Neurophysiology: **Electrically evoking sensory experience**

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Monkeys trained to distinguish touch stimuli that ‘flutter’ with different frequencies can similarly distinguish electrical stimulation of the somatosensory cortex according to its frequency; the implication is that the electrically-evoked patterns of cortical activity cause flutter sensations similar to those induced by touch.

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Current Biology 1998, 8:R412–R414
http://biomednet.com/elecref/09609822008R0412

Decades of studies involving electrical recording of the activities of single neurons in the brain have demonstrated that activity in cortical sensory areas is correlated with sensory events. That such activity actually mediates sensory perception is widely assumed, but much less frequently tested. The direct activation of neurons using electrical stimulation is one of few techniques that can actually address this issue. Romo and colleagues [1] have now used this technique in primate somatosensory cortex, examining whether the electrically-induced percept is comparable to naturally-occurring ones. They conclude that the two types of sensation can be extremely similar. We shall consider the persuasiveness of this claim.

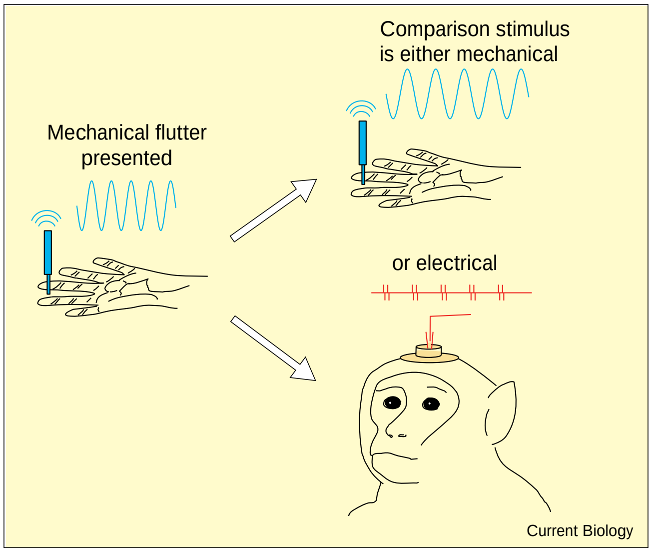
Romo *et al.* [1] trained monkeys to determine which of two mechanical ‘flutter’ stimuli was higher in frequency. The flutter stimuli were applied sequentially to the fingertip and had frequencies that varied from 5–50 Hz. After the animals were fully trained to discriminate the mechanical flutter stimuli, periodic electrical stimulation of primary somatosensory cortex (area S1) was substituted for the second mechanical flutter on some of the trials. This microstimulation was conducted at locations in S1 that responded selectively to mechanical flutter at the fingertip site in question (Figure 1).

After an initial period of parameter adjustment for the first monkey, the animals treated the electrical stimulation train as if it were a mechanical stimulus of the same frequency (Figure 2). In other words, the perceived frequency of the electrical stimulus corresponded to the frequency of the stimulation train. Thus, the same stimulation train could result in judgements of either ‘higher’ or ‘lower’ depending on the flutter frequency of the mechanical stimulus to which it was compared. Similarly, for a given mechanical stimulus, the animal’s judgement depended on the frequency of the stimulation train applied on that particular trial. Performance was nearly the same for mechanical and electrical stimulation. Does this mean that the percepts resulting from the two conditions are essentially identical?

The induction of realistic percepts by electrical stimulation has a long history, extending back to the first presurgical mapping of epileptics’ brains in the fifties. As Penfield’s probing so dramatically demonstrated [2], the sensations evoked from higher-order regions of the brain can be astonishingly realistic. Somatosensory cortex has itself been stimulated under such circumstances, producing tactile sensations [3]. But the population of neurons activated by microstimulation within a brain area has at best only an approximate correspondence to the population that would be activated by a natural stimulus. One could imagine, therefore, that artificial activation of these sensory areas might result in an obviously synthetic percept lacking the richness and complexity that characterizes natural input.

Nevertheless, other experiments have shown that microstimulation in cortical sensory areas produces sensations

Figure 1



The flutter frequency discrimination task employed by Romo *et al.* [1]. Monkeys were trained to judge whether the second stimulus was higher or lower in frequency than the first stimulus. The first stimulus (base) was always a mechanical oscillation, whereas the second (comparison) could be either mechanical or electrical on randomly interleaved trials. The microstimulation consisted of a train of ‘bursts’, each composed of two biphasic pulse pairs. The interburst frequency was considered to be the frequency of the stimulation train.

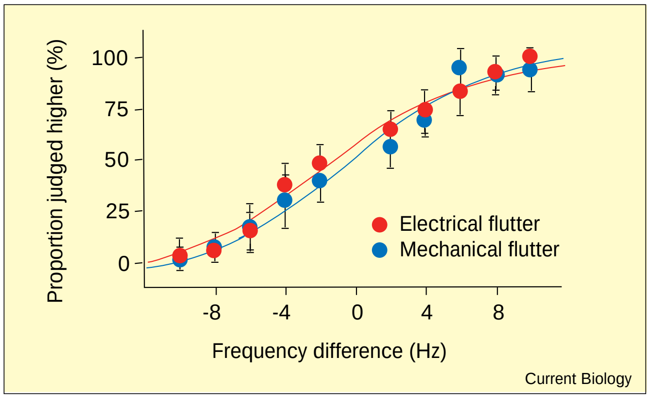
sufficiently realistic that monkeys can actually be fooled by them. Such work has been done in extrastriate visual areas MT and MST, where individual neurons show selectivity for the velocity of moving visual stimuli (reviewed in [4]). When they attempt to judge the overall direction of motion of a patch of dots, microstimulation biases the monkeys' decisions in favor of the preferred motion direction of the cells at the stimulation site [5–8]. Similarly, when they try to track a visual target using saccades and smooth pursuit eye movements, microstimulation causes the monkeys to alter their eye movements in a manner suggesting that the visual and electrical signals in MT are averaged together [9]. These studies found that the monkeys treated microstimulation as if it combined or competed with the sensory input, factoring it into their responses even when they were not rewarded for doing so. In many of these experiments [5–8], the monkeys were in fact rewarded for *ignoring* the microstimulation — the correct answer being determined solely by the visual display — yet they consistently treated the two forms of input as if they were indistinguishable.

An important difference between these earlier studies and that of Romo *et al.* [1] is that the MT/MST microstimulation was presented simultaneously with a sensory stimulus, whereas the new S1 experiment involved microstimulation in isolation. Microstimulation in MT in the absence of a visual input produced only minimal effects [10]. The experiment of Romo *et al.* [1], then, goes beyond the MT/MST studies to bolster the notion that microstimulation can substitute for sensory input altogether, and that it can do so with a time course in exact correspondence with external events.

Determining the exact degree of similarity between electrically induced and naturally occurring sensations, however, is very difficult. A percept that differed radically from the intended stimulus might nonetheless be sufficient for performing the task. In the experiment of Romo *et al.* [1], the monkeys were necessarily rewarded for properly identifying the frequency of the microstimulation train, as no 'correct' mechanical stimulus was presented. The reward criteria for the task encouraged the animals to ignore any potential dissimilarity with the natural stimulus and extract what relevant information was available.

Any alternative to the explanation that the monkeys' perception of the microstimulation was tantamount to mechanical flutter would have to account for the fact that the frequency of microstimulation was somehow discernible to the animal. Thus, even if the 'quality' of the sensation was something other than the tactile sense of flutter, the animals successfully perceived the temporal course of the stimulation train. It is indeed possible that this periodic microstimulation did not resemble flutter, but consisted of some other type of oscillating sensation whose frequency could be successfully compared to that of the oscillating mechanical stimulus. A more perverse possibility is that even a non-oscillating percept with some unknown property that covaried with the microstimulation frequency could be used to perform the task; in this case, however, the monkey would have had to learn quickly and accurately the correct relationship between this unknown property and flutter frequency.

Figure 2



Responses as a function of frequency difference for trials in which the comparison stimulus was mechanical (blue) or electrical (red). The flutter frequency of the base stimulus was 20 Hz for the data in this figure.

We consider these alternatives to be unlikely, for several reasons. First, the stimulation was conducted in an area where neurons are known to respond to the mechanical flutter stimuli. Second, the microstimulation patterns employed probably produced neuronal activity patterns similar to the natural responses to those stimuli [11,12]. Finally, and most compellingly, the monkeys' performance on microstimulation trials was virtually indistinguishable from their performance on interleaved mechanical trials (Figure 2). The most convincing explanation for this finding is that the evoked sensation is similar to the sensation of flutter. Further work in areas to which these S1 neurons project should illuminate how this information is actually used.

References

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