differences between the two sets of measurements. These include the differences between the detectors used, detector shielding, and differences in processing conditions. It is probable that the greatest difference was produced by the differences in shielding. The similarity in the shielding conditions experienced by our detectors and the averaging carried out in the modeling procedure help eliminate variability due to differences in shielding. The use of a single batch of Lexan on all missions, with a single processing cycle which included detectors from all nine missions, combined with a data acquisition carried out by the same observers, gives us a high level of confidence in the results reported here.

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References and Notes

1. C. A. Tobias, *Rep. UCRL-8915* (Lawrence Berkeley Laboratory, Berkeley, Calif., 1958); G. G. Fazio, J. V. Jelley, W. M. Chapman, *Nature (Lond.)* **228**, 260 (1970); C. A. Tobias, T. F. Budinger, J. T. Lyman, *ibid.* **230**, 596 (1971); T. F. Budinger, C. A. Tobias, J. T. Bichsel, J. D. Denney, W. B. Nelp, *Rep. LBL-31* (Lawrence Berkeley Laboratory, Berkeley, Calif., 1971); T. F. Budinger, J. T. Lyman, C. A. Tobias, *Nature* (*Lond.*) **239**. 209 (1972); D. Grahn, "HZE-Particle Effects in Manned Spaceflight" (National Academy of Sciences report, Washington, D.C., 1973); P. J. McNulty, V. P. Pease, L. S. Pinsky, V. P. Bond, W. Schimmerling, K. G. Vosburgh, *Science* **178**, 160 (1972); L. S. Pinsky, W. Z. Osborne, J. V. Bailey, R. E. Benson, L. F. Thompson, *ibid.* **183**, 957 (1974).
2. *Rep. UCRL-17357* (Lawrence Berkeley Laboratory, Berkeley, Calif., 1967); *Rep. LBL-529* (Lawrence Berkeley Laboratory, Berkeley, Calif., 1971); *Rep. LBL-2016* (Lawrence Berkeley Laboratory, Berkeley, Calif., 1973).
3. R. P. Henke, E. V. Benton, H. H. Heckman, *Radiat. Eff.* **3**, 43 (1970).
4. E. V. Benton and R. P. Henke, *Rep. AFWL-TR-72* (Air Force Weapons Laboratory, Albuquerque, N.M., 1972).
5. ———, *Rep. USF-TR-71-15* (University of San Francisco, San Francisco, Calif., 1971).
6. ———, *Rep. USF-TR-72-20* (University of San Francisco, San Francisco, Calif., 1972).
7. ———, *Rep. USF-TR-73-26* (University of San Francisco, San Francisco, Calif., 1973).
8. The response of plastic nuclear track detectors more closely follows the $\mathrm{LET}_{350\,\mathrm{ev}}$ rather than the LET_x of particles. For this reason the quantity $\mathrm{LET}_{350\,\mathrm{ev}}$ is used throughout this work. Over a wide range of particle velocities $\mathrm{LET}_{350\,\mathrm{ev}}$ can be converted to LET_x if one multiplies by a factor of ~ 1.6.
9. For details of this procedure and the measured fluences, please write to the authors.
10. H. J. Schaefer, E. V. Benton, R. P. Henke, J. J. Sullivan, *Radiat. Res.* **49**, 245 (1972).
11. C. M. Travis, personal communication.
12. S. B. Curtis and M. C. Wilkinson, *NASA Contract Rep. 1037* (1968); S. B. Curtis, W. R. Doherty, M. C. Wilkinson, *NASA Contract Rep. 1469* (1969).
13. R. L. Fleischer, H. R. Hart, Jr., G. M. Comstock, M. Carter, A. Renshaw, A. Hardy, *Science* **181**, 436 (1973).

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Self-Produced Locomotion Restores Visual Capacity after Striate Lesions

Abstract. *Rats permitted unrestrained movement in a patterned visual environment during the interval between two-stage bilateral lesions of the visual cortex reacquire a preoperatively learned pattern discrimination. Rats passively transported through the identical visual environment do not. This is the first demonstration that interoperative self-produced locomotion is essential for recovery of function in the visual system.*

Recovery of preoperatively learned tasks occurs in mammals when the brain areas relevant to the task are removed serially (*1*). Identical ablations or lesions made in a single operation may retard recovery of the task or prevent its reacquisition. Recovery is dependent upon the length of the interoperative interval (*2*), the size of the lesion (*3*), and the type of sensory stimulation experienced during the interoperative period (*4*). If animals subjected to two-stage lesions of the visual cortex are kept in the dark between surgeries, loss of visual function occurs just as though the ablation were performed in one stage. On the other hand, animals receiving various types of visual stimulation during the interoperative period recover visual capacity to varying degrees.

The nature of the interoperative experience is the subject of this research. Exactly what types of interoperative stimulation are required for complete recovery of visual function remained in question, but some clues were provided from a parallel area of research: neonatal visual deprivation.

In young animals, visual deprivation early in life precludes normal development of visual function (*5*). Furthermore, self-produced movement must accompany exposure to the visual environment for development of pattern vision. In view of this literature, we decided to investigate the effects of various kinds of sensory-motor deprivation upon the restoration of pattern vision after serial lesions of the striate cortex in rats. The data presented here demonstrate that self-produced movement is requisite for the recovery of pattern vision.

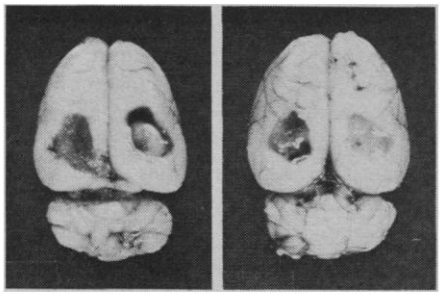

Fig. 1. Maximal (rat No. 6) and minimal (rat No. 23) cortical damage. Mean destruction was 14.6 percent of neocortex for all groups.

Fifty-two adult male Long-Evans rats were tested for ability to discriminate horizontal-vertical patterns, were given two-stage ablations of the striate cortex, and were retested for ability to discriminate visual patterns. During the 11 days between two-stage surgeries, the subjects were exposed differentially to visual stimulation 4 hours daily. The remaining 20 hours were spent in total darkness.

Rats were trained in a modified Thompson-Bryant Box (*6*). Prior to surgery, the animals underwent 5 days of pretraining consisting of ten trials per day. During days 1 and 2, the rats were taught to run to the goal box to escape or avoid shock. Over days 3, 4, and 5, two white translucent doors were gradually lowered over the goal box openings, and the rats were trained to push through the doors to enter the goal box.

The animals were then taught to discriminate between a vertical black-white striped door which led to the goal box and a horizontal black-white striped door which was always locked. The position of the correct door was varied randomly. Upon the lifting of the start gate, the animal was required to run through the vertically striped door into the goal box within 10 seconds to avoid or escape a constant-current, 1-ma shock of 2-msec duration, three times per second. A response to the negative stimulus was always shocked. Such a response involved the animal entering the wrong alley by two or more inches (5 cm). Preoperatively, animals were discarded if they failed to reach the criterion of nine out of ten correct discriminations within 12 days. Postoperatively, animals were run to an upper limit of 20 days to the same criterion. Recordings were made of the number of discrimination trials to cri-

Table 1. Median learning and retention scores.

Group	N	Preoperative learning		Postoperative retention (%)	
		Trials	Errors	Trials	Errors
Dark	10	85	37	−154	−202
Diffuse	12	80	37	−171	−170
Restrained	11	70	30	−171	−213
Unrestrained	11	90	35	+130	+ 20

terion and the number of discrimination errors committed before learning the task.

Surgery was performed under Nembutal anesthesia. Area 17 was aspirated with special care to leave subcortical tissue untouched. Lesions were performed in two stages with half the animals receiving left first-stage lesions and half receiving right first-stage lesions. Eleven interoperative days intervened between surgeries. Figure 1 shows the minimal and maximal extents of cortical damage.

After the first ablation, each rat was placed into one of four groups differentially exposed to visual stimuli. Group 1 remained in total darkness for the entire 11 days. Group 2 spent 4 hours daily in a light-diffusing plastic cylinder 15 cm in diameter and 60 cm in length. The cylinder was closed at both ends with the same material. The remaining 20 hours were spent in total darkness. Group 3 was transported through a patterned visual environment 4 hours daily while restrained in a holder fashioned from metal cans and grating. One end of the holder had a circular opening through which only the animal's head could protrude. The animal was held in position by a hairpin loop of wire passed through the grating at the other end of the holder. The environment was a circular alley 20 cm wide and 120 cm in diameter. Visual stimuli were painted on the alleys with black paint and included 1.25-cm-wide striations placed in various horizontal-vertical configurations. The holders were attached to a rotating apparatus turned by a variable-speed motor which transported the rats through the environment at speeds ranging from one revolution every 1 minute to one revolution every 5 minutes. The remaining 20 hours were spent in total darkness.

Group 4 was allowed free movement, 4 hours daily, in patterned visual alleys identical to those through which animals in group 3 were transported. The remaining 20 hours were spent in total darkness.

Four days after the second ablation, animals were tested for sparing of the pattern discrimination habit. Postoperative discrimination ability was compared to preoperative ability by means of savings scores for both trials to criterion and number of discrimination errors committed in reaching criterion.

For trials to criterion, we used the following formula for percent savings, trials:

$$\frac{(\mathrm{OL} - 10) - (\mathrm{RL} - 10)}{\mathrm{OL} - 10} \times 100$$

where OL refers to original learning and RL to relearning. Discrimination errors were computed according to the following formula for percent savings, errors:

$$\frac{\mathrm{OL} - \mathrm{RL}}{\mathrm{OL}} \times 100$$

Data for pre- and postoperative performance of all groups are summarized in Table 1. A Kruskal-Wallis analysis of variance revealed no differences among groups in preoperative learning in terms of trials or errors to criterion. A comparison of the postoperative retention scores indicates that only those animals allowed unrestrained movement during interoperative exposure to visual stimuli retained the pattern discrimination habit ($P < .001$). In addition, 7 of the 11 animals in this group demonstrated sparing, that is, postoperative performance was superior to preoperative performance. Virtually all animals in the dark, diffuse, and restrained groups failed to reach criterion on the visual task within the 20-day testing session.

Thus, visual deprivation during the interoperative period precludes two-stage recovery of visual function. Furthermore, self-produced locomotion must accompany exposure to a patterned visual environment for recovery to occur. These observations have implications for the treatment of patients after stroke or other trauma affecting the visual system. The findings are in accord with data from two parallel areas of research: neonatal visual-deprivation studies and visual-motor rearrangement experiments. Self-produced movement must accompany exposure to the visual environment for the normal development of pattern vision (*5*). Similarly, self-produced movement is essential in producing visual-motor adaptation to a prismatically rearranged visual environment (*7*). The similarity in findings suggests that related processes underlie visual-motor development, visual-motor adaptation, and visual-motor recovery.

Recovery of pattern vision after sequential removal of visual cortex is probably a consequence of functional reorganization of brain areas not primarily responsible for visual capacity. If synaptic geometry is important to restoration of function (*8*), then self-produced locomotion accompanying visual stimulation may enhance functional reorganization of synaptic terminals within the extravisual system.

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References

1. N. Butters, C. Butter, J. Rosen, D. Stein, *Exp. Neurol.* **39**, 204 (1973); S. Finger, R. A. Marshak, M. Cohen, S. Scheffs, R. Trace, D. Niemand, *J. Comp. Physiol. Psychol* **77**, 221 (1971); S. D. Glick and B. Zimmerberg, *ibid.* **79**, 481 (1972); J. Rosen and D. Stein, *Science* **173**, 353 (197 → D. G. Stein, J. J. Rosen, J. Graziedei, D. Mishkin, J. Brink, *ibid.* **166**, 528 (1969).
2. J. W. Stewart and H. W. Ades, *J. Comp. Physiol. Psychol.* **44**, 479 (1951).
3. L. J. Petrinovitch and T. J. Carew, *ibid.* **68**, 451 (1969).
4. D. D. Cole, W. R. Sullins, W. Isaac, *Psychopharmacologia* **11**, 311 (1967); R. L. Glendenning, *J. Comp. Physiol. Psychol.* **80**, 216 (1972); W. Isaac, *Psychol. Rep.* **14**, 151 (1964); K. A. Kircher, J. J. Braun, D. R. Meyer, P. M. Meyer, *J. Comp. Physiol. Psychol.* **71**, 420 (1970); D. R. Meyer, W. Isaac, B. Maher, *ibid.* **51**, 546 (1958); L. Petrinovitch and D. Bliss, *ibid.* **61**, 136 (1966); R. Thompson, *ibid.* **53**, 212 (1960).
5. A. Hein and R. M. Diamond, *J. Comp. Physiol. Psychol.* **76**, 219 (1971); R. Held and A. Hein, *ibid.* **56**, 872 (1963); R. Held and J. Bauer, *Science* **155**, 718 (1967); A. H. Riesen and L. Aarons, *J. Comp. Physiol. Psychol.* **52**, 142 (1969); A. H. Riesen, in *Symposium Bel Air II Desafferentation Experimentale et Clinique*, J. de Ajuriguerra, Ed. (Georg, Geneva, 1965).
6. R. Thompson and J. H. Bryant, *Psychol. Rep.* **1**, 393 (1955).
7. R. Held and R. Freedman, *Science* **142**, 455 (1963); R. Held and N. Gottlieb, *Percept. Mot. Skills* **8**, 83 (1958); R. Held and A. V. Hein, *ibid.*, p. → R. Held and M. Schlank, *Am. J. Psychol.* **72**, 603 (1959); R. Held and J. Bossom, *J. Comp. Physiol. Psychol.* **54**, 33 (1961).
8. D. C. Goodman and J. A. Horel, *J. Comp. Neurol.* **127**, 71 (1966); G. Lynch, S. Deadwyler, C. Cotman, *Science* **180**, 1364 (1973); G. Raisman, *Brain Res.* **14**, 25 (1969); G. E. Schneider, *Brain Behav. Evol.* **3**, 295 (1970).

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