gime similar to that regulated by other bluegills in tanks with a 2°C difference between sides (Fig. 2). Successful regulation in a tank without a temperature differential indicated that the bluegill learned to associate changes in its spatial position with eventual (but not immediate) changes in temperature.

We believe that our experimental system is amenable to several other modifications that may increase its versatility. If the tunnel is essentially curved on itself to form a doughnut-shaped swimming space, behavioral thermoregulation by continuously swimming fishes of the open sea, such as tunas (*8*), can be studied. Swimming direction (clockwise, counterclockwise) can control the direction of temperature change; swimming speed can control the rate of temperature change. Thus, fishes could be required to thermoregulate in continuous, gentle (0.1°C per 100 m) gradients of temperature in space that are simulated by changes in temperature through time.

Simultaneous behavioral regulation of temperature and a second, nonthermal factor may be investigated by using a tank with four compartments and two monitors. Concentrations of soluble substances (such as O_2, salts, pollutants) can be regulated by a fish-controlled mixing valve; light intensity can be regulated by fish-controlled dimmer circuitry. Movements of the fish in one dimension would regulate temperature and, in the other, the second variable (*9*). Such an approach would make it possible to measure the joint preferendum for two independently varying factors.

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References and Notes

1. F. E. J. Fry, in *Handbook of Physiology: Adaptation to the Environment*, J. Field *et al.*, Eds. (Williams & Wilkins, Baltimore, 1964), section 4, p. 715; *Univ. Toronto Stud. Biol. Ser.* **55**, 5 (1947).
2. P. N. Rozin and J. Mayer, *Science* **134**, 942 (1961).
3. B. Weiss and V. G. Laties, *J. Comp. Physiol. Psychol.* **53**, 603 (1960).
4. The circuit diagram of the monitor and other details are available on request from the authors.
5. The specimens 50 to 100 mm long that provided the data for Fig. 2 were taken from waters near Madison, Wisconsin, and were acclimated to 22°C prior to experiments.
6. The upper turn-around temperatures were local temperature maximums recorded from the warmer side of the tank. The *i*th local maximum, U_i, was the highest temperature recorded along the time sequence such that U_i was separated from adjacent maximums, U_{i-1} and U_{i+1}, by temperatures at least 0.5°C less than $\min(U_{i-1}, U_i)$ and $\min(U_i, U_{i+1})$, respectively. The lower turn-around temperatures were the corresponding local minimums recorded from the cooler side of the tank. The *i*th local minimum, L_i, was the lowest temperature recorded along the time sequence such that L_i was separated from adjacent minimums, L_{i-1} and L_{i+1}, by temperatures at least 0.5°C greater than $\max(L_{i-1}, L_i)$ and $\max(L_i, L_{i+1})$, respectively.
7. W. H. Neill, thesis, University of Wisconsin (1971).
8. Work proposed by the first two authors and A. Dizon for execution at the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service.
9. Systems analogous to those described here may be used to study behavioral regulation of nonthermal factors at various constant temperatures.
10. Development of the method described here and its initial application were part of a thesis submitted by W.H.N. to the graduate faculty of the University of Wisconsin, Madison, in 1971, in partial fulfillment of the requirements for the Ph.D. degree. The work was done at the Laboratory of Limnology and was supported in part by funds from the Wisconsin Utilities Association and the Office of Water Resources Research, Department of the Interior (MG OWRR B-028-Wis—WRC 70-010M). We gratefully acknowledge the technical assistance of Thomas C. Byles and Bruce K. Quirk.

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Rearing Complexity Affects Branching of Dendrites in the Visual Cortex of the Rat

Abstract. *Higher-order dendritic branching is considerably greater in Golgi-stained neurons from the occipital cortex of rats reared in groups in a complex environment than in similar neurons of littermates reared individually in laboratory cages. Littermates reared in pairs in cages have intermediate amounts of branching, while lower-order branching did not appear to be affected by any rearing environment.*

Alterations in the fine structure and ultrastructure of the cortex have been reported to follow extremes of sensory deprivation. Light deprivation has been found to alter the number of apical dendritic spines on pyramidal cells in the visual cortex of rodents (*1*) and to diminish higher-order dendritic branching in cats (*2*). Electron microscopic studies have indicated alterations in the size and density of individual synapses in the visual cortex after deprivation (*3*). Further, changes in spine density may be brought about by excess sensorimotor stimulation. Schapiro and Vukovich (*4*), for example, reported increased spine density and altered Golgi staining patterns after intense multimodal stimulation was given during the early postnatal period.

The above-mentioned changes have generally been reported only after animals were given differential stimulation far greater than that which the normal laboratory environment might provide. However, Rosenzweig, Bennett, and Diamond (*5*), along with others (*6*), have suggested that similar effects may be generated by milder forms of deprivation and enrichment. Increases in cortical weight and thickness, glial numbers, perikaryonal size, and enzyme activity have been found in rats subjected to a complex environment as compared to deprived littermates. Electron microscopic studies have indicated that average synaptic thickenings in some areas are longer after enriched rearing, but whether they also increase in number

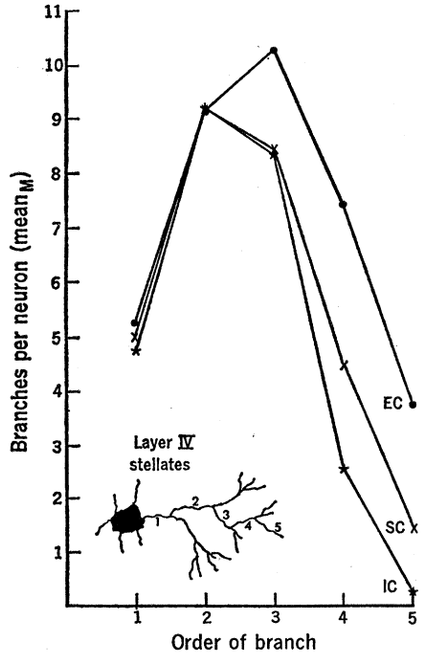

Fig. 1. Branches per layer IV stellate cell in the three rearing groups: *EC*, enriched; *SC*, social; and *IC*, isolated. Differences are confined to higher-order (3, 4, 5) branches. The diagram in lower left indicates scoring procedure. *Mean*$_M$ is the mean of mean scores for individual animals.

remains unclear (*7*). In a preliminary study, Holloway (*8*) reported increased dendritic branching in "layer II stellate" neurons of the occipital cortex of enriched rats as compared to deprived littermates. The overall effect for paired and unpaired animals was weakly significant, and only two of five significant comparisons of littermate pairs showed greater branching in the enriched animals. We now report that reliable differences in the number of higher-order dendritic branches in four types of Golgi-stained visual cortical neurons are found in animals reared in different environments.

Members of 12 male littermate triplet sets of Long-Evans hooded rats (*9*), matched for body weight, were assigned at 22 to 25 days of age to one of three environmental conditions (*4*). Enriched (EC) rats were housed in a group of 12 in a large wire mesh cage (45 by 60 by 70 cm) provided with a set of wood, metal, and plastic "toys," which were changed daily. Additionally, they were allowed 30 minutes of free play in a square box (1.2-m sides) equipped with similar toys. Isolated (IC) littermates were housed in standard sheet metal cages with wire mesh fronts and bottoms (22 by 25 by 30 cm). Social (SC) littermates were housed in pairs in identical cages. Diurnal lighting was on a 12-hour cycle, and all subjects had free access to food and water.

After 29 to 31 days in the differential environments, the animals were coded to prevent experimenter effects, anesthetized with sodium pentobarbital, and perfused with physiological saline. Triplet set members were perfused sequentially, the order randomized within each set. Coronal slabs 3 mm thick were excised from an area beginning 1.5 mm in front of the posterior cortical pole; a stereotaxic apparatus equipped with a scalpel blade was used. The tissue blocks were placed for 3 days in a solution of 2.4 percent potassium dichromate, 6 percent chloral hydrate, 1.5 percent potassium chlorate, and 4 percent formaldehyde (changed twice daily); transferred for 3 days to 3 percent potassium dichromate (changed daily); and then placed in 1 percent silver nitrate for 3 days; all solutions were at room temperature. This is a slight modification of the technique of Ramon Moliner (*10*). After staining, frozen 100-μm coronal sections were taken from the central 2 mm of the tissue slab and mounted in Permount with a coverslip. Of the eleven triplet sets processed (one member of the EC group died shortly after beginning the environmental treatment), six usable triplet sets (that is, sets in which all three animals showed satisfactory staining) were analyzed for dendritic branching.

From the area between 2 and 4 mm lateral to the midline, camera lucida drawings at ×400 were made of layer II pyramidal cells, layer IV pyramidal cells, layer IV stellate cells, and giant pyramidal cells of layer V (*11*). This area corresponds well to the occipital, or visual, cortex (*11*). Ten to fifteen neurons of each type were traced from the ten to twenty sections of each animal while the depth of focus was varied. No correction was made in converting the three-dimensional structure to two dimensions. Each drawing of a single neuron was analyzed (Fig. 1) for the number of dendritic branches and the order of branching; an order 1 branch is from the cell body, an order 2 branch is from an order 1 dendrite, and so forth (*2*). Data for basal and apical dendritic fields of pyramidal cells were combined.

The results for dendritic branching in the four cell types studied are shown in Table 1. Standard error values are based on the means for each animal, rather than on all individual neurons (the calculation used gives a more conservative estimate). Figure 1 indicates the relative magnitude of the differences at each order for layer IV stellate neurons. The probability of higher-order branching increases with increasing complexity of the rearing environment, at least within the range of conditions we used, while lower-order branches appear not to be affected.

The comparison between EC and IC animals is particularly clear in order 5 dendrites. In all possible cell types with all possible animal pairs, there is no case where order 5 branching in the IC rat exceeds that of his EC littermate ($P < 1 \times 10^{-6}$ for two-tailed sign test). In most of the other comparisons of order 3, 4, and 5 dendrites in animal pairs, EC animals have more branches than their SC and IC littermates. Differences between paired SC and IC animals are not quite so clear, but SC animals generally have more higher-order dendrites. Few if any re-

Table 1. Dendritic branching as a function of rearing condition: EC, enriched; SC, social; and IC, isolated. $Mean_M$ is the mean of the mean scores for individual animals, and N is the total number of neurons. Paired comparisons were scored as the number of pairs in which the mean branches per neuron for a particular pair member exceeded that value for his littermate. Significance values of comparisons were determined by analysis of variance.

Dendrite order	Branches per neuron ($mean_M$ ± standard error of $mean_M$)			Paired comparisons (pairs out of total pairs)		
	EC	SC	IC	EC > SC	EC > IC	SC > IC
			Layer II pyramidals			
	$N = 61$	$N = 60$	$N = 67$			
1	4.80 ± .39	4.90 ± .19	4.65 ± .18	3/6	3/6	4/6
2	8.85 ± .54	8.38 ± .38	8.20 ± .62	3/6	3/6	3/6
3	8.78 ± .67	7.42 ± 1.12	7.30 ± .86	5/6	4/6	4/6
4	4.42 ± .41	2.55 ± .86	1.78 ± .29	5/6	6/6*	4/6
5	1.60 ± .39	0.42 ± .19	0.08 ± .17	5/6*	6/6†	4/6
			Layer IV stellates			
	$N = 62$	$N = 64$	$N = 68$			
1	4.80 ± .16	5.03 ± .27	4.75 ± .13	3/6	3/6	3/6
2	9.10 ± .38	9.20 ± .44	9.22 ± .39	3/6	2/6	4/6
3	10.27 ± .66	8.24 ± 1.02	8.35 ± .91	5/6	5/6	2/6
4	7.40 ± 1.02	4.47 ± 1.10	2.63 ± 1.03	4/6	5/6†	5/6
5	3.73 ± 1.41	1.47 ± .39	0.27 ± .11	5/6	6/6*	5/6*
			Layer IV pyramidals			
	$N = 62$	$N = 64$	$N = 64$			
1	4.77 ± .31	4.53 ± .18	4.63 ± .08	3/6	2/6	2/6
2	8.97 ± .52	7.95 ± .75	8.95 ± .48	4/6	3/6	2/6
3	10.14 ± 1.03	7.45 ± .58	5.97 ± 1.10	5/6*	6/6*	4/6
4	5.51 ± 1.12	3.88 ± .84	1.68 ± .40	4/6*	6/6*	5/6*
5	2.70 ± .94	1.30 ± .24	0.42 ± .26	3/6	6/6*	4/6
			Layer V pyramidals.			
	$N = 64$	$N = 60$	$N = 66$			
1	4.90 ± .24	4.60 ± .13	4.68 ± .08	4/6	3/6	1/6
2	8.80 ± .62	7.93 ± .76	8.83 ± .36	4/6	2/6	2/6
3	9.98 ± .54	7.77 ± .58	7.65 ± .71	4/6*	6/6*	4/6
4	6.70 ± .81	3.87 ± .84	2.72 ± .76	5/6*	5/6†	4/6
5	3.53 ± .95	0.90 ± .24	0.47 ± .24	6/6*	6/6†	4/6

* $P < .05$. † $P < .01$.

liable differences appear in order 1 and 2 dendrites.

The data provide evidence for regulation of neuronal growth, at least during maturation, by "use," that is, by the degree of stimulation involved in the environmental situation in which the animal is reared. A possible explanation of the differences in synaptic size which have been reported to follow this differential rearing procedure (*7*) is that the additional synapses formed on higher-order branches may be larger than those more central in the neuron.

The failure to find such clear differences in dendritic branching in the Holloway study (*8*) may be related to several factors, such as the relatively small number of neurons examined and the particular neuronal population studied ("layer II stellate" neurons). Holloway's scoring technique—simple totals of intersections of dendrites with concentric rings—may have been insensitive to selective effects on higher-order branching, and the apparent variability in staining from animal to animal may have resulted in differences in the staining of higher-order dendrites. Finally, the longer treatment period in his study has been found to produce smaller cortical weight differences (*5, 6*).

Our results are compatible with previously reported differences in cortical depth, perikaryon size, and acetylcholinesterase activity, and suggest that the larger cell bodies may be involved in the support of the more extensive dendritic trees. It is possible that the differences in branching patterns are generated entirely or in part by some indirect effect of the environments through hormonal or general metabolic intermediates. However, most of the reported gross differences (*5*) are confined to selected brain regions; this suggests selective effects of environmental stimulation. In any case, the increased branching presumably provides increased surface for synaptic contacts, and this greater potential for interneuronal interaction suggests a greater capacity for information processing, loosely defined, in the brain of the animal reared in a more stimulating environment. One can also conceive that such processes, combined with the reported alterations in the size of individual synapses (*7*), might underlie some forms of information storage in the brain.

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References and Notes

1. F. Valverde, *Exp. Brain Res., Berlin* **3**, 337 (1967); A. Globus and A. B. Scheibel, *Exp. Neurol.* **19**, 331 (1967).
2. P. D. Coleman and A. H. Riesen, *J. Anat.* **102**, 363 (1968).
3. E. Fifkova, *J. Neurobiol.* **1**, 285 (1970); *ibid.* **2**, 91 (1970).
4. S. Schapiro and K. R. Vukovich, *Science* **167**, 292 (1970).
5. M. R. Rosenzweig, E. L. Bennett, M. C. Diamond, in *Macromolecules and Behavior*, J. Gaito, Ed. (Appleton-Century-Crofts, New York, 1971); *Sci. Amer.* **226** (No. 2), 22 (1972).
6. ———, S. Wu, R. W. Slagle, E. Saffran, *Brain Res.* **14**, 427 (1969).
7. R. W. West and W. T. Greenough, *Behav. Biol.* **7**, 279 (1972); W. T. Greenough, R. W. West, T. B. Fleischmann, paper presented at 1st annual meeting, Society for Neuroscience, Washington, D.C., October 1971; K. Møllgaard, M. C. Diamond, E. L. Bennett, M. R. Rosenzweig, B. Lindner, *Int. J. Neurosci.* **2**, 113 (1971).
8. R. L. Holloway, *Brain Res.* **2**, 393 (1966).
9. Parent stock obtained from Simonsen Laboratories, Gilroy, California.
10. E. Ramon Moliner, *Stain Technol.* **32**, 105 (1957).
11. S. Polyak, *The Vertebrate Visual System* (Univ. of Chicago Press, Chicago, 1957); W. Zeman and J. R. M. Innes, *Craigie's Neuroanatomy of the Rat* (Academic Press, New York, 1963); D. A. Sholl, *The Organization of the Cerebral Cortex* (Methuen, London, 1956).
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Target-Set and Response-Set Interaction: Implications for Models of Human Information Processing

Abstract. *In binary character-classification tasks, reaction time generally has been reported to increase substantially with the number of target elements. However, when the targets formed a familiar set and subjects were not required to make explicit "no" responses, reaction time did not increase significantly as the target set increased in size from one to three.*

In the most commonly used paradigm for the study of character classification, subjects are presented with a single stimulus, such as a letter or a digit, and must indicate whether or not it matches any of the stimuli contained in a previously memorized target set. Typically, results obtained with this experimental task indicate that the time taken to determine that a stimulus is indeed a member of the target set increases linearly with the size of the target set, at a rate of about 35 msec for each additional character. This result has been taken to mean that the characters in the target set are represented individually in memory, and that these memorial representations are searched serially at about 30 characters per second to determine if a match exists (*1*).

The target sets used in character classification experiments usually vary randomly in composition from trial to trial. Even when the same set is used for a block of trials, however, there is seldom any logical connection among the characters in the set. Thus, it is possible that the conclusions drawn about the process of character classification are limited to situations in which subjects may have difficulty dealing with a set of characters that are unfamiliar as a set (*2*). The initial pur-

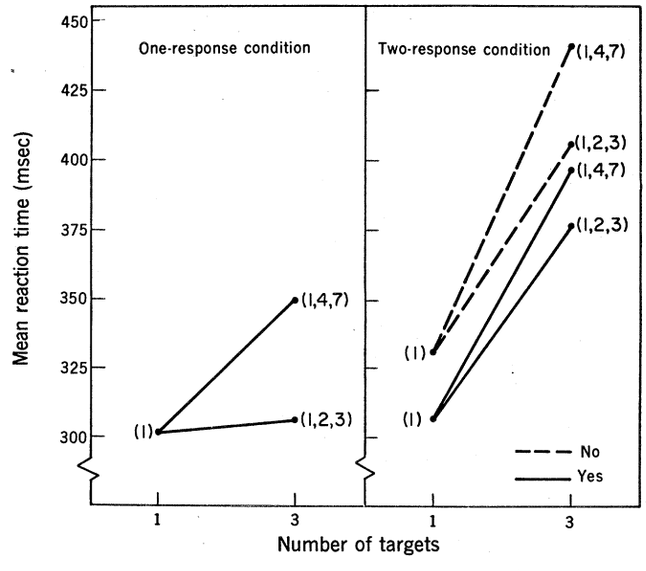

Fig. 1. Mean reaction time as a function of number of target elements for one- and two-response tasks. The numbers in parentheses represent the target set used at each point.