TOUCH AND GO: Decision-Making Mechanisms in Somatosensation

Ranulfo Romo
Instituto de Fisiología Celular, Universidad Nacional Autónoma de México, 04510 México, D.F. México; e-mail: rromo@ifisiol.unam.mx

Emilio Salinas
Computational Neurobiology Laboratory, Howard Hughes Medical Institute, The Salk Institute, La Jolla, California 92037; e-mail: emilio@salk.edu

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Abstract A complex sequence of neural events unfolds between sensory receptor activation and motor activity. To understand the underlying decision-making mechanisms linking somatic sensation and action, we ask what components of the neural activity evoked by a stimulus are directly related to psychophysical performance, and how are they related. We find that single-neuron responses in primary and secondary somatosensory cortices account for the observed performance of monkeys in vibrotactile discrimination tasks, and that neuronal and behavioral responses covary in single trials. This sensory activity, which provides input to memory and decision-making mechanisms, is modulated by attention and behavioral context, and microstimulation experiments indicate that it may trigger normal perceptual experiences. Responses recorded in motor areas seem to reflect the output of decision-making operations, which suggests that the ability to make decisions occurs at the sensory-motor interface.

INTRODUCTION

Decision making involves weighing evidence in favor of several possible courses of action. This process may be conceived as a chain of neural operations: encoding recent sensory stimuli, extracting from them currently relevant features, maintaining these features in working memory, comparing them to prior information (which might include the conditions of the task), and communicating the result to the motor apparatus so that an action is produced accordingly. The divisions between these steps may be artificial, but breaking the problem into pieces is helpful. Here we discuss several such pieces, although, in the long run, we aim for an integrated understanding of the decision-making process, at least to the extent possible within the minimalist environment of a laboratory task.
In many paradigms, the strictly sensory and motor components seem relatively well understood. But in the past decade, neurophysiologists have unearthed a wealth of complexity in the intermediate decision-making steps (Salzman et al 1990, 1992; Leon & Shadlen 1998; Kim & Shadlen 1999; Schall & Thompson 1999; Gold & Shadlen 2000). Physiologists in the motor system would call this the sensory-motor interface. However, the problem should not be understated. To explore decision-making, two key elements are required: first, comprehending the neural codes of the cells activated during the task (DeCharms & Zador 2000) and second, experimental preparations in which behavioral and neuronal activity are quantified simultaneously. Thus, psychophysical techniques are essential (Werner 1980, Newsome et al 1989, Hernández et al 2000). The rationale underlying these experiments is that the responses of neurons involved in the decision-making process should correlate with the animal’s behavior, and the specifics of these correlations should provide an indication of functional significance.

In the somatosensory system, combined psychophysical/neurophysiological experiments have a long tradition that goes back to Mountcastle and colleagues, who pioneered this approach almost four decades ago (Werner & Mountcastle 1965, Talbot et al 1968). Here we focus on recent studies that take this approach using controlled behavioral tasks based on tactile stimuli. We also mention some important studies in vision that are germane to our subject. After a brief section on the general organization of the somatosensory system, we discuss the cortical representation of somatosensory stimuli, its relation to behavior and perception, its dependence on behavioral context, and its persistence in working memory, all crucial ingredients in decision making. The final set of results describes neural responses found in areas traditionally implicated in motor control that seem to reflect the output of a categorical decision-making process.

OVERVIEW OF THE SOMATOSENSORY SYSTEM

Cutaneous Primary Afferents

Four types of cutaneous afferent fibers can be found in humans (Darian-Smith 1984, Vallbo & Johansson 1984, Vallbo 1995). Two of them adapt rapidly to constant skin indentations and two adapt slowly. The rapidly adapting fibers are anatomically associated with Meissner (RA) and Pacini (PC) mechanoreceptors under the skin, and the slowly adapting fibers are linked to Merkel (SA) and Ruffini receptors. These primary afferents transmit cutaneous information to the central nervous system; other fibers exist that transmit proprioceptive information, but these are not discussed here. Monkeys have the first three kinds of afferents but lack those linked to Ruffini organs. Although all these fibers respond to stimulation on the skin surface, they are selective for different spatiotemporal features (Talbot et al 1968; Phillips & Johnson 1981a,b; Phillips et al 1988, 1992). Signals from the mechanoreceptive transduction process are conveyed with exquisite fidelity to
the cortex: Even a single spike from a single RA primary afferent may be reliably perceived (Vallbo & Johansson 1984, Vallbo 1995).

Anatomical Pathways: From Sensation to Action in the Neocortex

After a relay in the nuclei of the dorsal column and the basal complex of the thalamus, somatosensory information reaches primary somatosensory cortex (S1). In primates, S1 is composed of four areas, areas 3a, 3b, 1, and 2. In each of them, the receptive fields of the neurons form an orderly map of the body (Kaas et al. 1979, Nelson et al. 1980). Areas 3b, 1, and 2 are interconnected (Shanks et al. 1985) and are the most heavily involved in processing tactile information. Neurons in S1 are traditionally classified as RA, SA, or PC because their firing is typically similar to that of the corresponding afferent fibers (Mountcastle et al. 1969, Powell & Mountcastle 1959, Talbot et al. 1968). These three subtypes are organized in columns (Mountcastle 1957, Powell & Mountcastle 1959, Talbot et al. 1968).

In the visual system, information originating in primary visual cortex flows along two pathways, the dorsal and ventral streams, which show some degree of functional specialization (Mishkin 1979, Ungerleider & Mishkin 1982, Goodale & Milner 1992). It is interesting that somatosensory information from S1 also proceeds along dorsal and ventral routes that might also be specialized (Mishkin 1979, Murray & Mishkin 1984). The dorsal stream flows through the posterior parietal cortex, via areas 5 and 7b (Cavada & Goldman-Rakic 1989, Pearson & Powell 1985, Shanks et al. 1985), and the ventral stream flows through the lateral somatosensory areas (Burton et al. 1995; Krubitzer et al. 1995; Pons et al. 1987, 1992).

The dorsal stream projects to premotor and primary motor (M1) cortices (Cavada & Goldman-Rakic 1989, Godschalk et al. 1984, Leichnetz 1986, Tokuno & Tanji 1993) and could be important for self-initiated or stimulus-triggered voluntary movements involving somatic processing. The ventral stream is more likely associated with fine discrimination and recognition of stimulus patterns. This pathway reaches the lateral premotor area (Cavada & Goldman-Rakic 1989, Godschalk et al. 1984, Leichnetz 1986) and the prefrontal cortex (Preuss & Goldman-Rakic 1989, Carmichael & Price 1995) and might be associated with fine discrimination or identification of objects. As in vision, receptive-field size and complexity increase progressively (Sinclair & Burton 1993, Iwamura et al. 1994). Both streams reach M1 (Leichnetz 1986, Tokuno & Tanji 1993), so both should influence motor activity during sensory tasks that require limb movements. The functional specializations of these streams still need to be elucidated, but it would be very interesting if a clear distinction could be drawn.

Peripheral Neural Codes for Tactile Stimuli

**Coding of Flutter-Vibration**  In the somatosensory system there is a nice correspondence between perceptual and anatomical submodalities. When mechanical vibrations are applied to the skin, two sensations can be evoked. With stimuli of low
frequency, between approximately 5 and 50 Hz, the sensation of flutter is produced; with stimuli of higher frequency, between 60 and 300 Hz, the distinct sensation of vibration is felt. Talbot et al (1968) demonstrated that flutter is mediated by RA afferents, whereas vibration is mediated by PC afferents. They also found a close, quantitative correspondence between perceptual and neuronal detection thresholds, which was later confirmed by recording and microstimulation of afferent fibers in awake human subjects (Macefield et al 1990, Ochoa & Torebjörk 1983, Vallbo & Johansson 1984, Vallbo 1995). This work established the experimental paradigm in which psychophysical and neurophysiological responses are directly compared.

Two additional observations were made in the same study (Talbot et al 1968); we comment on them because they have had a strong influence in the field. First, when periodic, sinusoidal stimuli were used, the evoked spike trains from RA and PC afferents were also periodic, with individual action potentials being strongly phase locked to the mechanical inputs. Second, the firing rates of PC afferents increased with increasing stimulus frequency (within their range of 60–300 Hz), but the rates of RA afferents seemed to change little inside their 5- to 50-Hz range. This posed a problem: High frequencies could be encoded by firing rate but low frequencies could not, because the same number of RA action potentials would be seen in any given time window regardless of frequency. Talbot and colleagues (1968) concluded that some mechanism downstream had to identify or distinguish the intervals between incoming RA spikes (see Ahissar & Vaadia 1990, Ahissar 1998) in order to generate different percepts for different frequencies. In other words, a temporal neural code (Shadlen & Newsome 1994, Singer & Gray 1995) had to be used. Subsequent studies reported similar findings in S1 (Mountcastle et al 1969).

Although some contradicting evidence appeared (Ochoa & Torebjörk 1983), the suggestion that a temporal code is used to represent flutter frequency in the cortex remained unchallenged until recently (Hernández et al 2000, Salinas et al 2000a). The new results do not eliminate this possibility, but they show, first, that the firing rate of S1 neurons is substantially modulated by flutter frequency and, second, that the observed rate modulations are highly consistent with psychophysical performance in flutter discrimination (see below).

**Coding of Spatiotemporal Patterns** Johnson & Hsiao (1992) and Johnson et al (1996) have studied the neural representations of texture and form in primary afferents. First they characterized the responses of SA, RA, and PC fibers to embossed letters of the alphabet scanned across afferent receptive fields. Experiments using anesthetized monkeys (Phillips et al 1981a,b) and attending humans (Phillips et al 1992) showed that the spikes of SA and RA afferents provided high-quality spatiotemporal images of the letters, which could account for human psychophysical performance in pattern recognition. Another study (Phillips et al 1988) suggested that neurons in area 3b with SA properties could also account for psychophysical performance, but that neurons with RA properties could not.
Johnson and coworkers also investigated the neural basis of texture perception (Johnson & Hsiao 1992, Johnson et al 1996). In this case a more rigorous comparison between neural and behavioral responses could be made because the stimuli consisted of arrays of raised dots of different textures, and texture could be parameterized. Subjective roughness estimates were made by human subjects, where roughness was manipulated by varying dot diameter, dot height, and inter-dot spacing, and recordings were again obtained from single SA, RA, and PC afferents in anesthetized monkeys. The question they asked was, what measures of neural activity may provide a consistent code for texture, where consistency simply referred to the condition that any given value of the response measure had to correspond to a single value of subjective roughness. Their approach to this problem is a textbook example of the scientific method: A large number of neural codes were methodically eliminated, until only one was left (Connor et al 1990, Connor & Johnson 1992, Johnson et al 1996, Blake et al 1997). Their conclusion was that information about texture had to be conveyed mostly by the differences in activity between SA fibers with receptive fields at different locations, which they referred to as SA spatial variations (Johnson et al 1996, Blake et al 1997). This led to the prediction that cortical somatosensory neurons should have receptive fields with excitatory and inhibitory subregions, which is what was indeed found later (DiCarlo et al 1998).

The results reviewed in this section highlight the roles that different cutaneous afferents play in representing somatosensory stimuli. The SA system transmits information regarding spatial features, whereas the RA and PC systems encode temporal features. The response properties of primary afferents must limit the psychophysical capacity to detect, recognize, and discriminate tactile stimuli, and indeed, a quantitative agreement has been observed repeatedly.

NEURAL ACTIVITY IN SOMATOSENSORY CORTEX DURING BEHAVIOR

The first step in studying central decision-making mechanisms is to understand which neurons encode the quantities being decided on and how they do it. Important developments concerning this issue are reviewed in this section.

Stimulus Representations in S1

The flutter submodality provides a convenient channel to study decision-making mechanisms and cognitive tasks based on temporal patterns (Talbot et al 1968; Mountcastle et al 1969, 1990, 1992; Recanzone et al 1992; Hernández et al 1997, 2000; Romo et al 1998, 1999, 2000). First, the same set of afferent fibers are activated regardless of stimulus frequency, because the stimulator moves perpendicularly to the skin. Second, this sensation is conveyed by a highly specific set of primary afferents and primary somatosensory neurons: those with RA properties.
Third, humans and monkeys have similar detection thresholds and discrimination capacities (Mountcastle et al 1990, Hernández et al 1997). However, for a long time the neural code for flutter frequency remained a subject for speculation because it seemed to depend on the temporal configuration of fixed numbers of spikes.

Mountcastle and colleagues investigated not only the responses of cutaneous afferents (Talbot et al 1968), but also those of S1 neurons, both in anesthetized (Mountcastle et al 1969) and in behaving (Mountcastle et al 1990) monkeys. They concluded that RA cortical neurons were similar to RA afferents: They responded briskly to flutter, firing in phase with applied mechanical oscillations, and their firing rates changed little as functions of frequency. A later study by Recanzone and coworkers (1992) agreed with these conclusions, which were further supported by comparisons between psychophysical performance and variations in periodic spike firing (Mountcastle et al 1969, Recanzone et al 1992). It indeed appeared that “frequency discrimination is made by a central neural mechanism capable of measuring the lengths of the dominant periodic intervals in the [evoked] trains of impulses” (Mountcastle et al 1967).

However, the key piece of evidence here, that the firing rate of S1 neurons is insensitive to flutter frequency, was based on a small sample (17 neurons) (Mountcastle et al 1990), and on tests within a narrow range of frequencies using anesthetized animals (Recanzone et al 1992). Recent studies focusing on this particular issue have reached other conclusions (Hernández et al 2000, Salinas et al 2000a).

Hernández et al (1997) trained monkeys to discriminate between the frequencies of two flutter stimuli presented sequentially on a fingertip; a schematic diagram of the task is shown in Figure 1a. They then recorded neurons with RA properties in areas 3b and 1 of S1 while the monkeys performed the task (Hernández et al 2000, Salinas et al 2000a). They confirmed that the evoked periodic spikes of S1 neurons were indeed extremely regular, but they also found that the firing rates of more than 50% of the neurons were significantly modulated by stimulus frequency (Hernández et al 2000, Salinas et al 2000a). This showed that the neural code for flutter frequency could be based on firing rate, but how could such a code be compared with one based on periodicity?

As a first approach to this problem, Shannon’s information (Cover & Thomas 1991) was used to quantify how well stimulus frequency was encoded (a) by the firing rates of the neurons and (b) by a response measure based on the periodicity of the interspike intervals (Salinas et al 2000a). On average, the periodicity-based response provided 1.71 bits of information about frequency, which roughly means that, by measuring the periodic intervals evoked in any single trial, stimulus frequency could be perfectly localized within a range of about 6.1 Hz (i.e. the full frequency range used, of approximately 20 Hz, could be divided into $2^{1.71} = 3.3$ perfectly distinguishable bins). For the neurons with the highest periodicity, the accuracy was about 3.5 Hz. In contrast, firing rate modulations carried much less information about stimulus frequency, giving accuracies of 16.6 and 10 Hz for average and best neurons, respectively.
Figure 1  Comparison between neuronal and psychophysical responses during vibrotactile discrimination. (a) Sequence of events in the task. The probe moves down (PD) and indents a fingertip. The monkey reacts by holding a key (KH). After a delay, the probe oscillates vertically at a base frequency. After another delay, the probe oscillates again, now at a comparison frequency. The monkey releases the key (KR) after the end of the comparison period and presses one of two push buttons (PB) to indicate whether the comparison frequency was higher or lower than the base. (b) Percentage of trials in which the comparison was called higher than the base. Continuous lines are sigmoidal fits to the data; for each curve, the threshold is proportional to its maximum steepness (see text). Open circles and gray curves indicate the monkey’s performance during one discrimination run using periodic stimuli. Filled circles and black curves indicate performance of an ideal observer that based his decisions on the evoked firing rates of a single neuron recorded while the monkey discriminated. (c) Numbers of S1 neurons with the indicated threshold ratios. Thick lines correspond to neurometric thresholds based on evoked firing rate; gray bars correspond to neurometric thresholds based on periodicity of evoked spike trains. Data are from all neurons with significant rate modulation. (d) As in panel a, but the observer discriminated based on the periodicity of the evoked interspike intervals of another neuron recorded in a different session. (e) As in panel c, but data are from all neurons with significant periodic entrainment. (f) As in panel a, but aperiodic stimuli were applied. Data are from another neuron. (g) Threshold ratios from all neurons tested with both periodic and aperiodic stimuli. Neurometric thresholds were computed from the firing rates in periodic (thick lines) and aperiodic (gray bars) conditions. (Modified from Hernández et al 2000.)
Thus, a neural code for flutter frequency based on firing rate was entirely possible, but in principle, a code based on spike periodicity could be up to three times more accurate.

**Neuron Versus Monkey**

*Discrimination Based on Periodic Stimuli*  Given the large discrepancy in information between neural codes based on firing rate and periodicity, Hernández and collaborators (2000) used the methods of signal detection theory (Green & Swets 1966) to find out which code, if any, was in agreement with the observed psychophysical behavior of the monkeys. In the flutter discrimination task, two stimuli, called base and comparison, are presented one after the other, with a pause in between, and the subject has to indicate whether the frequency of the comparison was higher or lower than the frequency of the base. Hernández et al. (2000) first computed the expected performance of an ideal observer who solved the task using the following simple (but optimal) rule: If the number of spikes evoked during the comparison period is higher than the number evoked during the base, then the comparison frequency was higher than the base. This rule is applied in each trial. An example of the resulting neurometric curve for a single S1 neuron is shown in Figure 1b. The threshold of the curve is defined as the stimulus frequency identified as higher than the standard in 75% of trials, minus the frequency identified as higher in 25% of the trials, divided by 2. Lower thresholds correspond to steeper curves and better performance. For the neurometric data shown in Figure 1b, the threshold was 2.5 Hz. The sigmoidal fit for the psychophysical performance of the monkey in the same trials had a threshold of 3.2 Hz, so the threshold ratio (behavior/neuron) was 1.3, close to 1. In this example the neurometric and psychometric curves were in excellent agreement. This was the case for a large number of S1 neurons whose firing rates varied significantly as functions of frequency, as shown in Figure 1c. Therefore, the recorded rate modulations accounted for the observed psychophysical performance.

The strategy of the ideal observer can be used with other response measures (Green & Swets 1966), so Hernández et al. (2000) also applied it to the periodicity-based response used before (Salinas et al 2000a). Again, the procedure simply consisted of determining whether the response was larger during the base or during the comparison periods. A neurometric function constructed from the periodicity-based responses of a single S1 neuron is shown in Figure 1d, along with the monkey’s performance in the recording trials. In this case, neurometric and psychometric thresholds differed by a factor of 10; using the periodicity-based response, the ideal observer could perform the task much more accurately than the monkey. Similar results were obtained with other neurons that fired in phase with the stimuli, as shown in Figure 1e. On average over all neurons analyzed, discrimination thresholds based on periodicity were about four times smaller than those based on firing rate, in agreement with the previous information analysis (Salinas et al 2000a). Therefore, according to the psychophysics, either a firing
rate code was being used efficiently or a periodicity-based code was being used very inefficiently.

Discrimination Based on Aperiodic Stimuli  Having practiced the discrimination task for months using periodic stimuli, the monkeys were presented with aperiodic stimulation patterns. These consisted of trains of short, mechanical pulses separated by random times. The numbers of pulses, however, still depended on the chosen frequency; for instance, if the stimulation period lasted 0.5 s, 20 Hz corresponded to 10 pulses. These stimuli were designed so that even highly stimulus-entrained neurons could not carry information about stimulus frequency in their periodicity; in this case the periodicity-based response was essentially random (Salinas et al 2000a). Experiments with these patterns produced three results. First, the monkeys’ performance was, from the initial sessions, practically the same as with periodic stimuli; they effortlessly extracted a mean frequency from the new patterns (Romo et al 1998, Salinas et al 2000a). Second, firing rate modulations in S1 were, on average, equally strong with periodic and aperiodic stimuli (Salinas et al 2000a). And third, consistent with the latter result, neurometric and psychometric curves were again in good agreement (Figure 1f,g) (Hernández et al 2000).

In conclusion, when periodicity was broken, both monkeys and firing rates behaved essentially the same as with periodic stimuli.

Single-Trial Covariations in Activity  A further test of association between neural activity and behavior is to search for changes in response properties between correct and incorrect discriminations (hits and errors) in trials with identical sensory stimuli (Britten et al 1996). This analysis can also be applied to different kinds of responses. Salinas et al (2000a) found no significant covariations between periodicity and behavior; the chances of the monkey making a correct discrimination were the same whether the spike trains were more periodic or less periodic than average. In contrast, a few single cells were found whose firing rates fluctuated along with the monkeys’ decisions; the numbers of cells that did this were small but highly significant. In addition, this effect was evident at the population level.

Stimulus Representations in S2  What is the neural representation of flutter stimuli in structures central to S1? An interesting area to explore is the secondary somatosensory cortex (S2), which belongs to the ventral somatosensory stream (Mishkin 1979; Murray & Mishkin al 1984). S2 is strongly connected to S1 (Burton et al 1995, Krubitzer et al 1995), and at least in primates, information seems to be processed mostly serially from S1 to S2 (Pons et al 1987, 1992).

When S2 neurons were recorded during the flutter discrimination task, significant firing rate modulations were observed, as in S1, but several differences were found between the two areas (Salinas et al 2000a). First, very few neurons in S2
were significantly entrained by flutter stimuli (less than 8%, versus 84% in S1). Second, although in both areas the firing rates were approximately monotonic functions of frequency, negative slopes were uncommon in S1 (8%), whereas in S2 they were almost as abundant as positive slopes (40% were negative). It is interesting that a similar change in representation from S1 to S2 has been reported using textured surfaces (Sinclair & Burton 1993; see also Jiang et al 1997). Third, several neurons in S2 (13%), but none in S1, sustained their responses for a few hundred milliseconds after stimulus offset, carrying information about the base frequency into the early component of the delay period. Fourth, attentional or task-dependent changes in firing rate were observed in both areas but were much stronger in S2 (see Hsiao et al 1993). Finally, single-trial covariations between behavioral and neuronal responses were detected in both areas, but these were again much more evident in S2. Here about 9% of the neurons showed significant differences in responses in correct versus incorrect discriminations, and the effect at the population level was strong (Salinas et al 2000a).

Thus, although periodicity is a prominent feature of the activity evoked by flutter in S1, comparisons between neuronal and behavioral responses suggest that the neural code for flutter frequency in this area probably relies on firing rate. In addition, neurons in S2 show a minimal trace of periodicity but still modulate their firing rates as functions of frequency, and most important, they seem to be more strongly correlated with the animal’s decision on a single-trial basis.

INSERTING ARTIFICIAL PERCEPTS THROUGH MICROSTIMULATION

Lesion effects, electrophysiological recordings, and imaging techniques can reveal correlations between neuronal activity and observable behavior, but a causal relationship is usually hard to prove. Intracortical microstimulation can produce results that are much closer to such proof (Salzman et al 1990, 1992; Britten & van Wezel 1998; Romo et al 1998, 2000). For this technique to work, the coactivated neurons should have similar functional properties. Flutter is thus well suited for microstimulation experiments because S1 is known to be organized in modules of specific submodalities. In particular, neurons with RA properties are found in columns (Mountcastle 1957, Powell & Mountcastle 1959, Jones et al 1975, Sur et al 1984). Another advantage of flutter is that humans and monkeys have comparable discrimination capacities (Mountcastle et al 1990, Hernández et al 1997).

Romo and colleagues (1998, 2000) injected microstimulation current in area 3b of monkeys trained in the flutter discrimination task (Figure 1a). In this paradigm subjects pay attention to the frequency of the first (base) stimulus, store a trace of it during a delay period, and compare it with the frequency of a second (comparison) stimulus (Hernández et al 1997). Microstimulation sites in S1 were required to have RA neurons with receptive fields on the fingertip at the location of the mechanical stimulating probe. In the initial experiment (Romo et al 1998), the second
stimulus was substituted in half of the trials with a train of current bursts delivered at the comparison frequency. Regular discrimination trials included natural stimuli only and were intermixed with microstimulation trials. Figure 2a shows a diagram of this paradigm and a plot with the results. The monkeys were able to discriminate between mechanical (base) and electrical (comparison) signals with performance profiles that were indistinguishable from those obtained with natural stimuli only (Romo et al. 1998). In view of the high discrimination accuracy with electrical signals, the artificially induced sensation probably resembled natural flutter quite closely (Romo et al. 1998, Wickersham & Groh 1998). Further experiments supported this conclusion.

The microstimulation experiment was repeated using aperiodic stimuli during the comparison period (Romo et al. 1998) (see above). During aperiodic stimulation, the same average frequencies were used, and the monkeys had to judge the differences between base and comparison frequencies as before. Figure 2b illustrates the two kinds of trials that were compared in this experiment. The graph shows that performance in microstimulation trials was again practically identical to performance with natural stimuli. Monkeys had no difficulty working with aperiodic vibrations, not even in the first sessions, so spike periodicity was not critical for flutter discrimination (see also Salinas et al. 2000a).

By design, in this task the frequency of the second stimulus is compared against a memory trace of the first stimulus (Hernández et al. 1997). To test whether the artificially induced percept could be stored in memory, the base stimulus was substituted with electrical microstimulation patterns while the comparison remained natural, mechanical (Romo et al. 2000). This paradigm is schematized in Figure 2c. The graph shows that, once more, performance with artificial sensations was indistinguishable from that observed with mechanical stimuli only. This experiment showed that monkeys can memorize the frequency of an artificial stimulus just like that of natural flutter.

Going one step further, both base and comparison stimuli were substituted with electrical pulses in the same trials (Romo et al. 2000). As shown in Figure 2d, in this condition the monkeys did not reach the same discrimination levels as with natural stimuli only, but their performance was only slightly worse, still well above chance levels. However, in 2 out of 11 sessions, this experiment with two artificial stimuli did not work; average performance dropped way below 75% correct. The reason for this failure is uncertain, but it may have to do with the location of the stimulating microelectrode relative to clusters of RA and SA neurons. The flutter sensation is mediated specifically by RA primary afferents (Mountcastle et al. 1969, Ochoa & Torebjörk 1983) and previous studies suggested that the specificity of the RA circuit for flutter is maintained in S1 (Mountcastle et al. 1990, Recanzone et al. 1992). This was also tested.

Figure 3 shows the results of a single experimental session in which the stimulating microelectrode encountered clusters of SA and RA neurons at different depths along the same penetration (Romo et al. 2000). Separate discrimination runs were performed with the electrode positioned at three locations. The same paradigm
was used in the three runs: In microstimulation trials, the base stimulus was electrical and the comparison was mechanical; in interspersed trials, both stimuli were natural (as in Figure 2c). When the electrode tip was placed near neurons with SA properties, the monkey performed at chance levels in microstimulation trials (Figure 3b), although it had no problem discriminating with natural stimuli. On the other hand, performance in microstimulation trials was just as good as with natural stimuli when the electrode tip was placed around RA neurons. When microstimulation was delivered near the border between RA and SA clusters, performance was better than chance but significantly below the levels seen with mechanical stimuli. The results of Figure 3 were confirmed in four other sessions.

In summary, neuronal activity elicited by direct electrical microstimulation in area 3b is localized (at least in a functional sense) and can trigger perceptual experiences. Furthermore, as far as can be measured psychophysically, this activity can be stored in memory and used to make quantitative comparisons and decisions in practically the same ways as naturally evoked activity.
ATTENTIONAL AND CONTEXT-DEPENDENT MODULATION OF ACTIVITY IN S1 AND S2

The responses of neurons to sensory stimuli may be affected by their behavioral context; holding someone’s hand may lead to completely opposite reactions, depending on whose hand is held. Interactions between stimulus-driven and contextual information should become stronger as activity reaches stages where decision-making becomes imminent.

Attentional effects have been thoroughly investigated in vision (Desimone & Duncan 1995). In several experimental paradigms and visual areas, attention sets a gain factor by which whole stimulus-response curves are multiplied (Connor et al 1997, McAdams & Maunsell 1999a, Treue & Martínez-Trujillo 1999). Whether attention acts similarly on somatosensory responses is unknown, but it should be investigated. Other interactions related to spatial or feature selection have been described as well (Reynolds & Desimone 1999). In somatosensory areas, modulations in firing rate have been documented, as in vision, but in addition, effects on spike timing have also been observed. This is discussed below.

Hyvarinen et al (1980) and Poranen & Hyvarinen (1982) first attempted to record attentional effects in S1 neurons. Neural responses to flutter stimuli were compared with artificial, electrical stimuli. Monkeys were trained in the flutter discrimination task (Figure 1a). (Left) The protocols used in four experiments. In all cases, two kinds of trials were interleaved: In natural discrimination trials, the monkeys compared two mechanical vibrations (black traces) delivered on a fingertip; in microstimulation trials, one or both stimuli were replaced by trains of current bursts (gray traces) microinjected into area 3b at the corresponding frequencies. Base and comparison frequencies varied across trials. (Right) The animals’ average performance in the situations schematized on the left. Filled circles and black lines indicate discrimination with natural stimuli; open circles and gray lines indicate discrimination in microstimulation trials. (a) The base stimulus consisted of periodic, mechanical vibrations (sinusoidal); the comparison stimulus was periodic and could be either mechanical (sinusoidal) or electrical. (b) The base stimulus consisted of periodic, mechanical vibrations (sinusoidal); the comparison stimulus was aperiodic and could be either mechanical (a series of short, single-sinusoid pulses) or electrical. (c) The base stimulus was periodic and could be either mechanical (single-sinusoid pulses) or electrical; the comparison stimulus was always periodic and mechanical (single-sinusoid pulses). (d) In half of the trials, both base and comparison stimuli were periodic and mechanical (single-sinusoid pulses). In the other half, both stimuli were periodic and electrical. In all experiments, natural and microstimulation trials were interleaved and were equally frequent. Scale bars equal 500 ms. Data points shown are means (± 1 standard deviation) over the indicated numbers of data collection runs. In panels a and b, only a subset of the collected data for which the base frequency was 20 Hz is shown. In panels c and d, only the subset of points for which the comparison frequency was 20 Hz is shown. (Modified from Romo et al 1998, 2000.)
Figure 3  Psychophysical performance in natural and microstimulation trials for three electrode locations. Neurons with slowly adapting (SA) and rapidly adapting (RA) properties were encountered along the same penetration. (a) Electrode depths. Asterisks mark microstimulation sites along the track. (b) Psychophysical performance measured when microstimulation was applied at the sites indicated in panel a. (Top) Microstimulation delivered around SA neurons; (center) microstimulation delivered near the border between RA and SA clusters; (bottom) microstimulation delivered around RA neurons. Symbols have the same meaning as in Figure 2; the protocol was the same as in Figure 2c. Each data point represents 10 trials collected during successive runs on the same day. (Modified from Romo et al 2000.)

in two conditions: when stimuli were delivered passively to the fingertips, without any behavioral reaction, and when the monkeys performed a simple detection task. A few neurons did fire at higher rates during the task compared with the no-task condition, but the effects were small. In retrospect this is not surprising, for two reasons. First, no effort was made to divert attention away from the stimulus in the passive condition, and second, attentional effects may increase substantially with increasing task difficulty (Posner et al 1978, Whang et al 1991). Much larger effects on firing rate were found later, both in S1 and S2, using more challenging paradigms (Hsiao et al 1993, Burton et al 1997, Steinmetz et al 2000). Studies using noninvasive techniques are consistent with these findings (Mima et al 1998,
Burton et al 1999). As in other modalities, typically stronger activity is seen when attention is focused on a stimulus that is relevant to the recorded neurons.

**Attentional Effects on Spike Timing**

Motivated by models of cortical interactions in which spike timing plays a key role (Niebur & Koch 1994), Steinmetz et al (2000) recorded pairs of neighboring S2 neurons to investigate whether attention is related to spike synchrony. In their experiments, tactile and visual stimuli were always presented simultaneously. Their monkeys were trained to switch between visual and somatosensory discrimination tasks, depending on a cue at the beginning of each block of trials. Across conditions, stimulus sets and arm motions used to indicate behavioral choices were identical. To perform the somatosensory task accurately, monkeys had to pay attention to the tactile stimuli and ignore the visual display, and vice versa during the visual task; mistakes indicated that attention was misdirected.

As in earlier work (Hsiao et al 1993), these investigators observed that the firing rates of a large proportion of S2 neurons (80%) changed significantly between conditions (Steinmetz et al 2000). They also found that 66% of all neuron pairs were significantly synchronized, regardless of the task. This was simply a consequence of receptive field overlap because neurons sharing common inputs should exhibit some degree of synchrony. The most novel finding was that, on average, synchrony was stronger during tactile discrimination than during visual discrimination: About 9% of all S2 neuron pairs fired more synchronously when the monkeys attended the tactile stimuli. Changes in synchrony also increased with task difficulty and could not be explained in terms of variations in firing rate. The implication is that shifting the attentional focus has an impact on spike synchrony. Two facts cannot be overlooked, however. First, we do not know whether changes in synchrony in S2 translate into functional changes downstream (Niebur & Koch 1994, Shadlen & Newsome 1994, Salinas & Sejnowski 2000). And second, the attentional modulation of firing rate seems much more prominent, at least judging from the fractions of neurons with significant effects (Hsiao et al 1993, Steinmetz et al 2000).

Other experiments using flutter stimuli confirmed that attention may influence the timing of evoked spikes. Salinas et al (2000a) compared neural responses in S1 recorded during active discrimination (Figure 1a) versus responses obtained during passive stimulation. In blocks of passive trials, the same stimuli used for discrimination were applied, but the responding arm was restrained, no behavioral reaction was required, and no reward was delivered. A measure of periodicity was constructed based on the Fourier spectrum of the evoked spike trains; this was just the fraction of total power found around the frequency of stimulation. Periodicity was significantly higher in active than in passive tests (Salinas et al 2000a). In other words, the timing of evoked S1 spikes relative to the mechanical stimulation pulses was more regular during active discrimination; tighter phase locking occurred in this condition.
As with the results of Steinmetz et al (2000), the functional implications of these timing effects are uncertain, but they are extremely interesting, if nothing else, because they constrain the microcircuitry that may underlie attentional modulation of stimulus-evoked activity.

Attentional Effects on Signal Quality

It is not surprising that Salinas et al (2000a) also observed that firing rates changed between active and passive conditions in S1 and S2. However, they noticed that the rates depended more strongly on stimulus frequency during active discrimination. Several measures were computed to evaluate the association between firing rate and frequency in the two conditions. These measures included the mean trial-to-trial variability in spike count, a signal-to-noise ratio, and Shannon’s information (Cover & Thomas 1991). The same conclusion was reached with all quantities tested: When the animals performed the task and presumably paid attention to the stimuli, the evoked firing rates were less variable across trials and were better correlated with frequency (Salinas et al 2000a). For this analysis, the random cofluctuations in firing rate between pairs of neurons, which could, in principle, limit the quality of the overall population signal (Zohary et al 1994, Abbott & Dayan 1999), were taken into account. Thus, the quality of the rate-based representation of flutter frequency was higher during active discrimination than during passive stimulation. These effects were seen in both S1 and S2, although they were stronger in S2. Attention is commonly thought of as a mechanism that amplifies or selects relevant signals, filtering out irrelevant ones (Desimone & Duncan 1995, Connor et al 1997, McAdams & Maunsell 1999a, Reynolds & Desimone 1999), but it may also produce clearer signals (McAdams & Maunsell 1999b).

Thus, context or attention typically modulate the intensity of stimulus-evoked neural responses, but they can also influence the times at which spikes are fired and the effective signal-to-noise ratio, even in a primary sensory area.

NEURAL CORRELATE OF SOMATOSENSORY WORKING MEMORY IN THE PREFRONTAL CORTEX

In the flutter discrimination task described above (Figure 1a), a neural representation of the base frequency needs to be remembered during the delay period following the base stimulus. Where in the brain is such mnemonic trace kept and what is the stimulus representation?

Salinas et al (2000a) found neurons in S2 that prolonged their frequency-specific responses into the early component of the delay period. Their rates typically varied with base frequency in the same direction as during stimulation. This sustained activity typically lasted a few hundred milliseconds (one second at most) and was not seen in S1 (but see Zhou & Fuster 1996). Its functional role is unknown but could be related to working memory.
Romo and colleagues (1999) recorded in the prefrontal cortex, a structure known to be involved in memory processes (Funahashi et al. 1989, Fuster 1989). They found delay responses whose dependence on stimulus frequency was monotonic, like that observed in S2 (Salinas et al. 2000a): Some prefrontal neurons increased their firing rates steadily with increasing frequency, whereas others had firing rates that varied in the opposite direction, firing most intensely at low base frequencies (Figure 4). Most delay neurons fell into one of three groups: early, late, or

![Figure 4](image_url)

**Figure 4** Responses of two neurons in the prefrontal cortex with delay activity during the flutter discrimination task (Figure 1a). (a) Spike raster plot. Each row of dots corresponds to one trial, and each dot represents one action potential. Trials are shown sorted into blocks of equal base frequency (left), in hertz. Long horizontal lines divide groups with equal base but different comparison frequency (right), in hertz. Intervals in gray indicate base and comparison stimulation periods (500 ms). The time axis is shown on the plot below. The firing rate of this neuron increased as a function of base frequency. (b) As in panel a, but for a neuron whose firing rate decreased as a function of base frequency. (c,d) Spike densities (firing rate as a function of time) for the data shown above. Base frequency is indicated by the level of gray: The lightest line corresponds to 10 Hz and the darkest to 34 Hz. (e,f) Mean firing rate (±1 standard error of the mean) averaged over the entire delay period as a function of base frequency. Gray lines are sigmoidal fits to the data. (Modified from Romo et al. 1999.)
persistent. Persistent neurons carried a significant signal related to base frequency during the full delay period, early neurons carried it during the first second of the delay but not during the last one, and late neurons carried such signal during the last second of the delay but not during the first. Thus, early neurons resembled those units in S2 with prolonged activity, which is consistent with the anatomical projections from S2 to prefrontal cortex (Preuss & Goldman-Rakic 1989, Carmichael & Price 1995).

The response characteristics of these prefrontal neurons were not static. When the delay was extended from three to six seconds, most late neurons shifted the onset of their response, again developing a significant signal about 1 s before the end of the delay period (Romo et al 1999; see also Kojima & Goldman-Rakic 1982). These shifts took place in the course of a few trials and probably reflect temporal expectations: With a fixed delay, the monkey can anticipate the onset time of the comparison stimulus.

Anticipation is a crucial factor in memory tasks because it blurs the distinction between sensory- and motor-related activity (Romo et al 1999). When monkeys use different arm movements to indicate their choices, delay responses seen to vary across sensory conditions may actually be associated with the timing (Fuster 1989) or identity (Kojima & Goldman-Rakic 1982, Funahashi et al 1989, Hoshi et al 1998) of the various motor acts. Therefore, the observed delay activity (Romo et al 1999) could have been related to motor preparation or motor intention. To test this, a special stimulus set was designed in which approximately equal numbers of arm motions were made toward the two push-buttons for any given base frequency (only those two arm motions were possible). If the sustained responses had been related to motor anticipation only, no variation in firing rate should have been obtained as a function of base frequency, but this is not what happened. With this set the same kinds of monotonic responses were observed. Thus, it is unlikely that these delay neurons are involved in motor preparation. The observed monotonic encoding might be a general, basic kind of sensory representation used in working memory because, in principle, it may be used for any scalar, analog quantity.

### NEURONAL REPRESENTATIONS OF A DECISION

#### A Categorization Task for Exploring Decision-Making Mechanisms

Romo and colleagues (1993, 1996) designed a task in which the speed of a moving tactile stimulus could be categorized as either low or high. Figure 5a shows the sequence of events. In each trial, a mechanical probe traversed a fixed distance across a fingertip at either of 10 speeds: Five of them were considered low (12, 14, 16, 18, and 20 mm/s), and five were considered high (22, 24, 26, 28, and 30 mm/s). The monkey had to decide whether the stimulus belonged to the low or high category, and the choice was indicated by pressing one of two push buttons.
Figure 5  Responses related to categorical decision making.  

(a) Sequence of events in the categorization paradigm. The tip of a probe was lowered (PD) and touched a fingertip. The monkey reacted by holding a key (KH). Following a delay, the probe started moving (ON) at one of ten speeds. After traversing a constant distance, the probe stopped moving (OFF). The monkey released the key (KR) and pressed one of two push buttons (PB) to indicate whether the speed was low (<20 mm/s) or high (>20 mm/s).  

(b) Spike rasters from an M1 neuron that fired more intensely at low speeds. Each line corresponds to one trial, and each small tick represents an action potential. Large squares indicate behavioral events: onset (ON) and offset (OFF) of probe movement, or key release (KR), which marked initiation of the hand-arm movement toward the buttons. Responses are shown for only two speeds, 12 and 30 mm/s.  

(c) Spike rasters from the same neuron in panel b recorded while the monkey made identical arm movements to the medial (M) or lateral (L) buttons but was cued by the dimming of an LED (light emitting diode) light, with no tactile stimulation. In each trial, the first square indicates the visual go signal (OFF), and the second square indicates key release.  

(d) Mean firing rate (±1 standard error of the mean) as a function of stimulus speed averaged over a population of 27 S1 neurons. Continuous line indicates best linear fit.  

(e) As in panel d, but for a population of 40 supplementary motor area (SMA) neurons that fired significantly more strongly at high speeds than at low speeds. Continuous line indicates sigmoidal fit. Similar responses were also recorded in M1.  

(f) As in panel e, but for a population of 20 M1 neurons selective for low speeds. Similar responses were also recorded in the SMA. (Modified from Salinas & Romo 1998a,b.)
The animal had to discover which speeds belonged to which category by trial and error.

Three quantities are essential in this paradigm: stimulus speed, speed category, and arm motion (which could take two values). Here, computing-speed category is equivalent to reaching a decision, and understanding the decision-making process amounts to answering three key questions. (a) Where are the neural representations of the three quantities, and what are the neural codes used? (b) How are these representations constructed? (c) How do they correlate with a subject’s observable behavior? The second question is the hardest (but see Gold & Shadlen 2000), but neurophysiological experiments have provided some insight into the other two.

Representation of Tactile Motion

Neurons in S1 respond to motion on the skin. DiCarlo & Johnson (1999, 2000) characterized this dependence in detail using random-dot patterns. When a single moving probe is used, the evoked S1 activity can be represented by a population vector (Georgopoulos et al 1988) whose direction and magnitude correspond to the direction and speed, respectively, of the moving tactile stimulus (Ruiz et al 1995).

Recordings from S1 were obtained from monkeys performing the categorization task (Romo et al 1996). Two kinds of neurons were found. One kind increased their firing rates during stimulation regardless of stimulus speed; these neurons signaled the presence of a stimulus but not its properties. However, other neurons fired at rates that increased monotonically with increasing speed, and the relationships were, to a good approximation, linear (Romo et al 1996, Salinas & Romo 1998b; see also DiCarlo & Johnson 1999) (Figure 5d). These neural responses did not covary with behavior: For any given speed, the firing rates for correct and incorrect categorizations were indistinguishable (Salinas & Romo 1998b). In addition, when the same stimuli were delivered passively, the responses were unchanged (in passive trials the monkey’s responding arm was restrained, no movements were performed, and no reward was given).

These results differ from those of Salinas et al (2000a), who found attentional effects and single-trial covariances between neuronal and behavioral responses in S1. Two factors (other than differences in stimuli) might account for the discrepancy. First, fewer data were available in the categorization experiments, so small effects could have been missed. Second, categorization is easier than discrimination (Hernández et al 1997), and attentional effects may depend on task difficulty (Posner et al 1978, Whang et al 1991).

Thus, S1 neurons responded in a purely sensory fashion: First, the firing rate curves reflected stimulus speed, not speed category; second, passive and active responses were indistinguishable; and third, no cofluctuations with behavior were detected. However, lesions in S1 (areas 3b, 1, and 2) drastically impair the capacity to categorize, with deficits persisting for months (Zainos et al 1997). This suggests that S1 is not directly involved in the categorization process, although it provides
a neural representation of tactile motion that is essential for downstream decision-making mechanisms, and probably for perception as well (Romo et al 1998, 2000).

Categorical Decision-Making in Motor Networks

Where should one search for the decision-making mechanisms that operate during somatosensation? The motor areas of the frontal lobe are good candidates, first, because they must be kept informed about any decisions in order to generate the appropriate motor actions (Shadlen & Newsome 1996, Leon & Shadlen 1998, Schall & Thompson 1999) and second, because they receive strong projections from somatosensory areas. For instance, the supplementary motor area (SMA) (also known as medial premotor cortex) receives direct inputs from the posterior parietal cortex and the lateral somatosensory areas (Jurgens 1984, Cavada & Goldman-Rakic 1989, Luppino et al 1993). Neurophysiologists have characterized the SMA as related to motor preparation or execution (Alexander & Crutcher 1990a,b; Kurata & Tanji 1985; Tanji & Kurata 1985), but strong responses to visual, auditory, and somatic stimuli are also seen when animals use them to initiate arm movements (Kurata & Tanji 1985, Tanji & Kurata 1985, Romo & Schultz 1987). Therefore, the role of motor areas in sensory-motor integration (and possibly decision-making processes) may be more important than generally accepted (Shen & Alexander 1997, Zhang et al 1997).

This possibility was investigated by recording the activity of single neurons in the SMA (Romo et al 1993, 1997) and in primary motor cortex (M1) (Salinas & Romo 1998a) of awake monkeys performing the tactile categorization task. Many neurons in these areas displayed activity related to hand-arm motions, as expected from previous reports (Schwartz et al 1988; Alexander & Crutcher 1990a,b; Georgopoulos 1994). These responses did not vary as functions of stimulus speed. However, a small but significant fraction of the neurons in these areas (191/745 in SMA, 71/477 in M1) responded differentially to speed category. These neurons were recorded along the same microelectrode penetrations as the classical motor-related units (Salinas & Romo 1998a). Their firing rates did not vary linearly with stimulus speed, as in S1. Instead, they typically traced sharp sigmoids that either increased or decreased (Figures 5e,f). These neurons showed an almost binary specificity for one or another category. In both areas, about equal proportions of differential neurons preferred low and high speeds (Romo et al 1993, 1997; Salinas & Romo 1998a,b).

Motor and premotor neurons are typically tuned to the direction of arm motion (Georgopoulos et al 1988, Schwartz et al 1988, Georgopoulos 1994). Because low and high speeds always corresponded to the same two push buttons, did the observed differences in rate arise simply from differences between movement trajectories? This is unlikely because tuning curves for movement direction are much broader than the 11 degrees of separation used between push buttons. Based on this distance, the maximum change in firing rate expected for a typical M1 neuron was about 1 spike/s (Salinas & Romo 1998a; see also Schwartz et al 1988).
The observed rate modulation was, on average, much larger than expected from classic directional tuning (Figures 5e,f).

**Distinguishing Responses Related to Sensory, Motor, and Decision-Making Processes**

The plots of firing rate versus speed suggested that the differential responses could represent the output of a decision-making mechanism (speed category), but other possibilities had to be considered (see Horwitz & Newsome 1998). For instance, they could still have been related to preparation or execution of arm movements, but with an exceptionally sharp tuning. What were these neurons coding? Additional control experiments and analyses were performed to address this.

First, none of the differential neurons responded to passive stimulation (0/30 in SMA, 0/5 in M1) (Romo et al 1997, Salinas & Romo 1998a). These cells were not just driven by the sensory stimulus, as in S1.

Second, the animals were also trained to make arm movements toward the push buttons in response to visual cues only, in the absence of tactile input. In this condition, the category-specific neurons either stopped responding altogether or did fire at higher rates compared with baseline, but with the same intensity for both arm movements (Romo et al 1997, Salinas & Romo 1998a) (Figure 5b,c). Overall, about three quarters of the differential neurons tested during visually guided reaching stopped responding differentially (57/71 in SMA, 29/42 in M1). The category-specific responses did not correlate unconditionally with motor behavior.

Third, the psychophysical performance of the monkeys was compared with the performance of an ideal observer who based his judgements on the responses of a population of neurons (Salinas & Romo 1998a,b; see also Britten et al 1992, Shadlen et al 1996). The neurometric curves constructed from S1 responses and the measured psychometric curves had different shapes, which suggests that behavioral performance is based on a different representation of speed. However, the neurometric curves derived from category-specific neurons in the SMA and M1 were almost identical to the monkeys’ performance curves (Salinas & Romo 1998a,b), indicating that the output of the categorical decision-making process is likely to be coded by units that have sharp, increasing and decreasing sigmoidal dependencies on speed.

Fourth, the category-specific responses were compared in correct (hits) versus incorrect categorizations (errors) to determine whether they covaried with sensory input, motor behavior, or both (Salinas & Romo 1998b; see also Britten et al 1996). For example, at any given speed, an ideal motor neuron should produce different responses in hit trials and error trials because, having fixed the sensory input, hits and errors correspond to different arm movements. The resulting patterns of hit-and-error responses exhibited both sensory and motor characteristics in a variety of combinations. This was consistent with an analysis of response latencies, which were not consistently time locked to either sensory (stimulus onset and offset) or
motor (key release) events (Salinas & Romo 1998a). These neurons seemed part of a sensory-motor interface.

Widely Distributed Category Signals

In additional experiments, category-specific neurons were also found in the neostriatum, and these failed to respond differentially during visually guided reaching and during passive stimulation, as in the SMA and M1 (Romo et al 1995, Merchant et al 1997). This is not entirely surprising, considering the bilateral inputs that originate in the SMA (Kunzle 1975, Jurgens 1984, McGuire et al 1991) and the similarities between striatal and motor cortical responses (Alexander & Crutcher 1990a,b; Schultz & Romo 1992; Romo et al 1992; Romo & Schultz 1992; Salinas et al 2000b). Whatever the message the category-specific neurons are sending, it is widely broadcast throughout vast motor networks.

The results in this section can be summarized as follows. In S1, firing rate varies linearly with the speed of tactile motion (Romo et al 1996). This representation is essential for categorization (Zainos et al 1997), but the animal’s choice, low or high, is probably encoded by category-specific neurons or by units with similar responses (Salinas & Romo 1998a,b). These neurons are found in a large number of motor structures, but to activate them, both sensory and motor components of the task are required (Romo et al 1997, Merchant et al 1997, Salinas & Romo 1998a). On the other hand, their activity covaries with both sensory and motor variables in single trials (Salinas & Romo 1998a,b). Therefore, category-specific neurons might represent an interface between the output of the sensory categorization process and the motor command used to indicate the monkey’s choice. Studies in vision have also revealed a tight association between sensory and motor activity during decision making (Leon & Shadlen 1998, Kim & Shadlen 1999, Schall & Thompson 1999, Gold & Shadlen 2000). Whether other areas contain dedicated neurons that encode independently of motor activity the categorical decision being made has yet to be investigated (Horwitz & Newsome 1998).

CONCLUDING REMARKS

Decision making is present even in the simplest tasks. When the afferent input needs to be heavily transformed or analyzed, sensory areas become more involved in the process, and at least in some cases, their activity matches psychophysical performance (Newsome et al 1989, Vogels & Orban 1990, Britten et al 1992, Hernández et al 2000). Thus, the relevant sensory properties—receptive field, feature selectivity, response sensitivity, etc—should be thoroughly investigated, as has been done, for instance, for visual motion or for flutter. This is critical in studying decision making because we need to understand the neural codes for the sensory quantities being decided on (DeCharms & Zador 2000, Salinas et al 2000a), as well as their dependence on factors such as attention or memory.
(Romo et al 1999, Salinas et al 2000a). Intuitively, the circuits that generate motor commands should stand at the other end of the decision-making processes because their output needs to be expressed physically. But is this intuition correct?

First, decision-making might involve neural mechanisms and interactions not yet understood or maybe not even identified so far. The problem of timing may be one of greatest importance. Consider, for example, the following result. When S1 is lesioned, monkeys can no longer categorize the speed of a moving tactile stimulus (Zainos et al 1997). However, they can still detect its presence, so they keep performing the task. A crucial component of the decision-making process is clearly missing, but a decision to press one switch or the other is made anyway; in fact, it is made with the right timing because the reaction times of lesioned animals remain normal (Zainos et al 1997). This result is the converse of the experiment by Seidemann et al (1999), who found that neural activity that would normally have a strong influence on a perceptual decision had absolutely no effect when it was out of synch relative to the normal sequence of events in the task (although this could be modified through training). Therefore, the decision-making process seems to proceed as if it were part of an encompassing, established plan. Maybe it is better to think of making a decision as the creation of a highly flexible motor plan that can be delayed (if the action requires a go signal to be triggered) or rapidly reconfigured (if the motor output is not specified ahead of time), for example. As illustrated in the previous section, the signals that come closest to encoding the output of a decision-making process have been found in areas involved in motor control: the SMA (Romo et al 1997, Salinas & Romo 1998b), M1 (Zhang et al 1997, Shen & Alexander 1997, Salinas & Romo 1998a), and the lateral intraparietal area (Shadlen & Newsome 1996). Is there any difference between making a decision and planning a motor action that can be postponed indefinitely? The recent study by Gold & Shadlen (2000) is particularly revealing. They recorded neural activity and injected microstimulation current in the frontal eye field of monkeys performing a two-alternative motion-discrimination task. The frontal eye field is involved in generating eye movements. Gold & Shadlen found that this area gradually accumulates evidence for motion in one or another direction, such that the process of forming a decision and motor preparation seem to be indistinguishable.

Another intriguing consideration is this. Making decisions may involve information coming from various sources and gathered at widely different times, such as information arriving from sensory areas, working memory, or long-term memory. Thus, the circuits toward which multiple pieces of information converge would seem to require a common format for the incoming signals, a common code. McAdams & Maunsell (1999b) pointed out that sensory events and internal behavioral state may affect cortical responses in equivalent ways, through similar circuits and synaptic mechanisms that differ only in the information they deliver. It is interesting that in several instances, the firing of somatosensory neurons has been shown to be linearly related (approximately) to stimulus parameters and to subjective intensity (Mountcastle et al 1963, Sinclair & Burton 1993, Jiang et al...
1997, Johnson et al 1996, Blake et al 1997, Romo et al 1996, Salinas et al 2000a). This includes the prefrontal responses that encode flutter frequency during a delay period (Romo et al 1999). Is there a common neural substrate, independent of modality or of stimulus parameters, shared by most discrimination tasks or decision-making processes?

These and related questions will probably be central to future neurophysiological studies of decision making in all modalities.

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FROM SENSATION TO ACTION


CONTENTS

PDZ DOMAINS AND THE ORGANIZATION OF SUPRAMOLECULAR COMPLEXES, Morgan Sheng, Carlo Sala 1

THE ROLE AND REGULATION OF ADENOSINE IN THE CENTRAL NERVOUS SYSTEM, Thomas V. Dunwiddie, Susan A. Masino 31
LOCALIZATION AND GLOBALIZATION IN CONSCIOUS VISION, S. Zeki 57

GLIAL CONTROL OF NEURONAL DEVELOPMENT, Greg Lemke 87

TOUCH AND GO: Decision-Making Mechanisms in Somatosensation, Ranulfo Romo, Emilio Salinas 107

SYNAPTIC MODIFICATION BY CORRELATED ACTIVITY: Hebb’s Postulate Revisited, Guo-qiang Bi, Mu-ming Poo 139
AN INTEGRATIVE THEORY OF PREFRONTAL CORTEX FUNCTION, Earl K. Miller, Jonathan D. Cohen 167

THE PHYSIOLOGY OF STEREOPSIS, B. G. Cumming, G. C. DeAngelis 203

PARANEUROPLASTIC NEUROLOGIC DISEASE ANTIGENS: RNA-Binding Proteins and Signaling Proteins in Neuronal Degeneration, Kiran Musunuru, Robert B. Darnell 239

ODOR ENCODING AS AN ACTIVE, DYNAMICAL PROCESS: Experiments, Computation, and Theory, Gilles Laurent, Mark Stopfer, Rainer W Friedrich, Misha I Rabinovich, Alexander Volkovskii, Henry DI Abarbanel 263

PROTEIN SYNTHESIS AT SYNAPTIC SITES ON DENDRITES, Oswald Steward, Erin M. Schuman 299

SIGNALING AND TRANSCRIPTIONAL MECHANISMS IN PITUITARY DEVELOPMENT, Jeremy S. Dasen, Michael G. Rosenfeld 327

NEUROPEPTIDES AND THE INTEGRATION OF MOTOR RESPONSES TO DEHYDRATION, Alan G. Watts 357

THE DEVELOPMENTAL BIOLOGY OF BRAIN TUMORS, Robert Wechsler-Reya, Matthew P. Scott 385

TO EAT OR TO SLEEP? OREXIN IN THE REGULATION OF FEEDING AND WAKEFULNESS, Jon T. Willie, Richard M. Chemelli, Christopher M. Sinton, Masashi Yanagisawa 429

SPATIAL PROCESSING IN THE BRAIN: The Activity of Hippocampal Place Cells, Phillip J. Best, Aaron M. White, Ali Minai 459

THE VANILLOID RECEPTOR: A Molecular Gateway to the Pain Pathway, Michael J Caterina, David Julius 487

PRION DISEASES OF HUMANS AND ANIMALS: Their Causes and Molecular Basis, John Collinge 519

VIKTOR HAMBURGER AND RITA LEVI-MONTALCINI: The Path to the Discovery of Nerve Growth Factor, W. Maxwell Cowan 551

EARLY DAYS OF THE NERVE GROWTH FACTOR PROTEINS, Eric M. Shooter 601

SEQUENTIAL ORGANIZATION OF MULTIPLE MOVEMENTS: Involvement of Cortical Motor Areas, Jun Tanji 631

INFLUENCE OF DENDRITIC CONDUCTANCES ON THE INPUT-OUTPUT PROPERTIES OF NEURONS, Alex Reyes 653
NEUROTROPHINS: Roles in Neuronal Development and Function, Eric J Huang, Louis F Reichardt

CONTRIBUTIONS OF THE MEDULLARY RAPHE AND VENTROMEDIAL RETICULAR REGION TO PAIN MODULATION AND OTHER HOMEOSTATIC FUNCTIONS, Peggy Mason

ACTIVATION, DEACTIVATION, AND ADAPTATION IN VERTEBRATE PHOTORECEPTOR CELLS, Marie E Burns, Denis A Baylor

ACTIVITY-DEPENDENT SPINAL CORD PLASTICITY IN HEALTH AND DISEASE, Jonathan R Wolpaw, Ann M Tennissen

QUANTITATIVE GENETICS AND MOUSE BEHAVIOR, Jeanne M Wehner, Richard A Radcliffe, Barbara J Bowers

EARLY ANTERIOR/POSTERIOR PATTERNING OF THE MIDBRAIN AND CEREBELLUM, Aimin Liu, Alexandra L Joyner

NEUROBIOLOGY OF PAVLOVIAN FEAR CONDITIONING, Stephen Maren

{α}-LATROTOXIN AND ITS RECEPTORS: Neurexins and CIRL/Latrophilins, Thomas C Südhof

IMAGING AND CODING IN THE OLFACTORY SYSTEM, John S Kauer, Joel White

THE ROLE OF THE CEREBELLUM IN VOLUNTARY EYE MOVEMENTS, Farrel R Robinson, Albert F Fuchs

ROLE OF THE REELIN SIGNALING PATHWAY IN CENTRAL NERVOUS SYSTEM DEVELOPMENT, Dennis S Rice, Tom Curran

HUMAN BRAIN MALFORMATIONS AND THEIR LESSONS FOR NEURONAL MIGRATION, M Elizabeth Ross, Christopher A Walsh

MORPHOLOGICAL CHANGES IN DENDRITIC SPINES ASSOCIATED WITH LONG-TERM SYNAPTIC PLASTICITY, Rafael Yuste, Tobias Bonhoeffer

STOPPING TIME: The Genetics of Fly and Mouse Circadian Clocks, Ravi Allada, Patrick Emery, Joseph S. Takahashi, Michael Rosbash

NEURODEGENERATIVE TAUOPATHIES, Virginia M-Y Lee, Michel Goedert, John Q Trojanowski

MATERNAL CARE, GENE EXPRESSION, AND THE TRANSMISSION OF INDIVIDUAL DIFFERENCES IN STRESS

REACTIVITY ACROSS GENERATIONS, Michael J Meaney

NATURAL IMAGE STATISTICS AND NEURAL REPRESENTATION, Eero P Simoncelli, Bruno A Olshausen

Nerve Growth Factor Signaling, Neuroprotection, and Neural Repair, Michael V Sofroniew, Charles L Howe, William C Mobley

FLIES, GENES, AND LEARNING, Scott Waddell, William G Quinn