

Neurophysiology: Sensing and categorizing

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Objects differ along many stimulus dimensions, but observers typically group them into fewer ‘categories’ according to their potential use or behavioral relevance. New experiments in awake, behaving monkeys open a window onto the process of stimulus categorization within the central nervous system.

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Our ability to categorize sensory stimuli allows us to interact efficiently with arrays of objects that are physically different, yet functionally similar. A pewter beer stein only vaguely resembles a porcelain teacup, yet they are equivalent in the sense that either can be used to hold a beverage. A clay flowerpot, on the other hand, looks a bit like both but serves an entirely different purpose. The category to which an object belongs largely determines how we interact with it; a complete physical description of the object is often superfluous. Although it feels effortless to us, categorizing sensory stimuli is a notoriously difficult computational problem [1].

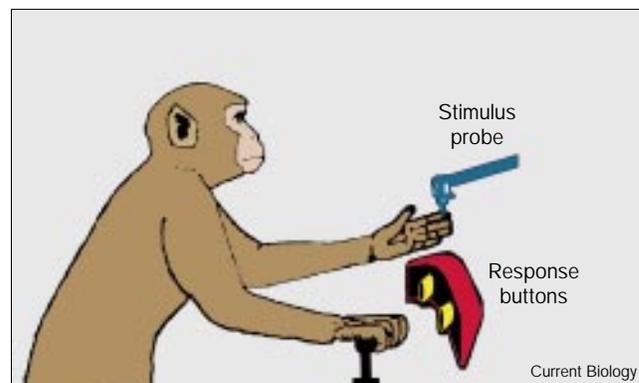
In early sensory areas of the cerebral cortex, stimulus representation appears to depend almost exclusively on elementary physical attributes, such as the orientation of visual edges, the frequency of an auditory tone, or the pressure of a somatosensory stimulus applied to the skin. Neural responses in these areas are thus largely independent of any perceptual category to which an object belongs. In contrast, a small population of neurons in the inferotemporal cortex — a higher order visual area in primates — responds specifically when the face of another monkey or human appears in the visual field [2]. ‘Face cells’ appear to encode a specific category of visual stimuli, irrespective of substantial variability in elementary physical attributes, such as the color, texture or shape of the skin, hair or eyes. Stimulus categorization, therefore, can be reflected in the responses of single neurons when the stimulus category has substantial behavioral significance to the animal.

Recently, Ranulfo Romo and his colleagues in Mexico City have pursued combined behavioral and neurophysiological experiments in rhesus monkeys which have provided insight into how somatosensory stimuli may be

categorized within the central nervous system [3–8]. In these experiments, somatosensory stimuli acquired behavioral significance through extensive training of the monkeys on a simple categorization task. Somatosensory stimuli, moving at various speeds, were applied to the fingers of the left hand as illustrated in Figure 1. The monkey was required to categorize each stimulus as ‘high speed’ or ‘low speed’ in order to obtain a liquid reward. Each trial began when the animal gripped a post with its right hand; categorical judgments of stimulus speed were indicated subsequently by reaching with the right hand to one of two contact buttons. The monkeys developed their categorical sense of high versus low speed through thousands of trials of exposure to speeds that ranged from 12 to 30 millimeters per second, in 2 millimeter per second increments. The monkeys were rewarded for categorizing speeds of 20 millimeters per second or less as ‘low’ and speeds of 22 millimeters per second or greater as ‘high’.

Using microelectrodes inserted across the dura mater, the membranous sheath that covers the brain, Romo and

Figure 1



The experimental set-up employed by Salinas and Romo [8]. The monkey sat on a primate chair, facing a pair of response buttons. Tactile stimuli were applied to the fingers of the left hand, which was immobilized in the palm-up position by means of a half-cast. The monkey placed his right hand on an immobile post to initiate each trial. The probe moved along the fingers of the left hand from distal to proximal at one of ten equally spaced speeds. Once the probe had traveled 6.5 mm, the monkey had 1100 msec to release the key and press a button indicating the speed category of the stimulus (the medial button corresponded to low speeds and the lateral one corresponded to high speeds). The fact that the stimulus excursion was constant across all speeds forces stimulus duration to vary systematically with speed. Thus the monkeys may have been attending to the duration of the stimulus rather than to the speed, but this distinction is not critical for analysis of categorization signals, which is the main topic of the study. (Adapted from [7].)

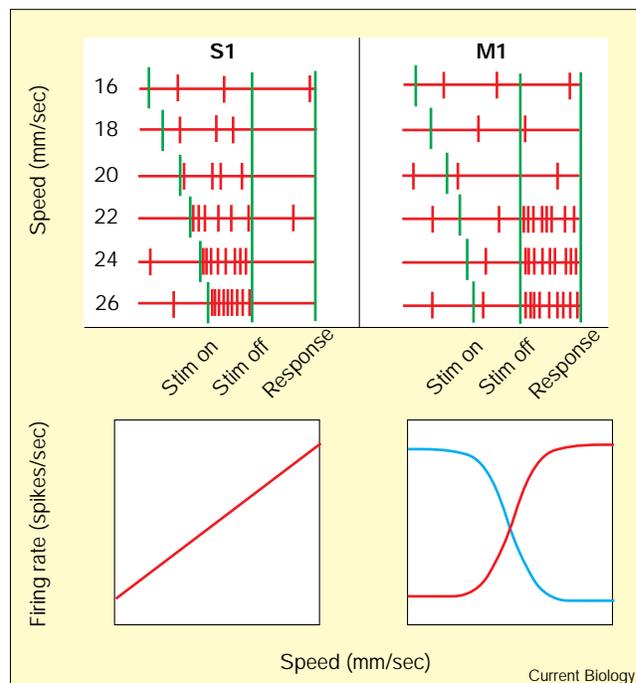
colleagues recorded the activity of single neurons in several brain areas while the monkeys performed the categorization task. The recording technique is minimally invasive, allowing multiple sessions to be conducted without excessive tissue damage. Task-related activity was observed in several areas of the brain, from the primary somatosensory cortex to the primary motor cortex. The central conceptual and technical challenge of these experiments was to distinguish neural activity related to the act of categorization from sensory activity related simply to the representation of the stimulus, or motor activity related specifically to the operant arm movement.

The monkey's sense of touch is obviously critical for performing this task. Indeed, lesions of the primary somatosensory cortex (S1), the first cortical area specialized for processing tactile stimuli, severely impaired performance on the categorization task [6]. Does speed categorization occur in S1? Several lines of evidence suggest that this is not the case [4]. Firstly, S1 neurons that are sensitive to stimulus speed typically increase their responses linearly with the speed of the tactile stimulus, irrespective of its category (Figure 2, left). Thus, the primary variable speed, and not speed category, is explicitly represented in the firing rates of S1 neurons. Secondly, tactile stimulation induces identical activity in S1 whether or not a trained monkey is actively engaged in the task. Lastly, there is no discernible difference in the responses of S1 neurons to these stimuli in trained and untrained monkeys; the trained monkeys' knowledge of stimulus category is not manifest in S1.

More promising candidates for 'categorical' neural signals were identified, however, in the premotor cortex [5], putamen [3,7] and primary motor cortex (M1) [8]. In the most elegant of these studies, Salinas and Romo [8] found that roughly 15% of 477 neurons examined in M1 exhibited category-specific responses. They restricted their search to the region of the M1 motor map representing the right arm (the arm making the operant reaching response). This region of M1 contains neurons that discharge in conjunction with movements of the right arm, and it is therefore the most likely region of M1 to contain categorical signals related to performance on this task. In this region of M1, Salinas and Romo [8] found that some category-specific neurons responded optimally to high-speed stimuli, whereas others responded best to low-speed stimuli. Within each category, however, firing rates were remarkably constant, despite broad variation of stimulus speed within the category.

These properties are the hallmarks of category selectivity, and can be visualized in the nearly step-shaped response functions depicted in the lower right panel of Figure 2. The stimulus-response functions measured in M1 contrast strikingly with those measured in S1 (compare the lower two panels of Figure 2), and the two groups of neurons

Figure 2



Typical results obtained by Romo and colleagues in the primary somatosensory cortex (S1) and primary motor cortex (M1) of monkeys trained on the task illustrated in Figure 1. At the top are shown twelve examples of neural recordings (red), six from S1 (left) and six from M1 (right). All traces are aligned on stimulus (Stim) offset (all event times are indicated by green lines). Each vertical red tick indicates an action potential. S1 neurons discharge action potentials during tactile stimulation at a rate proportional to stimulus speed. M1 neurons respond later in the trial, at one of two rates corresponding to the speed category. At the bottom, the rates of action-potential discharge are plotted as a function of stimulus speed for typical S1 and M1 neurons. Some M1 neurons (right graph) are preferentially excited by fast stimuli (red curve and example recordings above), while others display the reverse tuning (cyan curve). In contrast, none of the S1 neurons (left graph) were preferentially excited by slow stimuli.

also differed in the timing of their activity during the trial (also compare in Figure 2). S1 neurons responded best during application of the stimulus to the skin, whereas M1 neurons responded best during the reaction time interval after application of the stimulus but before execution of the arm movement.

From these data, Salinas and Romo [8] drew the provocative conclusion that neural signals recorded in a small population of M1 neurons represent the speed category of the tactile stimulus. In this view, the categorical neurons would provide a high-level signal that could guide the selection of a specific operant arm movement, which is then conveyed to motoneuron pools in the spinal cord. The most serious difficulty for this conclusion is that the categorical judgment made by the monkey correlates perfectly with the arm movement made to report the judgment (left button for low speeds; right button for high

speeds). Thus, it is possible that the apparent ‘categorical’ signals in M1 are no more than premotor signals for one of the two operant arm movements, which might be expected under standard notions of M1 physiology.

Salinas and Romo [8] present two arguments against the latter interpretation, both of which are strongly suggestive, but neither of which is completely compelling. Firstly, they performed control experiments on a number of identified ‘categorical’ neurons, in which the monkey pressed the same two buttons in response to a simple visual instruction, completely outside the context of the somatosensory categorization task. About half of the ‘categorical’ neurons ceased to respond differentially to the two arm movements in this control experiment, suggesting that a simple motor explanation is not sufficient to explain the differential activity observed during the categorization task. This result strongly supports the argument that the M1 neurons in question actually signal the perceptual categorization, but the argument is not airtight as no quantitative measurements were made to confirm that various parameters of the arm movements — latency, speed, trajectory and accuracy — were identical in the two tasks.

Secondly, Salinas and Romo [8] argue that the known physiology of M1 neurons could not possibly support the large differences in category-related firing they observed in their experiments. Georgopoulos *et al.* [9] have shown that many reach-related neurons in M1 are tuned for the direction of the reach: they respond optimally when the monkey reaches in a particular direction, and their responses fall off gradually as the direction of reaching changes from the optimal. Salinas and Romo deliberately positioned their two operant response buttons side by side, separated by only 11 degrees of reach angle (see Figure 1). From the tuning curves published by Georgopoulos and others, an 11 degree difference in reach angle should result in a very modest difference in firing rate for the two movements. Thus a strictly motor explanation of the categorical responses would appear unlikely. Again, this is a strong, but not completely compelling, argument. Salinas and Romo could make their case much stronger by actually measuring the reach tuning curves of each neuron they study, in order to demonstrate firmly that the categorical signals are not accounted for by motor tuning curves.

The control measurements we have suggested are tedious to perform and analyze, but they are critical if we are to establish beyond doubt the existence of high-level signals related to sensory categorization in M1. Salinas and Romo are ideally positioned to gather even more compelling evidence with experiments of this nature. Looking to the future, Salinas and Romo could provide a coup de grâce by training monkeys on a more complex version of the task, in which the association between stimulus speed and response movement are reversed on interleaved trials.

This could be accomplished by simply marking the ‘fast’ and ‘slow’ buttons uniquely (by color, for example) and randomly swapping them between the two button locations. If the neurons maintain consistent category tuning in both conditions, their activity would undeniably reflect speed categorization. If, on the other hand, their category preference reversed when the button locations reversed, the activity would be more indicative of the monkey’s intention to make a particular arm movement.

The division between sensory and motor functions in the cortex is perhaps not as sharp as was once believed. Some M1 neurons carry signals that are not easily classified as sensory or motor, but appear to be intermediate between the two. This complexity is not entirely unexpected. As we push the envelope of neurophysiological recording into the realm of processes linking sensation and action, the line between them is blurring rapidly. Nevertheless, fascinating questions are emerging, along with new opportunities for empirical investigation. For example, what exactly is the processing path that links sensation to action? What neural transformations are necessary to implement simple cognitive operations such as categorization, discrimination and motor planning? Must sensory signals be cast into an abstract internal model of the world before a motor response is planned, or might a more-or-less direct link exist between sensory and motor representations within the brain, at least for simple sensorimotor associations? Answers to questions of this nature will certainly shape how we think about neural information processing strategies and the neural basis of cognition. The answers are most likely to emerge from creative empirical studies like those of Romo and colleagues, which exploit well-designed behavioral paradigms in conjunction with the tools of neurophysiology.

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