



SMR.853 - 42

ANTONIO BORSELLINO COLLEGE ON NEUROPHYSICS

(15 May - 9 June 1995)

**"Neuronal Plasticity That Underlies Improvement
in Perceptual Performance"**

Ehud Zohary
Department of Neurobiology
Hebrew University
Jerusalem 91904
Israel

**These are preliminary lecture notes, intended only for distribution to
participants.**

Reprint Series
4 March 1994, Volume 263, pp. 1289-1292

SCIENCE

Neuronal Plasticity That Underlies Improvement in Perceptual Performance

Ehud Zohary,* Simona Celebrini,† Kenneth H. Britten,‡ and William T. Newsome

Copyright © 1994 by the American Association for the Advancement of Science

Neuronal Plasticity That Underlies Improvement in Perceptual Performance

Ehud Zohary,* Simona Celebrini,† Kenneth H. Britten,‡
William T. Newsome

The electrophysiological properties of sensory neurons in the adult cortex are not immutable but can change in response to alterations of sensory input caused by manipulation of afferent pathways in the nervous system or by manipulation of the sensory environment. Such plasticity creates great potential for flexible processing of sensory information, but the actual effects of neuronal plasticity on perceptual performance are poorly understood. The link between neuronal plasticity and performance was explored here by recording the responses of directionally selective neurons in the visual cortex while rhesus monkeys practiced a familiar task involving discrimination of motion direction. Each animal experienced a short-term improvement in perceptual sensitivity during daily experiments; sensitivity increased by an average of 19 percent over a few hundred trials. The increase in perceptual sensitivity was accompanied by a short-term improvement in neuronal sensitivity that mirrored the perceptual effect both in magnitude and in time course, which suggests that improved psychophysical performance can result directly from increased neuronal sensitivity within a sensory pathway.

Neural circuitry in sensory areas of the cerebral cortex is intricately organized, evoking the impression of an elegantly wired machine that performs stereotyped computations on sensory input. Recent experiments, however, have shown that this circuitry is subject to dramatic plastic changes. Topographic organization can be altered by damage to peripheral afferents or by chronic performance of a sensory task (1, 2). The stimulus-response properties of individual neurons can be modified by pharmacological intervention (3), by changes in the behavioral context in which a stimulus

is presented (4), and by direct manipulation of the sensory environment (5). Plasticity thus appears to be a common feature of the adult cortex and may be closely linked to the behavioral ability to respond flexibly to the environment.

We compared neuronal to behavioral plasticity in the context of visual discrimination of motion direction. The monkeys were familiar with this task, having developed asymptotically stable performance over months of training. Within daily sessions, however, the animals often exhibited a steady gain in discriminative ability over the first 300 to 500 trials of a particular task configuration. To search for neural correlates of this phenomenon, we examined the activity of single neurons in two extrastriate visual areas that play a prominent role in motion vision: the middle temporal (MT) and medial superior temporal (MST) visual areas. Neurons in these two areas are typically directionally selective; they respond optimally to motion in a particular

Department of Neurobiology, Stanford University School of Medicine, Stanford, CA 94305, USA.

*To whom correspondence should be addressed.

†Present address: Centre de Recherche Cerveau et Cognition, CNRS-UPS, Faculté de Médecine de Rangueil 133, Route de Narbonne, 31062 Toulouse Cedex, France.

‡Present address: Center for Neuroscience, University of California at Davis, 1544 Newton Court, Davis, CA 95616, USA.

"preferred" direction and are frequently inhibited by motion in the opposite, or "null," direction. We have recently demonstrated that the electrical activity of neurons in these areas influences judgments of motion direction in the psychophysical task used here (6). This system therefore provides a particularly promising opportunity to identify neuronal correlates of perceptual plasticity.

We trained four monkeys to discriminate between opposite directions of motion in a random dot visual display. In each trial, a percentage of the dots in the display moved coherently in a common direction while the remainder moved in random directions, creating a masking motion noise. The strength of the motion signal was varied from trial to trial by a change in the percentage of dots moving coherently, and the range of stimulus strengths was chosen so as to measure psychophysical and neuronal thresholds for discriminating the direction of motion in the display (7). Each experiment was divided into consecutive blocks of approximately 200 stimulus presentations, and psychophysical and neuronal thresholds were measured in each block. Data from areas MT (155 cells) and MST (73 cells) are presented together because we found no differences between the two areas that were relevant to this study.

The psychophysical data in Fig. 1A show the proportion of correct choices made by the animal as a function of motion strength (dot coherence level) in a single experiment. The neuronal data in Fig. 1B indicate the proportion of correct choices that could be achieved in principle if decisions were based on the responses of the single neuron under study (8). Both the neurometric and psychometric functions shifted leftward in the second block of trials, which indicates an improvement in the discrimination of weak motion signals. The proportional change in threshold represented by this shift (calculated by dividing the threshold in block 2 by the threshold in block 1) was 0.51 for the psychophysical data and 0.47 for the neuronal data. Thus, both psychophysical and neuronal sensitivity increased by a factor of 2 in the second block of trials (sensitivity = 1/threshold).

The distribution of threshold ratios observed in 202 experiments for which we obtained two full blocks of data is illustrated in Fig. 2. The geometric mean of the threshold ratios was 0.84 for the psychophysical data (Fig. 2A) and 0.88 for the neuronal data (Fig. 2B); both effects were significant (paired *t* test, $P < 0.0001$). On average, psychophysical sensitivity increased by 19.4% and neuronal sensitivity by 13.6%. The change in neuronal sensitivity was not correlated with the change in psychophysical sensitivity on an experiment-by-experiment basis, although the average change was similar.

We conducted an additional 26 experiments with a single monkey that was required to maintain his gaze on a fixation spot during presentation of the visual stimuli; this animal had never been trained on the discrimination task. The neuronal threshold ratios in these experiments are plotted as filled bars in Fig. 2B. These neurons also gained sensitivity during the course of the experiment, and the effect was indistinguishable from that observed in the trained monkeys (9). Thus, the enhancement of neu-

ronal sensitivity appears to be an automatic process that occurs irrespective of the behavioral significance of the stimuli (10). In this respect our data differ from those of Recanzone, Merzenich, and Schreiner, who observed changes in the sensitivity of cortical neurons while monkeys practiced a somatosensory discrimination task but did not observe such changes when the skin surface was passively stimulated (2).

To compare the time courses of the psychophysical and neuronal effects, we averaged across the entire data set to obtain composite thresholds as a function of time, where time is expressed as consecutive stimulus repetitions during a block of trials. Both psychophysical and neuronal thresholds decreased steadily as a function of stimulus repetition number (Fig. 3). The slopes of regression lines fitted to the two sets of data are not significantly different, which is consistent with the notion that the improvements in neuronal and psychophysical sensitivity occurred at the same rate (11). This temporal correspondence suggests that the improvement in psychophysical performance may be a direct consequence of the improvement in neuronal sensitivity.

To investigate the possible locus of neuronal plasticity, we tested whether im-

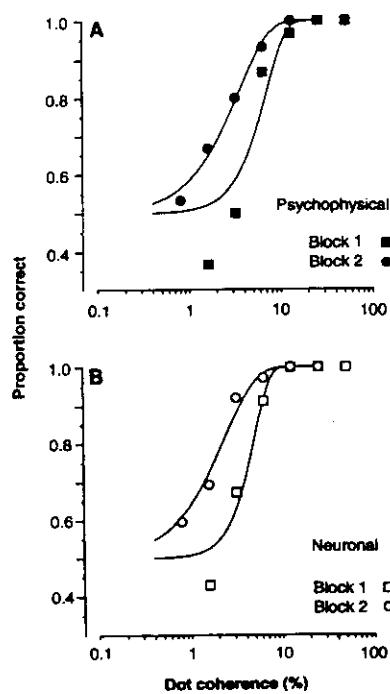


Fig. 1. An example of the effect of stimulus repetition on psychophysical and neuronal performance. Psychophysical performance (A) is given as the proportion of correct discriminations made by the monkey as a function of the percentage of coherently moving dots (motion strength). Neuronal performance (B) was calculated from the differential responses of the neuron to preferred and null direction motion. For each dot coherence level, we used a method based on signal detection theory to compute the performance expected of an ideal observer who reports the direction of motion in the display on the basis of the responses of the neuron under study (8). The neurons were highly directional for strong motion signals, and the performance expected of the ideal observer was therefore excellent. Weak motion signals elicited roughly equal responses to the two directions of motion, resulting in poor performance by the ideal observer. An experiment consisted of successive blocks of trials, and each block consisted of 150 to 210 stimulus presentations (30 stimulus repetitions—15 in each direction of motion—for each of 5 to 7 dot coherence levels). Sigmoidal functions were fitted to the data, and thresholds were calculated from the fitted curves (14). Threshold is defined as the dot coherence level that supports 82% correct performance.

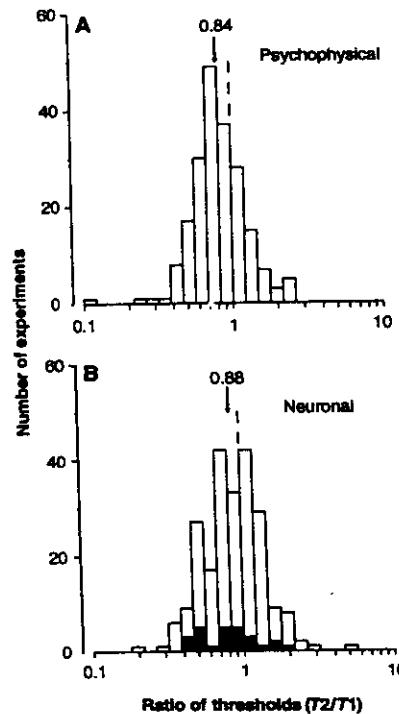


Fig. 2. Frequency histograms describing the ratio of threshold in the second block of trials (T_2) to threshold in the first block (T_1) for both psychophysical (A) and neuronal (B) data. Ratios less than unity indicate an improvement in sensitivity during the experiment, whereas ratios greater than unity indicate the converse. Arrows indicate means of the two distributions.

provement in neuronal sensitivity would "transfer" from a stimulated subregion of the receptive field to a subregion that was not stimulated. If enhanced sensitivity results from plastic changes occurring exclusively within afferent structures with considerably smaller receptive fields (such as the striate cortex) or at specific sets of synapses between small receptive field afferents and MT or MST cells, the increase in sensitivity should not transfer to the unstimulated subregion of the receptive field.

Fig. 3. The dependence of composite threshold on stimulus repetition number over the course of an experiment. Each stimulus was presented 30 times in the experiments included in this analysis. Composite psychophysical data were obtained by summing correct and incorrect responses across experiments for each repetition of each stimulus condition. For example, the proportion of correct choices was calculated across experiments for the first presentation of each dot coherence level (including both the preferred and null directions). The proportion of correct choices was then plotted as a function of stimulus coherence to form a composite psychometric function, and the threshold was computed from fitted functions as described (Fig. 1). This threshold is the psychophysical data point for stimulus repetition number 1. The process was repeated to obtain thresholds for each of the 30 stimulus repetition sequences. To compute composite neuronal thresholds, we generated "decisions" by comparing the physiological responses to preferred and null direction stimuli for each coherence level in each stimulus repetition sequence in an experiment. If the response to the preferred direction was greater, a "correct" decision was scored; if the response to the null direction was greater, an "incorrect" decision was scored. Correct and incorrect decisions were then summed across experiments and expressed as the proportion of correct choices for each coherence level for a given stimulus repetition sequence (as described above for the psychophysical data). The data were plotted to form composite neurometric functions, and thresholds were computed from sigmoidal curves fitted to the composite data. This process was repeated for each of the 30 stimulus repetition sequences to obtain the data illustrated in this figure. The psychophysical data point for stimulus repetition number 1 is an outlier because the monkeys frequently did not know the axis of motion to discriminate until the target light-emitting diodes appeared at the end of the first trial. Performance improved abruptly after the first trial. The first data point was not used, therefore, in the regression analysis of these data.

Fig. 4. (A) Spatial design of the experiment for studying the locus of neural plasticity. After mapping each cell's receptive field (shaded), we selected two nonoverlapping regions inside the receptive field whose direction properties were qualitatively similar. An initial block of 100 stimuli was presented in one of the two sites; this site was selected randomly at the beginning of the experiment and designated site 1. Then a test block of trials was presented (200 stimuli), with half of the stimuli presented at site 1 and half at site 2; the site of presentation was chosen randomly on each trial. In each block of trials, stimuli were presented at several dot coherence levels to permit measurement of neuronal thresholds. The location of the fixation point for this example experiment is indicated by FP. (B) Flow diagram illustrating the sequence of measurements in an experiment. A rectangle represents a block of trials at a given site. An arrow represents a comparison between neuronal thresholds measured in the two blocks connected by the arrow, and the arrow points toward the block having greater sensitivity (lower thresholds). The number accompanying each arrow indicates the increase in sensitivity between the two blocks, averaged across all 36 experiments.

If, however, the neuronal plasticity occurs at the level of MT and MST, conditioning at one location in the receptive field should lead to an increase in sensitivity at the other location as well.

Using the experimental design illustrated in Fig. 4, we compared the effect of conditioning stimuli at site 1 on thresholds measured subsequently at both test sites. The effect of the conditioning stimuli on sensitivity at site 1 could be measured directly by comparison of thresholds obtained during

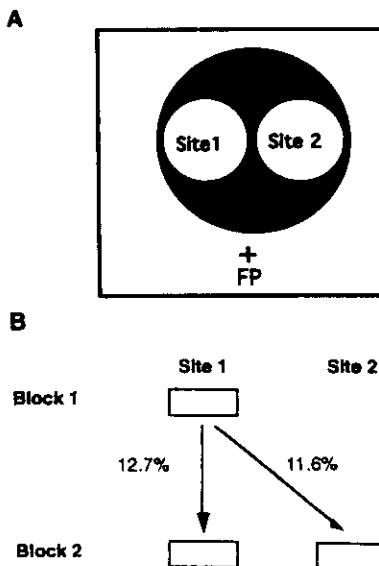
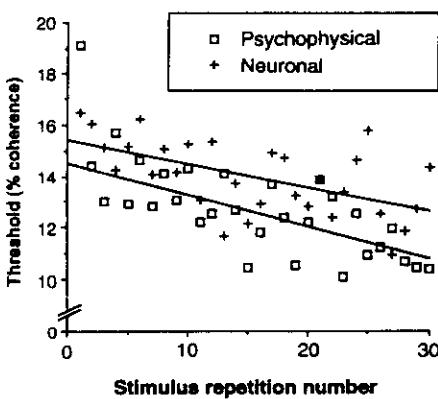
the conditioning and test blocks. However, transfer of the effect to site 2 was inferred indirectly, because any attempt to measure a "preconditioning" threshold at site 2 would itself condition the site. To test transfer to site 2, therefore, we compared across all experiments the average postconditioning threshold at site 2 to the average conditioning threshold at site 1. Average thresholds were used because threshold differences between site 1 and site 2 can arise trivially in any single experiment as a result of spatial inhomogeneities in the receptive field. Across experiments, however, receptive field inhomogeneities average out because the conditioning and test subregions were selected randomly in each experiment.

The experimental design is schematized and the main results summarized in Fig. 4B. Compared with initial thresholds measured during the conditioning trials at site 1, average neuronal sensitivity increased by 12.7% at site 1 and by 11.6% at site 2. On average, conditioning of one subregion of the receptive field appeared to enhance sensitivity equally in conditioned and unconditioned regions of the receptive field. These data suggest that the plastic mechanisms reside, at least in part, locally within the superior temporal sulcus. An alternative hypothesis is that the plastic changes result from spatially nonspecific mechanisms located at an earlier level, perhaps involving lateral connections between cells with nonoverlapping receptive fields (12).

Humans frequently exhibit long-term improvements in discriminative ability as they learn and practice a particular psychophysical task (13). Are the short-term effects demonstrated here related mechanistically to long-term perceptual learning? In principle, perceptual learning could be based on enhanced sensitivity of sensory neurons like that demonstrated here, on more efficient "readout" of information encoded at the sensory level, or on some combination of the two. Comparing the sensitivities of MT and MST neurons before and after training in our direction discrimination task should provide an initial test of these alternatives.

REFERENCES AND NOTES

1. C. D. Gilbert and T. N. Weisel, *Nature* **356**, 150 (1992); J. H. Kaas, M. M. Merzenich, H. P. Killackey, *Annu. Rev. Neurosci.* **6**, 325 (1983); T. P. Pons *et al.*, *Science* **252**, 1857 (1991).
2. G. H. Recanzone, M. M. Merzenich, C. E. Schreiner, *J. Neurophysiol.* **67**, 1071 (1992).
3. Y. Fregnac, D. Shultz, S. Thorpe, E. Bienenstock, *Nature* **333**, 367 (1988); *J. Neurosci.* **12**, 1280 (1992); J. M. Greuel, H. J. Luhmann, W. Singer, *Science* **242**, 74 (1988); D. Shultz and Y. Fregnac, *J. Neurosci.* **12**, 1301 (1992).
4. E. Ahissar *et al.*, *Science* **257**, 1412 (1992); J. H. R. Maunsell, G. Sclar, T. A. Nealy, D. D. DePriest, *Visual Neurosci.* **7**, 561 (1991); E. K. Miller, L. Li, R. Desimone, *Science* **254**, 1377 (1991); J. Moran and R. Desimone, *ibid.* **229**, 782 (1985); N. M.



Weinberger, R. Javid, B. Lepan, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 2394 (1993).

5. M. W. Pettet and C. D. Gilbert, *Proc. Natl. Acad. Sci. U.S.A.* **89**, 8366 (1992).

6. C. D. Salzman, C. M. Murasugi, K. H. Britten, W. T. Newsome, *J. Neurosci.* **12**, 2331 (1992); C. M. Murasugi, C. D. Salzman, W. T. Newsome, *ibid.* **13**, 1719 (1993).

7. The responses of single neurons were recorded while the monkey performed the direction discrimination task. In each experiment, we placed the stimulus so that it matched the size and location of the neuron's receptive field, and we adjusted the speed of the coherently moving dots to elicit an optimal response from the neuron. The motion signal was presented either in the cell's preferred direction or in the opposite (null) direction. In an individual trial, the monkey was required to fixate a stationary point of light for 2 s while the stimulus was presented. After the viewing period, the monkey indicated his judgment by making a saccadic eye movement to one of two light-emitting diodes corresponding to the two possible directions of motion. Eye movements were measured continuously with the scleral search coil technique [D. A. Robinson, *IEEE Trans. Biomed. Eng.* **10**, 137 (1963)]. The monkey received a liquid reward for a correct choice. Incorrect choices were punished by a brief time-out period. If the monkey broke fixation prematurely, the trial was aborted and the data discarded. Cells were included in our data sample on the basis of direction selectivity—we required that their responses to strong motion in the null direction be consistently smaller than their responses to strong motion in the preferred direction. For most cells, the response in the null direction was equal to or less than the spontaneous firing rate.

8. K. H. Britten, M. N. Shadlen, W. T. Newsome, J. A. Movshon, *J. Neurosci.* **12**, 4745 (1992).

9. The average neuronal threshold ratio in the untrained monkey was 0.79, corresponding to an increase in neuronal sensitivity of 26.4%. The difference in thresholds measured in the first and second blocks of trials was statistically significant (paired *t* test, $P = 0.005$, $df = 25$). Although the mean threshold ratio was lower for neurons recorded in the untrained monkey than for those recorded in the trained monkeys, the overall distributions of threshold ratios were not significantly different for the two groups (unpaired *t* test, $P = 0.15$, $df = 226$).

10. In general, enhanced discriminative capacity of single neurons can result either from changes in neuronal responsiveness or from a decrease in response variability. An analysis of our data supports the first possibility. We assessed the change in responsiveness by measuring, for each neuron, the slope of the response function relating motion coherence level to firing rate. Slopes were computed separately for the preferred and null direction response functions in each block of trials. These correlation-response functions were fitted well by straight lines for roughly half of the MT neurons [K. H. Britten, M. N. Shadlen, W. T. Newsome, J. A. Movshon, *Visual Neurosci.* **8**, 1157 (1993)], and this analysis was done only on these cells. The slopes of the coherence-response functions for preferred-direction motion were significantly steeper in the second block of trials, which indicated increased responsiveness (paired *t* test, $P < 0.0002$, $df = 151$). Across coherence levels, firing rates in response to preferred-direction motion increased by an average of 6.6% in the second block of trials. The slopes of the null direction coherence-response functions were significantly more negative, on average, in the second block of trials (paired *t* test, $P < 0.0001$, $df = 116$). Response variance, normalized for firing rate, was unchanged between the first and second blocks of trials.

11. We did an analysis of covariance to determine whether the composite neuronal and psychometric thresholds depended on stimulus repetition number in the same fashion. We used an interaction term between stimulus repetition number and data set (psychophysical or neuronal) to test the null hypothesis that the two data sets were fit as well with the same as with different slopes. The interaction term was not significant ($P = 0.17$).

12. D. Y. Ts'o, C. D. Gilbert, T. N. Wiesel, *J. Neurosci.* **6**, 1160 (1986).

13. M. Ahissar and S. Hochstein, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 5718 (1993); K. Ball and R. Sekular, *Vision Res.* **27**, 953 (1987); N. Berardi and A. Fiorentini, *J. Physiol.* **384**, 633 (1987); A. Kami and D. Sagi, *Proc. Natl. Acad. Sci. U.S.A.* **88**, 4966 (1991); T. Poggio, M. Fahle, S. Edelman, *Science* **256**, 1018 (1992).

14. R. F. Quick, *Kybernetik* **16**, 65 (1974).

15. We thank M. N. Shadlen for suggesting the time course analysis, C. Koch for helpful suggestions during the course of this work, C. D. Salzman for useful comments on the manuscript, and J. Stein for excellent technical assistance. Supported by the National Eye Institute and by training fellowships from the McDonnell-Pew program in cognitive neuroscience and the CNRS of France.

22 September 1993; accepted 7 January 1994