Cortical microstimulation influences perceptual judgements of motion direction

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NEURONS in the visual cortex respond selectively to perceptually salient features of the visual scene, such as the direction and speed of moving objects, the orientation of local contours, or the colour or relative depth of a visual pattern. It is commonly assumed that the brain constructs its percept of the visual scene from information encoded in the selective responses of such neurons. We have now tested this hypothesis directly by measuring the effect on psychophysical performance of modifying the firing rates of physiologically characterized neurons. We required rhesus monkeys to report the direction of motion in a visual display while we electrically stimulated clusters of directionally selective neurons in the middle temporal visual area (MT, or V5), an extrastriate area that plays a prominent role in the analysis of visual motion information.

Microstimulation biased the animals’ judgements towards the direction of motion encoded by the stimulated neurons. This result indicates that physiological properties measured at the neuronal level can be causally related to a specific aspect of perceptual performance.

Like other cortical sensory areas, MT is organized in a columnar fashion so that clusters of neighbouring neurons have similar physiological properties. In MT, neurons in a single cortical column discharge a burst of action potentials in response to motion in a ‘preferred’ direction, but yield little or no response to motion in the opposite or ‘null’ direction. The preferred direction of motion varies systematically from column to column so that MT contains a complete representation of motion direction at each location in the visual field. Consequently, a microstimulation current that selectively elevates the discharge rate of a small cluster of MT neurons should enhance the intracortical signal related to a particular direction of motion. In primate motor cortex, a 10-μA pulse of cathodal current directly activates neurons within ~85 μm of the electrode tip. To activate local clusters of MT neurons, we therefore applied 10 μA stimulating pulses (0.2-msec pulses, 200 Hz, biphasic) to selected sites in which neurons encountered over 150 μm of electrode travel had similar preferred directions. Although we attempted to confine direct excitation to a local cluster, neurons remote from the stimulation site were probably activated trans-synaptically.

But activation of remote neurons does not necessarily imply a loss of functional selectivity; there is increasing evidence that cortical columns are preferentially connected with other columns having similar response properties. These considerations suggest that microstimulation in our experiments may have activated a circuit of neurons encoding a particular direction of motion.

Our methods for electrophysiological recording and for monitoring eye movements in trained rhesus monkeys were adapted from those of Wurtz and colleagues, and our psychophysical methods were based on those described by Newsome and Paré. Figure 1 illustrates the procedures used in the present experiments. In brief, three rhesus monkeys were trained to discriminate the direction of motion in a random dot display shown on a video screen. In the display, a specifiable percentage of the dots carried a constant-velocity or ‘correlated’ motion signal while the remaining dots moved in random directions, creating a masking motion noise. We varied the strength of the motion signal by changing the percentage of dots in

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correlated motion. For each experiment a new stimulation site was selected and the motion display was placed in the multi-neuron receptive field mapped at the stimulation site. On a given trial the monkey maintained visual fixation on a stationary point of light while viewing the random dot stimulus for one second. The correlated motion signal was randomly selected to be in either the preferred or null direction of the local cluster of neurons. After the viewing interval, the monkey indicated its judgement of motion direction by making a saccadic eye movement to one of two light-emitting diodes corresponding to the possible directions of the motion stimulus. The monkey received a liquid reward for a correct choice. An experiment consisted of 640 randomly interleaved trials. On half of the trials we applied electrical stimulation that began and ended simultaneously with the onset and offset of the random dot stimulus. The monkeys performed trials at four correlation levels—0% correlation and three levels near psychophysical threshold. The reward contingencies were identical on stimulated and non-stimulated trials.

If microstimulation enhances the extracortical signal related to the preferred direction of motion of the local cluster of neurons, we would expect stimulation to bias the animal’s psychophysical judgements towards that direction. Figure 2 shows the results of two experiments in which microstimulation had such an effect. For both experiments, the proportion of decisions in favour of the preferred direction (‘preferred decisions’) is plotted against the strength of the motion signal expressed as the percentage of dots in correlated motion. The closed symbols represent trials with electrical stimulation; open symbols correspond to nonstimulated trials. Positive correlations indicate motion in the preferred direction and negative correlations represent motion in the opposite direction. Comparing performance on stimulated and nonstimulated trials, one can see that at every correlation level the monkey made more preferred decisions when electrical stimulation accompanied the visual stimulus, with a net increase of 43 preferred decisions in Fig. 2a and 118 preferred decisions in Fig. 2b. In both experiments of Fig. 2, the increase in preferred decisions due to microstimulation can be described as a leftward shift of the psychometric function. The magnitude of the leftward shift quantifies the microstimulation effect in units of the visual stimulus. In other words, the magnitude of the leftward shift, expressed as percentage of correlated dots, corresponds to the visual stimulus change that would mimic the behavioural effect of microstimulation. We employed logistic regression analysis18 to measure the magnitude and statistical significance of the stimulation-induced shift of the psychometric function. For the experiment of Fig. 2a, the effect of microstimulation was behaviourally equivalent to the addition of 7.7% correlated dots to the visual stimulus and was highly significant (P < 0.0001). For the much larger effect in Fig. 2b, the effect of microstimulation was behaviourally equivalent to the addition of 20.1% correlated dots (P ≈ 0.0001).

Microstimulation caused statistically significant shifts in the psychometric function (P < 0.05) in 18 of 38 experiments in one monkey, in 9 of 16 experiments in a second monkey, and in 3 of 8 in a third. Figure 3 shows for each experiment the magnitude of the stimulation-induced shift expressed as percentage of correlated dots. Positive values correspond to leftward shifts in the psychometric function and negative values correspond to rightward shifts. Stripped bars indicate experiments in which the shift of the psychometric function was statistically significant. In 29 of the 30 experiments that yielded significant effects, microstimulation shifted the psychometric function leftwards, indicating an increase in preferred decisions. In the remaining experiment, microstimulation caused a highly significant rightward shift, an observation that could be explained if microstimulation had a large effect on nearby columns whose preferred direction was opposite to that of the target column. This is a plausible explanation for the single counterintuitive result as adjacent columns of MT neurons sometimes have opposite

![FIG. 2. Effect of microstimulation on psychophysical performance for two stimulation sites in MT. The abscissa indicates the strength of the motion signal in percentage of correlated dots. Positive correlation values indicate motion in the neurons' preferred direction; negative values correspond to motion in the opposite—null—direction. The ordinate shows the proportion of trials in which the monkey judged motion to be in the preferred direction of the stimulated neurons (preferred decision). Each data point is based on 40 trials, except for 0% correlation for which 80 trials were conducted. The correlation levels were selected so that the monkey would judge the direction of motion correctly in ~70% of the trials in a block. In half the trials the microstimulation was applied simultaneously with the visual stimulus; the other trials contained no microstimulation. For each experiment we employed logistic regression analysis18 to fit sigmoidal curves of equal slope to the stimulated and nonstimulated data; the curves thus derived provided an acceptable fit to most of the data. a, Typical experiment in which stimulation biased the monkey's perceptual decisions towards the preferred direction of the stimulated neurons. The psychometric functions for the stimulated trials was shifted leftwards by 7.7% correlated dots. The magnitude of the shift indicates that the behavioural effect of microstimulation could have been reproduced by adding to the visual stimulus 7.7% correlated dots in the preferred direction. b, Experiment in which microstimulation induced a leftward shift of 20.1% correlated dots; one of the larger effects we observed. The different appearance of the 'no stimulation' curves in a and b results largely from differences in choice bias in the two experiments. In the no stimulation condition in a the monkey favoured the preferred direction on 56% of the trials at 0% correlation. Note that with no choice bias, the monkey would have made 50% preferred decisions at 0% correlation; in this experiment, therefore, the monkey had a very small choice bias. In the no stimulation condition b, however, the monkey made preferred decisions on only 33% of the trials at 0% correlation. In this experiment, the monkey had a pronounced bias towards the null direction response LED; the effects of this bias are evident at other points on the no stimulation curve as well. Choice bias is a common phenomenon in human and animal psychophysics, and its presence and intensity in any particular experiment is difficult to predict. Most bias values observed in the present experiments were within the range observed in previous experiments that did not involve electrical microstimulation.

preferred directions9. The data in Fig. 3 show that microstimulation biased the monkeys' perceptual decisions towards the preferred direction of the stimulated neurons. The result is consistent with the notion that focal microstimulation enhances the sensory representation of one direction of motion relative to others. As an alternative explanation, however, is that microstimulation had a direct effect on the operant response, a saccadic eye movement. The latter hypothesis seems unlikely for several reasons. First, physio-