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Behavioral Choice-related Neuronal Activity in Monkey Primary Somatosensory Cortex in a Haptic Delay Task

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Abstract

The neuronal activity in the primary somatosensory cortex was collected when monkeys performed a haptic–haptic DMS task. We found that, in trials with correct task performance, a substantial number of cells showed significant differential neural activity only when the monkeys had to make a choice between two different haptic objects. Such a difference in neural activity was significantly reduced in incorrect response trials. However, very few cells showed the choice-only differential neural activity in monkeys who performed a control task that was identical to the haptic–haptic task but did not require the animal to either actively memorize the sample or make a choice between two objects at the end of a trial. From these results, we infer that the differential activity recorded from cells in the primary somato-sensory cortex in correct performance reflects the neural process of behavioral choice, and therefore, it is a neural correlate of decision-making when the animal has to make a haptic choice.

INTRODUCTION

Perceptual decision-making refers to a cognitive process leading to an action selected among several alternatives. In this process, current information collected from sensory systems is compared and integrated with prior information stored in the brain to make a judgment toward an appropriate behavioral choice (Gold & Shadlen, 2007; Platt, 2002; Schall, 2001). The neural mechanism of decision-making has been studied at the single-unit level in monkeys performing sensory (e.g., visual or tactile) discrimination tasks (Pesaran, Nelson, & Andersen, 2008; Huk & Shadlen, 2005; Romo, Hernandez, & Zainos, 2004; Romo, Hernandez, Zainos, & Salinas, 2003; Hernandez, Zainos, & Romo, 2002; Romo, Hernandez, Salinas, et al., 2002; Romo, Hernandez, Zainos, Lemus, & Brody, 2002; Shadlen & Newsome, 2001; Kim & Shadlen, 1999; Newsome, Britten, & Movshon, 1989).

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In the somatosensory system, responses of neurons in the secondary somatosensory cortex (SII) have been found to be correlated with the monkey's behavioral decision in a tactile discrimination task (Romo, Hernandez, Zainos, et al., 2002). On the basis of evidence obtained in their study, Romo and colleagues proposed that neurons in SII cortex would combine past and present sensory information for decision-making. Nevertheless, the neuronal basis of decision-making in the somatosensory system during a haptic (active touch) choice still remains unknown. The haptic choice consists of multiple steps, including hand movements of palpating and pulling the tactile stimulus for the final choice. In the somatosensory cortex, studies have shown that some cells are attuned to both a touch of an object and movements of the hand and arm toward it (Lebedev, Denton, & Nelson, 1994; Jiang, Chapman, & Lamarre, 1991; Nelson & Douglas, 1989). This indicates that the primary somatosensory cortex (SI) participates not only in encoding sensory information but also in sensory–motor integration. Similar results have also been seen in the association cortex, Area 5 and Area 7 (Chapman, Spidalieri, & Lamarre, 1984; Kalaska, Caminiti, & Georgopoulos, 1983; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Hyvarinen & Poranen, 1974). However, up to now, it is still not clear whether neurons in SI are involved in the neural process of behavioral choice, including decision-making in haptic discrimination tasks.

In previous studies, we showed that neurons in SI cortex were activated during the delay period when the monkey performed a haptic–haptic (HH) DMS task (Bodner, Zhou, & Fuster, 1997; Zhou & Fuster, 1996). These findings suggested that SI cortex participates in active retention of haptic information in addition to being important for haptic perception of current information. Furthermore, SI cells in monkeys well-trained to perform a visuo-haptic (VH) cross-modal DMS task were observed to be activated by a visual icon that was associated with the haptic choice (Zhou & Fuster, 1997, 2000).

In a recent human study, Harris and colleagues (2002) found that performance of a tactile working memory task was significantly disrupted when a TMS pulse was delivered to the SI cortex, and they proposed a model in which the maintained neuronal activity in both higher level cortices and SI cortex was essential to optimal tactile working memory performance. Another recent human study (Bolognini, Rossetti, Maravita, & Miniussi, 2011) indicated that the disruption of SI activity by repetitive TMS selectively impaired visual processing of touch in a visual discrimination task with tactile stimuli. Those studies indicate that SI cortex, beyond just a modality-specific primary sensory cortical area as traditionally viewed, plays an important role in performance of tactile cognitive tasks.

We hypothesized that in the somatosensory system, neurons in SI cortex participate in the neural process of decision-making, because SI cortex functions in both receiving current haptic information and retaining prior haptic information. In this study, we tested this hypothesis by examining the activity of SI neurons recorded during the choice period of a haptic working memory task.

METHODS

Animals

Four (3 male and 1 female) rhesus monkeys (Macaca mulatta), each weighing 7–10 kg, were used for this study. Two of them were used as control animals. They were individually housed and fed an ad libitum diet, but water intake was restricted on experimental days. They obtained water only during experimental sessions as reward for correct behavioral responses (supplemented as needed out of the experimental sessions). Experiments were carried out in accordance with the guidelines published in the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publications No. 86-23, revised 1987), and protocols were approved by the animal care and use committee at the Johns Hopkins University.

Behavioral Tasks

The experiments were conducted in a sound-attenuated chamber. The monkey was trained to perform haptic DMS tasks (Figure 1) in a fully automated, computer-controlled apparatus. The details of the tasks have been described elsewhere (Zhou & Fuster, 1996, 2000). Basically, the test objects were a pair of vertical cylindrical rods of identical dimensions (axis = 150 mm, diameter = 19 mm) but different surface features. The rods differed in the direction of parallel ridges (6 mm apart) on their surface: One rod had the ridges along the axis of the cylinder (vertical edges), and the other had the ridges around its circumference (horizontal edges).

HH Task—The trial began with a click signaling that the sample (a vertical cylindrical rod, either the one with horizontal ridges on its surface or the one with vertical ridges) was accessible for the monkey to touch in a fixed central position in front of the animal. About 1.5 sec later, the monkey lifted its operating hand from a handrest and reached out to touch the rod. After the sample touch, the animal returned its hand to the handrest, thus initiating the delay period, which varied from 10 to 12 sec trial by trial. A second click signaled the beginning of the choice period. During that period, two rods (horizontal vs. vertical) were presented side by side. The monkey reached out again to grasp the objects and pull one. A pull of one rod ended the trial and led to an immediate reward of about 1.5–2 ml of water if the chosen rod matched the sample. The rod was entirely hidden from view throughout the task. The monkey could not see the objects either during training or during recording. The presentation of the sample rod and the position of the rods in the choice period were pseudorandomized from trial to trial. In the task, monkeys were trained to use only one hand to perform the task across both training and recording sessions. The other hand was physically restrained by a plate attached to the monkey chair.

VH Task—A trial started with the presentation of a white rectangular light display (duration of 0.5 sec) on the center of a computer screen in front of the animal at eye level. This light signaled the beginning of a trial. At 2 sec after the off-set of the white light, an icon (the visual cue for the trial, duration of 2 sec) was presented in the same position. A pair of black and white icons was used. Similar to the tactile rods in the HH task, one icon showed patterns of parallel stripes with horizontal direction, and the other showed those with vertical direction. The off-set of the visual cue signaled the beginning of the delay. The rest of the trial was the same as the corresponding part of the trial in the HH task. The visual cue and the position of the tactile objects for choice were arranged randomly between trials. Eye movements were monitored and recorded continuously by an eye tracking system (ISCAN ETL-200, ISCAN, Inc., Burlington, MA).

HH Control Task—Two monkeys were used in the control task. The procedure for this task was essentially identical to the HH task, except that, during the choice period, a pull of either rod led to immediate reward. That is, in the HH control task, the animal was not required to either discriminate the haptic objects or actively memorize them during the delay for the subsequent behavioral choice.

Implantation of Recording Chamber

After the animal's task performance (both the HH task and the VH task) reached 75% correct or above, a cylindrical recording chamber (Crist Instrument Co., Inc., Bethesda, MD) of 22-mm diameter was implanted. The location of the recording chamber on each animal was determined by the individual MRI atlas (3T, Johns Hopkins Hospital). During the surgery for implantation, the central sulcus and intraparietal sulcus were clearly visible in the skull opening. Digital pictures of the opening were taken after the chamber had been implanted, and by this, locations of recording sites in areas covered by the recording chamber could be calculated accurately.

Single-unit Recordings

For each recording session, two or three glass-coated tungsten electrodes (1–2 MΩ, Nano Biosensors Ltd., Nazareth, Israel) were introduced into the SI area through a multielectrode driver (NAN Electrode System, Plexon, Inc., Dallas, TX). The single-unit activity recorded extracellularly was collected by the Plexon System (Plexon, Inc., Dallas, TX). Before starting regular daily recording sessions, we first mapped the hand area in SI by examining receptive fields of cells in the animal's hand to ensure that recorded cells would be within that area. During recording— when obtainable—the receptive field of a cell was also examined. For a given unit in the VH task, the eye movement throughout a trial was monitored and recorded for off-line analysis to exclude the effect of eye movement on the unit firing. Trials in which the animal closed its eyes were excluded from analysis. Single units with at least 10 completed trials for each sample/cue (horizontal or vertical) were saved in database.

Data Analysis

The following events in the HH task were used for statistical analysis of unit firing with regard to frequency changes in temporal relation to them: (1) click before the sample period, (2) the first touch of the sample rod in the sample period, (3) hand-off of the sample rod, (4) the last touch of the object before the pull at the choice, and (5) the pull at the choice. Those events defined the end of baseline (period of 10 sec before the click, Event 1), the sample period (between Events 2 and 3), and the choice period (between Events 4 and 5). After off-line spike sorting by the Off-line Sorter (Plexon, Inc., Dallas, TX), files were exported to NeuroExplorer software (Plexon, Inc., Dallas, TX). The average firing frequency locked to a given event, such as first touch of the sample object, was calculated by using Matlab software (Mathworks, Natick, MA). Differences in average firing rate between each task period and the baseline were submitted to the Student's t test by using intertrial variance in the error term ($p < .05$). The difference of responsiveness of a unit between the group of horizontal object trials and the group of vertical object trials was also assessed by calculating the difference of the difference in average firing rate with respect to the baseline using the Student's t test ($p < .05$).

Significance of the difference in grand-averaged firing frequency of cells that showed differential activity only in the choice period (choice-only cells) was tested between the preferred and nonpreferred objects in both sample and choice periods of the task (where preferred object refers to the object that, when touched by the monkey, resulted in a significantly higher firing rate of a cell than that exhibited when the other object—nonpreferred— was touched in performance of the task). Frequency histograms for the preferred object and the nonpreferred object were made respectively (bin size = 50 msec). The separate histograms resulted from averaging firing of each cell. The procedure was as follows: The preferred and nonpreferred average firing frequency in sample and choice periods of each cell was calculated by normalizing the choice response (bin size = 50 msec) of each trial to the maximal preferred response (absolute value of maximal deviation from zero) in each cell. The grand-averaged firing frequency was created by taking the average of all the normalized values from the cells in the corresponding bins. Significance per period of the difference in grand-averaged firing frequency between the preferred and nonpreferred objects was then tested by the Student's *t* test.

RESULTS

Neuronal activities in correct task trials were collected from the hand representation area of SI cortex in two monkeys (Figure 2) performing the HH and VH DMS tasks (Figure 1).

Behavioral Observations

The monkeys used in our study were well trained (over 2 years). Their task-related behavioral performance was monitored by video camera, eye tracking system, and movement detection sensors in each individual trial. After their long period of training, the monkeys had learned to use a relatively consistent behavioral pattern (arm reaching and hand movements in manipulation of the object). Instead of moving their operating hand up and down when they explored a haptic object, as they did in early stages of training, during unit recording both the well-trained and control animals touched the object by holding it steadily (see Figure 1A). We did not find any pattern difference in haptic touch between the horizontal and vertical sample trials.

When performing the HH and VH DMS tasks, at their choice the two well-trained monkeys used the following strategy: (1) if the first object touched matched the sample, the monkey pulled the object after palpating it (direct choice, "first-last" touch trial); (2) if the first touched object was the nonmatching one, the monkey switched to the other object, palpated it, and then pulled it [indirect choice, "first-nonmatch" (FNM) trial]. In rare cases, the monkey moved its hand back and forth between the objects and then pulled the correct one.

Regardless of strategy, the monkey always palpated the chosen object before pulling it. There was no significant difference in performance accuracy between FNM and first-last trials. Control monkeys pulled the rod without palpating its surface features.

No spatial bias toward either location (right or left) was found in the analysis of a single-cell activity.

RT at Choice

The average RT (the time from "last touch" to "pull") was calculated for the two response strategies (Option 1/direct choice and Option 2/indirect choice) during the recording of 67 cells. There was no significant difference in RTs between the two groups of trials corresponding to the two options [direct choice (0.37 ± 0.05 sec) vs. indirect choice (0.39 ± 0.04 sec), $p > .5$], as in both conditions, the animal palpated the object before finally pulling it. The RT in control monkeys was 0.15 ± 0.05 sec (behavioral data from 235 cells), which was significantly shorter than that in the well-trained monkeys ($p < .001$), as the control monkeys pulled the rod without palpating it.

Analyses of Neuronal Activity

Neuronal Activity during Sample and Choice Periods—Among 402 recorded single units, 67 cells (16.7%, 39 horizontal-preferred cells and 28 vertical-preferred cells) showed significant differential activity only in the choice period (the period between the onset of the last touch of the chosen rod and the pull of it), but not in either the sample period or the delay (Figures 3 and 4). The results showed that the choice differential activity began around 500 msec before the pull, and the activity reached the peak right before the pull (choice action). In the sample period (the period for sample palpation from the hand-on to hand-off), 37 cells (9.2%) showed significant differential activity when the animal palpated the tactile rod. Neurons preferred either the horizontal rod (20 horizontal cells) or the vertical rod (17 vertical cells). Twelve of the 37 cells also showed the significant differential activity (three horizontal cells and nine vertical cells) in the choice period (no such differential activity shown in the delay). The selectivity of these 12 cells was similar between both periods ($p > .15$).

The difference in firing frequency at choice between preferred and nonpreferred objects tended to disappear in incorrect response trials (Figure 5). Compared with that in correct trials, the grand-averaged preferred firing frequency decreased significantly ($p < .005$) in incorrect trials, resulting in a significant ($p < .001$) diminution in grand-averaged differential activity. The average RT (the time between the onset of the last touch and the choice pull) differed between correct (0.41 ± 0.02 sec) and incorrect (0.57 ± 0.01 sec) trials ($p < .001$). Thirty-three of those 67 choice differential cells were also recorded in a VH task (Figure 2). More than half (17) of those cells showed significant differential activity at choice in both tasks (Figure 6A). The others (16) showed selectivity only in the HH task (Figure 6B).

Two hundred and thirty five neurons were recorded in SI cortex of two control monkeys who performed the control task that was identical to the HH task but did not require the animal to either actively memorize the sample or make a choice between the two objects at the end of the trial. That is, in the “choice” period, a pull of either of the rods would give the monkey an immediate water reward and end the trial. Among those 235 control cells, only three cells showed choice-only differential activities.

Neuronal Activity in FNM Trials (Indirect Choice)—The differential activity around the first-touch in the choice period in FNM trials was analyzed (Figure 7). Only 19 of the 67 cells (28.3%) were selected in this analysis, each of which had at least five trials for both preferred and nonpreferred objects. Significant ($p < .03$) difference in grand-averaged firing frequency was observed between preferred and non-preferred trials.

Comparison of Neural Activity between Two Different Response Strategies—The neural activity of the 67 choice differential cells was analyzed for the two response strategies. There was no significant difference in cell firing between the two options (Option 1 vs. Option 2, Figure 8).

DISCUSSION

The central finding of this study is that a substantial number of SI neurons in monkeys performing a haptic DMS task show significant differential activity specifically during the period when the animal has to make a correct haptic choice between two objects to receive a reward. We assume that this differential activity is likely a neural correlate of decision-making and thus conclude that SI cortex contains cells that participate in the cognitive process of decision-making.

In the cortical dynamics of the perception–action cycle (Fuster, 2001), SI cortex is the lowest cortical stage of the upstream somatic sensory processing hierarchy, and primary motor cortex (MI) is the lowest cortical stage of the downstream motor processing hierarchy. There are interactions between cortical stations at various levels of the two hierarchies. Evidence from past studies (Lebedev et al., 1994; Jiang et al., 1991; Nelson & Douglas, 1989) indicates that neuronal signals may arrive at SI before movement onset. In a recent study, Peterson and his colleagues (Matyas et al., 2010) found that SI directly drove whisker retraction, providing a rapid negative feedback signal for sensorimotor integration. Those studies indicate dynamic interactions between SI and MI. The close anatomical relationship between the two cortices (Stepniewska, Preuss, & Kaas, 1993; Jones, Coulter, & Wise, 1979) may provide a neural basis for the timely information exchange between the two during active tactile exploration. This exchange may play an essential role in the matching of a tactile memory trace and the present haptic stimulus represented by neural networks in SI cortex. Furthermore, this timely information exchange may be critical for fine hand movements during tactile exploration leading to proper decisions. It is therefore a reasonable assumption that the haptic decision-making during the choice period of our task requires a certain level of participation by SI cortex. As in the visual system (Nienborg & Cumming, 2009), other cortical areas at higher level in the somato-sensory system may also have influences through top–down pathways on the activity of SI networks in the process of decision-making.

Most choice differential cells in this study show selectivity only at choice but not in the sample period, suggesting that these cells are activated in a neural process beyond sensory analysis which is most likely carried out by those cells showing differential activity during both sample and choice periods in the task. The plausible interpretation of the choice-only differential activity is that it reflects the neural process of decision-making. It seems that two populations of SI neurons are linked respectively to the two choices (vertical or horizontal ridges). The animal's decision may be made by computing the difference in firing rates from those two populations of SI neurons (Romo & Salinas, 2003; Gold & Shadlen, 2001).

If there is an FNM touch in the choice period, the animal may have made its decision before the last touch and perform the last touch only for a double-check. As shown in Figure 7, the significant differential activity occurs right after the FNM touch, although this difference is less significant than that induced by the last touch. It seems that in those FNM trials, monkeys make a decision not to pull the stimulus after the first touch. Therefore, the significant difference in neural activity between preferred and nonpreferred FNM trials further indicates that the choice differential cells in this study are likely involved in the neural process of decision-making.

In a previous study, we found differential delay cells in SI, indicating that those SI cells were likely involved in haptic working memory (Zhou & Fuster, 1996). Therefore, one might argue that the choice differential cells found in the current study may also be a part of the neural networks of working memory, because some studies have indicated that the working memory and decision-making share the same neural networks (Curtis & Lee, 2010; Wang, 2008). However, it appears that the choice differential activity in the current study was more likely correlated with the neural process of decision-making than the delay-differential cells. The main reason is because the differentiation during the process of haptic choice builds up gradually, and the pull takes place right after this differential activity has reached its peak. This indicates a high correlation between the behavioral action and the neuronal activity. In this respect, our results agree with the decision-making model proposed by other studies (Wang, 2008; Romo & Salinas, 2003; Gold & Shadlen, 2001). Furthermore, compared with that exhibited during “FNM touch,” the differential activity of “Match touch” is significantly increased. This comparison, to a certain extent, shows the temporal integration of neural activity at the haptic choice, the outcome of decision-making. This type of integration has been proposed to be a process that enables the monkey to accumulate evidence in favor of or against choice options (Wang, 2008).

Our results also show that the action of final pull per se is not a determinant of the differential activity of the cells, because that activity, in fact, begins about 500 msec before the pull. That is, the action at choice (the pull of the rod) occurs not before but after the peak of the choice differential activity. In addition, the action of pulling the rod is essentially identical in all trials (both horizontal and vertical trials).

The diminished firing selectivity of cells in incorrect response trials further supports our inference that the choice differential activity is related to decision-making.

Furthermore, half of those HH choice differential cells whose activity was also recorded in the VH task did not show differential activity at haptic choice in the latter task, although in both tasks, the behavioral procedure for choice is identical (the animal discriminates between two haptic objects and chooses the one that matches the sample). This also supports the idea that the choice differential activity is not simply related to sensory analysis. Interestingly, the other half of VH cells showed choice differential activity in the VH task as well. This indicates that, in this task, the visual sensory information may modulate the neural activity in SI cortex through top–down influences. This finding is consistent with previous work showing that associated visual or auditory sensory stimuli may affect the neural activity in SI cortex in cross-modal tasks (Zhou & Fuster, 2000, 2004).

As expected, in our data from control animals, which did not need to make a choice at the end of a trial, very few cells were observed to show choice-only differential activity. This result again supports the assumption that the choice differential activity is very likely related to the process of decision-making.

Single neurons in the pFC and other areas have been found to encode task performance strategies or abstract rules (Muhammad, Wallis, & Miller, 2006; Wallis, Anderson, & Miller, 2001). In this study, we compared the neuronal activity between two response options (strategies) that the monkey took during the choice period. No significant difference was found in either the preferred trial group or the nonpreferred trial group. This result indicates that the choice differential activity between the preferred and non-preferred objects is not likely induced by task performance strategy but by the decision-making process. Our analysis of the choice RT also supports this assumption.

In the somatosensory system, neurons in SII cortex show activity consistent with their participation in the process of decision-making, as that activity is correlated with the monkey's behavioral judgment in a tactile passive discrimination task (Romo, Hernandez, Zainos, et al., 2002). Findings in our present study suggest that, in the cortical somatosensory system, SI cortex, the early somato-sensory cortical area also enters decision-making in tactile discrimination. However, we cannot draw the conclusion that the animal's decision-making is solely based on tactile information because during the choice period in our haptic task (an active touch task), there are movements of reaching, palpating, and pulling the object. In contrast to other studies (Meftah el, Shenasa, & Chapman, 2002; Romo, Hernandez, Zainos, et al., 2002; Hernandez, Zainos, & Romo, 2000; Tremblay, Ageranioti-Belanger, & Chapman, 1996), in which the tactile stimulus was passively perceived, our study was based on haptic tasks, where proprioceptive inputs induced by active choice, in addition to tactile ones, may lead to SI reactions. It is reasonable to suppose that the choice differential responses in our results were induced by both types of inputs. Decision-making, like all executive cognitive functions, is a distributed function, determined by many inputs and factors (Zhou, Ardestani, & Fuster, 2007). Thus, we cannot conclude that decision-making is based exclusively on what goes on in SI or any other single cortical area. In the neuronal process of decision-making for a haptic choice, the motor cortex and other higher associative areas are most likely involved.

There is increasing evidence that early sensory cortical areas play a more active role in cognitive processes than traditionally thought (Zhou et al., 2007; Shuler & Bear, 2006; Pasternak & Greenlee, 2005; Ress & Heeger, 2003). In our previous studies, we have shown evidence that neurons in SI cortex participate in working memory of tactile information in addition to being important for tactile perception (Zhou & Fuster, 1996). Furthermore, we have shown that SI neurons are activated by visual stimuli that have been associated with tactile stimuli through cross-modal task training (Zhou & Fuster, 2000). The findings in this study confirm and extend our previous findings by showing that, besides participation in working memory, SI cortex may also participate in other higher cognitive functions, including decisions between haptic choices. At a more general level, these findings suggest that the haptic network in SI is part of widely distributed cortical networks involved in decision-making.

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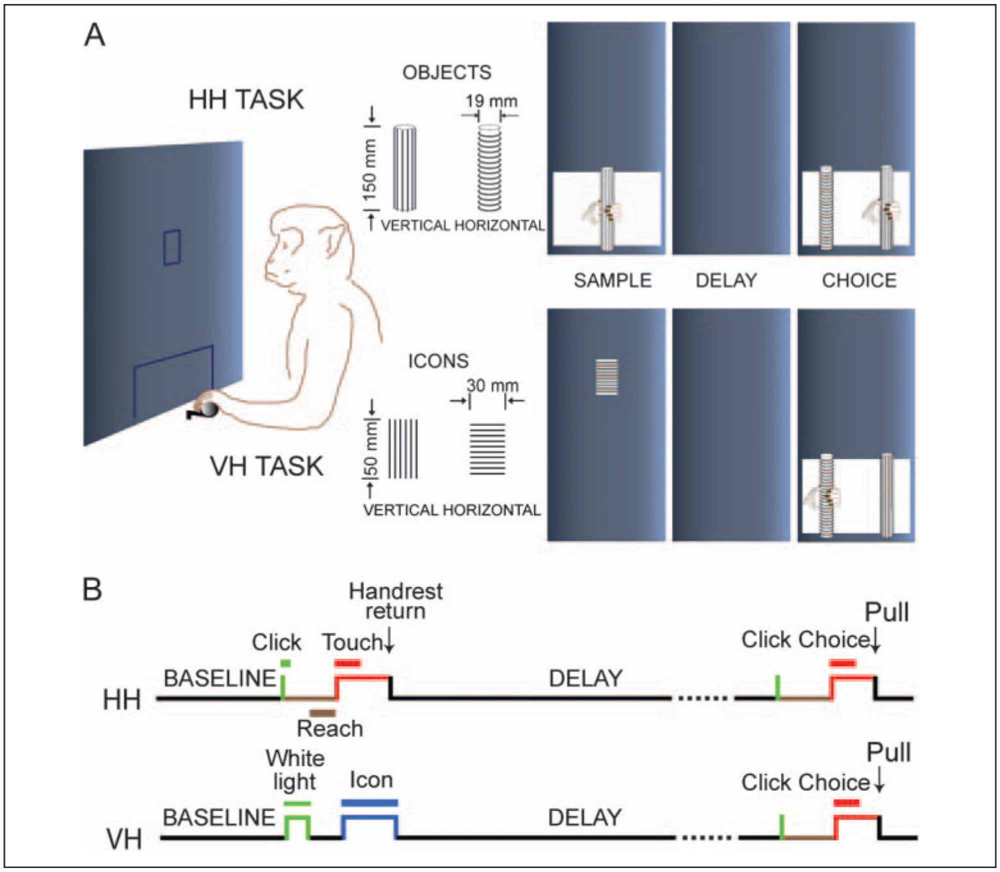

Figure 1.

Schematic diagram of behavioral tasks. (A) Top: Events of the HH task. The subject touches the sample that cannot be seen, one of two objects (rods) differing by a surface feature (orientation of parallel ridges or texture). The subject must memorize that feature through a delay period (10–12 sec) because at the end of it, he is presented with the two objects simultaneously, and he must choose by touch and pull the one that matches the sample. Bottom: In the VH task, the subject views an icon (the visual cue) of vertical or horizontal stripes and must memorize it through the delay to choose by touch one of two objects with ridges oriented in the same direction as the stripes of the sample icon. (B) Order of events in a task trial. In HH, the trial begins with a click signaling that the sample object is accessible to touch; the animal extends the hand toward the object and briefly palpates it, after which he returns the hand to its resting location. After the delay, a second click signals the accessibility of the objects for the choice. The animal again extends the hand toward the objects for palpating and pulling the one that matches the sample to get reward (see Behavioral Observations). In VH, the trial begins with the presentation of the icon. After the delay, the correct tactile choice is that of the object matching in ridge orientation the icon's stripe orientation.

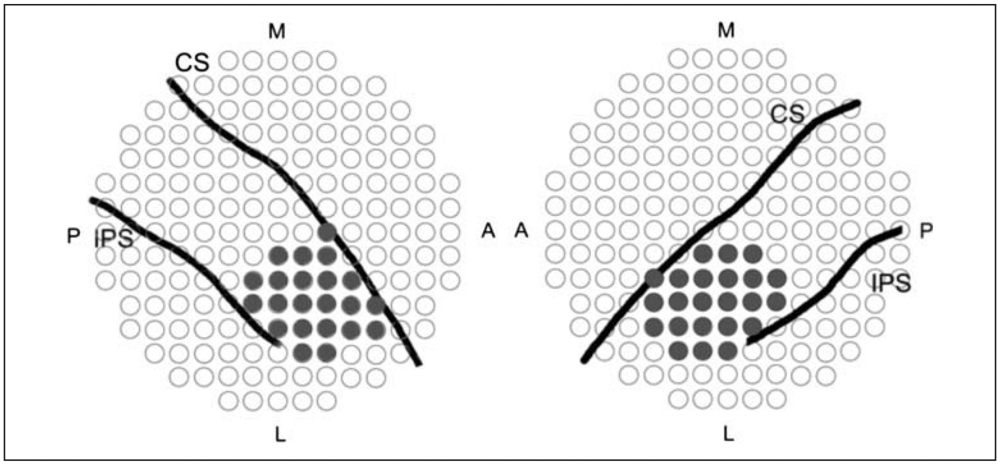

Figure 2.

Anatomical locations of recording sites in SI cortex of two monkeys in the HH task. CS = central sulcus; IPS = intraparietal sulcus; A = anterior; P = posterior; M = medial; L = lateral. Penetrations of electrodes are shown in dark gray color in recording grids.

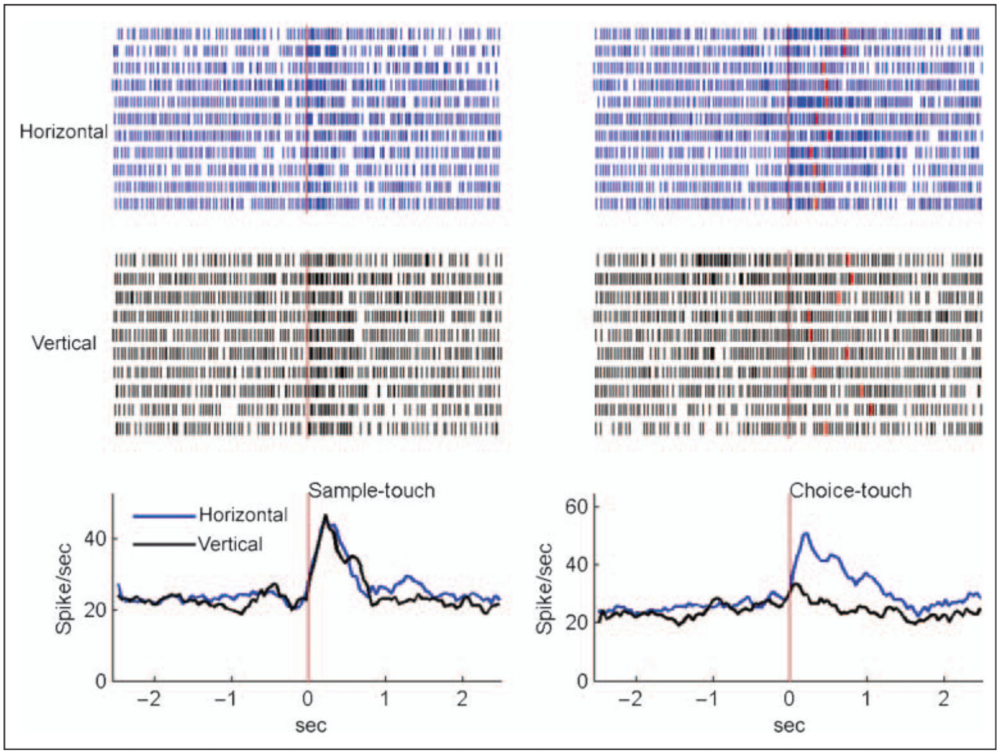

Figure 3.

Rasters and perievent histograms (bin size = 50 msec) of a cell recorded in the hand area of SI cortex in the HH task, showing the activity in both sample and choice periods. Left: The time-locking event for histograms is the first touch of the sample. This is a nondifferential touch-activated neuron ($p > .50$). The average firing rate for both rods in the sample period increases significantly from the baseline level. Right: The time-locking event for histograms is the onset of the last touch before the pull of the chosen rod. The red raster in each trial shown in this and the other figures indicates the onset of the choice (the pull). The firing rate of the cell is significantly higher in touch of the horizontal rod ($p < .001$).

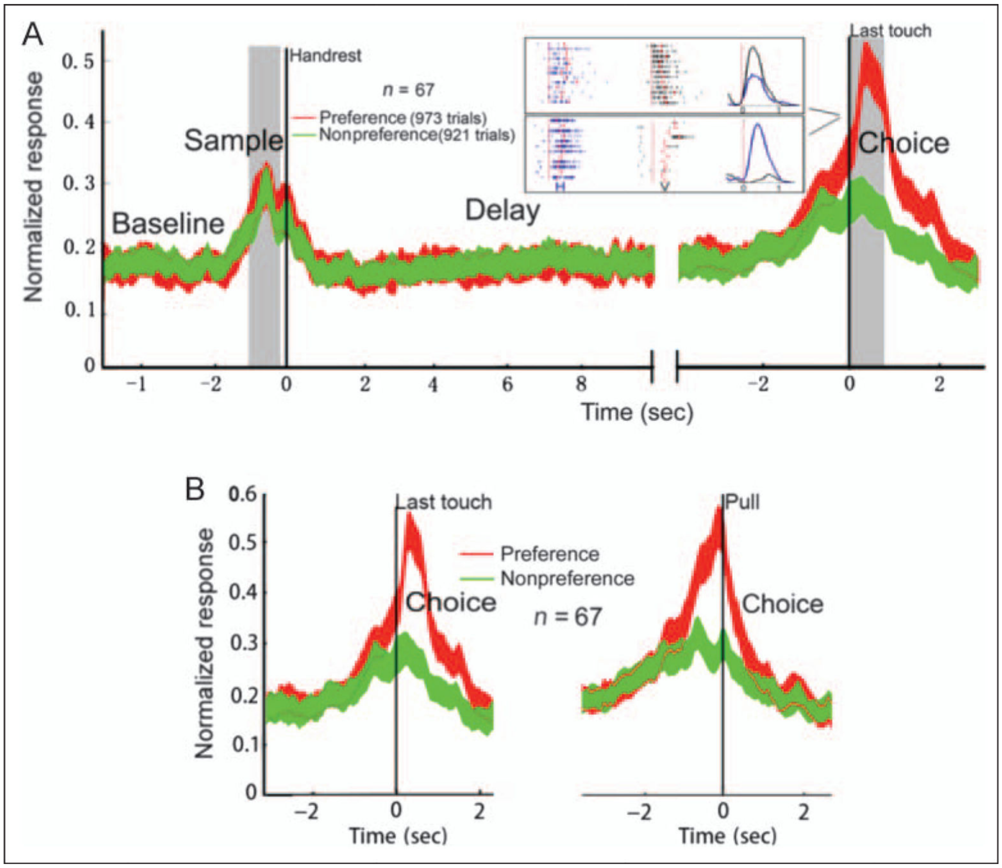

Figure 4.

(A) Grand-averaged firing frequency (bin size = 50 msec) in the HH task in 67 choice differential cells. The average firing frequency of cells ± 1*SEM* for the preferred haptic object at choice (preference determined by significant higher firing frequency to either object) is indicated by histograms in red, and for the nonpreferred object, it is indicated by histograms in green. Left: The time-locking event for histograms is the beginning of the delay period. The average length of the sample period for both preferred and non-preferred trials is indicated by the width (0.49 sec) of the shaded area. Note that there is no significant difference in firing rate between preferred and non-preferred trials during both sample and delay periods. Right: The time-locking event for histograms is the onset of the last touch at choice. The average length of the period between the last touch and the pull (RT = 0.41 sec) is also indicated by shading. The firing rate of the preferring cell responses, whether for the horizontal or vertical rod, is significantly higher than that of the nonpreferring cell responses. Two insets show preferred differential firing at choice in two cells, respectively. One cell is preferred for the vertical rod (top), and the other is preferred for the horizontal rod (bottom). H = horizontal, V = vertical. (B) Grand-averaged firing frequency in the 67 cells during the choice period. The time-locking events for histograms are the onset of the last touch (left) and the onset of the pull (right). Note that the choice differential neuronal activity begins around 500 msec before the pull.

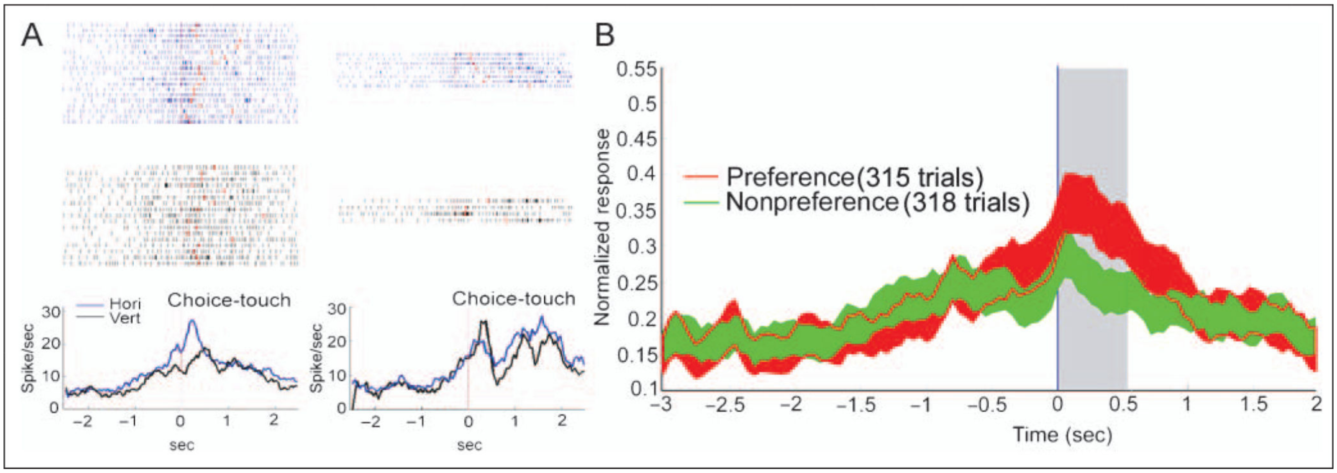

Figure 5.

(A) Rasters and perievent histograms (bin size = 50 msec) of a cell in the HH task, showing the significant differential activity at choice in correct (left, $p < .01$) trials. Note that the differential activity disappears in incorrect trials (right). Hori = horizontal rod; Vert = vertical rod. (B) Grand-averaged (67 cells) firing at choice in the HH task in incorrect trials.

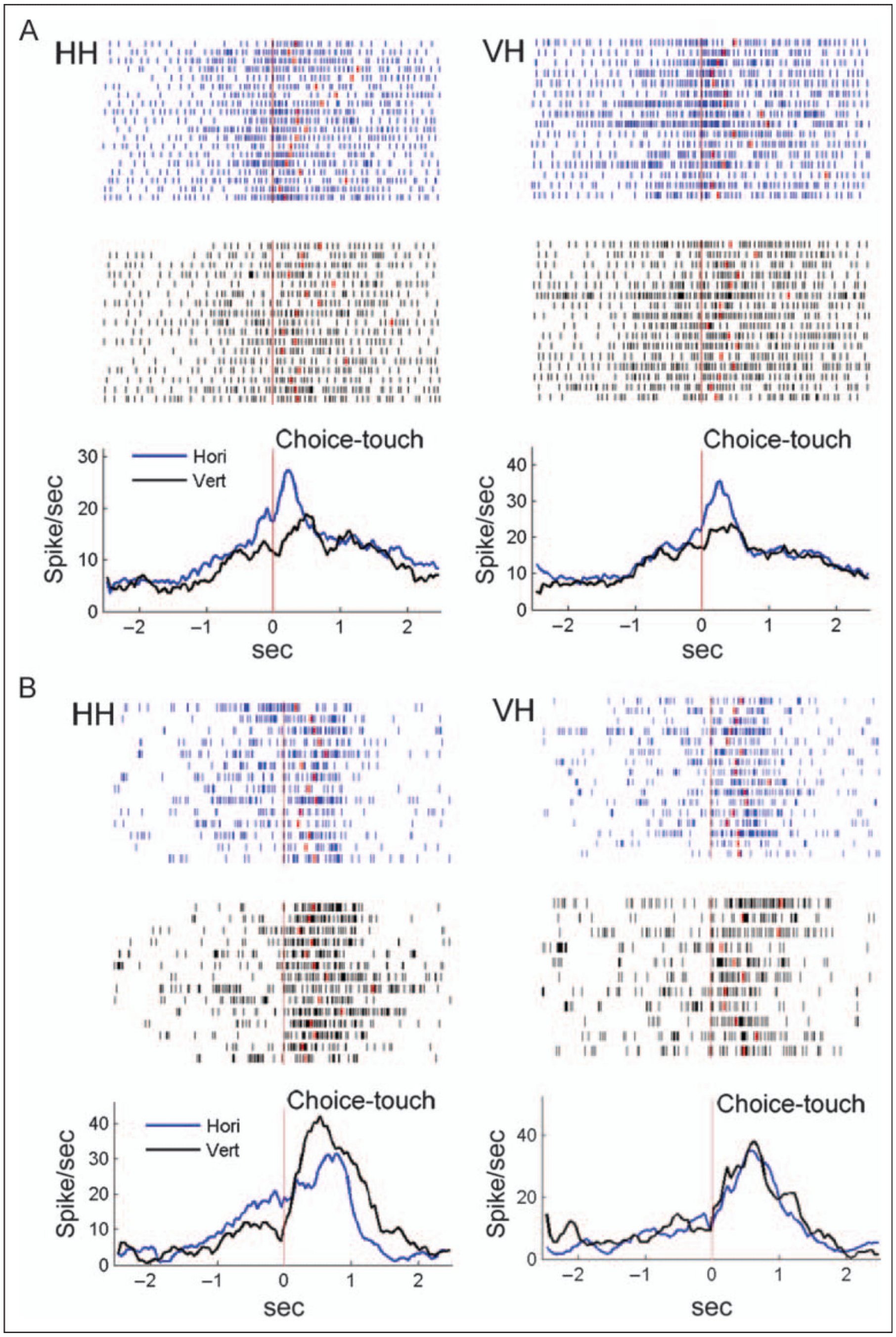

Figure 6.

Rasters and histograms (bin size = 50 msec) of two cells showing the activity at choice recorded in both HH (left) and VH (right) tasks. (A) Similar significant ($p < .01$) differential activities are shown in both tasks. (B) Significant ($p < .02$) differential activity is seen only in the HH task.

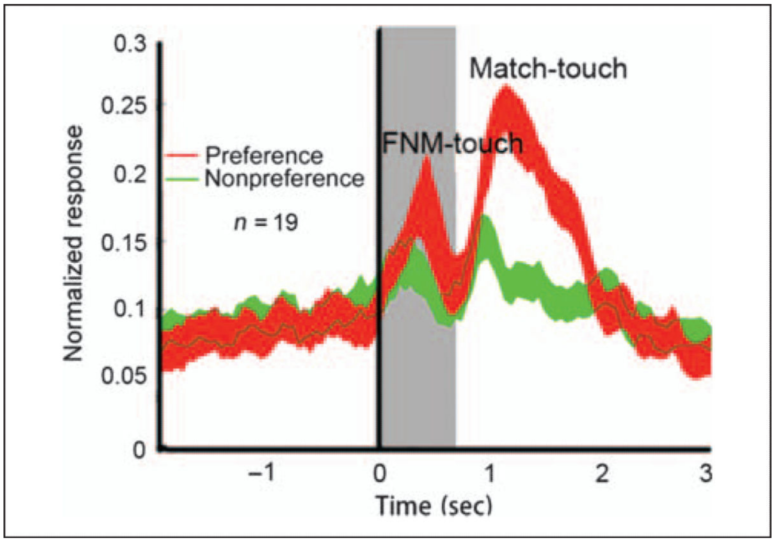

Figure 7.

Grand-averaged firing frequency (bin size = 50 msec) in 19 FNM differential cells in the HH task. The time-locking event for histograms is the first touch of the nonmatch object. The gray band indicates the average duration between the onset of the touch and the hand off from the object. Note the significant differential activity between preferred (trial number *n* = 103) and nonpreferred (*n* = 114) trials (*p* < .03, around the first touch; *p* < .001, around the last touch).

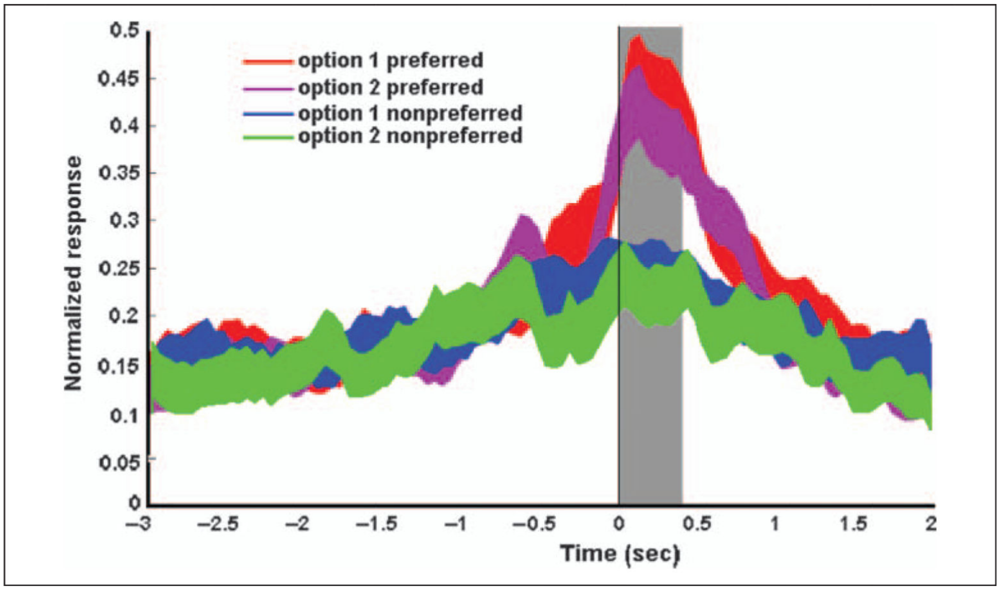

Figure 8.

Grand-averaged firing frequency from the 67 choice differential cells in two different response options in the HH task. For the preferred sample objects, the firing frequency of cells ± 1*SEM* is indicated by the red histogram in Option 1 and by the magenta histogram in Option 2, and for the nonpreferred sample objects, it is indicated by the blue histogram in Option1 and by the green histogram in Option 2. The time-locking event for histograms is the last touch at choice. No significant difference was found in either preferred or nonpreferred trials (preferred, Option 1 vs. Option 2, $p > .1$; nonpreferred, Option 1 vs. Option 2, $p > .2$).