare predictions and reality. Sensory information is therefore perceived in the context of the behavioral goals of the current task and may be attenuated in cases where the predictions are verified, or amplified when they fail.

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