Lecture 18: Decision-Making, part II

Series of experiments by Ranulfo Romo’s lab. Have used a tactile frequency discrimination task to study neurons at several stages of somatosensory system from S1 to motor cortex.

This task involves comparing the frequencies of two sequential stimuli (f1: base, f2: comparison) and deciding whether f2>f1 or f2<f1

This task involves:
- Encoding frequency of f1
- Remembering f1 during a delay period between f1 and f2
- Encoding frequency of f2
- Comparing f2 to f1
- Planning a motor response

Critically, the monkey cannot make his decision until he feels both f1 and f2
Frequency discrimination in the range of ‘flutter’ (5-50 Hz) is thought to be mediated by rapidly adapting (RA) neurons driven by Meissner’s corpuscles.

One class of RA neurons in S1 shows highly periodic modulations in response to the ‘flutter’ stimulus. Response is modulated at the frequency of the stimulus, with no response during the delay between f1 and f2. Neurometric functions based on periodicity (b, green), are generally steeper than the monkey’s psychometric function (b, blue). On average, these periodic responses have sensitivity several times higher than the monkey.
Another class of RA neuron in S1 shows responses that are less periodic, but firing rate increases monotonically with flutter frequency. For this class of neuron, neuronal thresholds are generally similar to psychophysical thresholds.
These results appear to suggest that monkeys should rely more heavily on periodic responses in S1.

BUT... choice probability measurements (Salinas et al. 2000, J. Neuroscience) show that firing rates of non-periodic neurons are correlated with perceptual decisions, whereas periodicity of periodic neurons was not correlated with decisions. Suggests that periodicity may not be crucial. To test this more directly, Romo et al. used microstimulation.

In half of the trials, a periodic train of electrical stimuli was applied to S1 instead of the comparison stimulus (f2). Monkeys continued to perform the task well (a)

Next, monkeys were asked to discriminate between a periodic f1 and an aperiodic f2 (b). They again performed well when the aperiodic f2 was either a tactile stimulus or microstimulation

Suggests that periodic responses are not essential for the task
Microstimulation was also an effective surrogate for tactile stimulation when it replaced the base (f1) stimulus (c).

Perhaps most surprisingly, microstimulation of S1 led to fairly normal performance when both f1 and f2 were substituted by electrical stimulation (d)!

This is different from Newsome experiments in which microstimulation always accompanied a real stimulus.

When microstimulation was applied to clusters of slowly adapting (SA) neurons (open symbols on right), monkeys were unable to perform the task based on microstimulation.
Secondary somatosensory cortex (S2)

S2 receives much of the output from S1 in the somatosensory system.

During the flutter discrimination task, several differences emerged between processing in S1 and S2:

1) Whereas responses of most neurons in S1 are at least somewhat periodic, responses of most S2 neurons are *aperiodic*. Firing rate is modulated with frequency, but not time locked to flutter.

2) For most neurons in S1, firing rate increases with flutter frequency. In S2, there are two types of neurons: those that increase firing rate with frequency, and those that decrease firing rate.

**Example S2 responses**

![Firing rate vs. Stimulus frequency](image)
3) Responses of S2 neurons continue to represent f1 into the delay period of the task, whereas S1 responses terminate at the end of the stimulus. Thus, some S2 neurons appear to maintain a memory trace of f1 into the delay period. But they don’t maintain this memory trace until the end of the memory period (d).

4) Choice probabilities for S2 neurons are significantly larger, overall, than CPs for S1 neurons. Suggests that S2 neurons are more strongly coupled to perceptual decisions.
5) Critically, S2 neurons come to represent the *difference* \((f_2 - f_1)\) during the comparison period and before the motor response.
To quantify this, Romo et al. modelled the responses of neurons as:

\[
\text{Firing rate} = a_1 \times f_1 + a_2 \times f_2 + \text{constant}
\]
Why do cells cluster along negative diagonal?

Firing rate = \( a_1 \times f_1 + a_2 \times f_2 + \text{constant} \)

If cells are on negative diagonal:
\[ a_2 = -a_1 \]

Firing rate = \( a_1 \times f_1 - a_1 \times f_2 \)
\[ = a_1 (f_1 - f_2) \]

Cells are directly coding difference between \( f_1 \) and \( f_2 \)
To quantify this, Romo et al. modelled the responses of neurons as:

\[
\text{Firing rate} = a_1 \times f_1 + a_2 \times f_2 + \text{constant}
\]

Overall, S2 contains a more complex representation than S1. Does S2 represent the critical difference frequency \((f_2 - f_1)\) or does it represent the motor plan to push a particular button? How would you decide?
Prefrontal Cortex (PFC)

S2 neurons cease responding shortly into the delay period of the task. Where is the memory of f1 stored in the brain? PFC neurons begin to represent f1 during the base stimulus, and many maintain activity related to f1 throughout the delay period. Thus, PFC may contain the memory trace.

During the comparison period, PFC neurons come to strongly represent the difference frequency (f2 – f1). Responses of PFC neurons with persistent delay activity tend to show high choice probabilities. Neurons in PFC represent (f2 – f1) before neurons in S2: suggests a possible top-down signal from PFC -> S2.
Medial Premotor Cortex (MPC)

MPC projects directly to the primary motor cortex (M1) and the spinal cord. Thus, it is typically thought to be involved in generating movements. Romo et al show that this area is not simply involved in planning the motor response.

MPC neurons show some activity during the base stimulus (f1) and carry some information about f1 in the delay. F1-related delay activity occurs mostly late in the delay. During the comparison, MPC comes to strongly represent (f2 – f1).
Are MPC responses consistent with a simple representation of the motor plan to press one of the buttons?

Some observations suggest not:

-MPC neurons carry some information about f1 during the base and late in the delay. But f1 alone cannot specify the motor response; monkey needs to know f1 and f2.

-If purely motor, activity should be related to the *sign* of (f2-f1) but not necessarily the magnitude of the difference. Romo et al. show that MPC neurons do represent the magnitude of the difference. This is somewhat analogous to LIP neurons ramping up in proportion to motion coherence.