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A Developmental Theory of Environmental Enrichment
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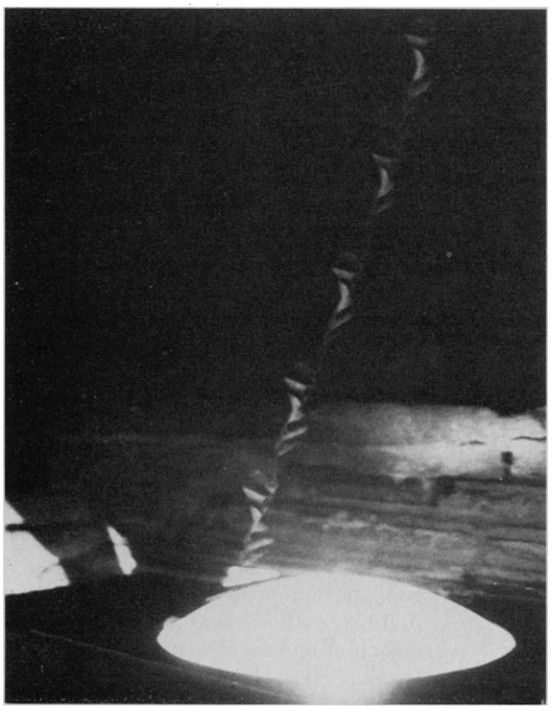

Fig. 2. A tulip key drifts in the wind as it falls toward a vertical searchlight. The camera shutter is open, the illumination steady. The key alternates between bright and dark as it shows its illuminated bottom or its shadowed top to the camera.

pare the seed-dispersing ability of the different modes of flight (as opposed to that of the actual samaras themselves, which have widely differing sizes and weights). I ballasted four wings, 12.7 by roughly 2.52 cm, cut from file cards, to about 1.2 g apiece, with the weights located so they flew like the four types of samara. The heaviest model weighed 1.36 g, the lightest 1.12 g. The widest wing was 1.036 times as wide as the narrowest. Sinking speeds, measured by ruler and stopwatch, were multiplied by

$$\left(\frac{\text{wing width}}{\text{model weight}} \times \frac{1.2}{2.52} \right)^{1/2}$$

to give the values expected for 1.2-g models with wings exactly 2.52 cm wide (Table 1).

Because the models were heavier than the samaras they flew at higher Reynolds numbers (*5*), which probably exaggerated the proportional spread in sinking speeds. Even so, except for the plate, the highest sinking speed was only 2.4 times the lowest. Sinking speed is proportional to the inverse square root of the aerodynamic forces that would be produced if each model were ballasted so all sank at the same speed. The upward force coefficient,

$$2\,(\text{weight}) \,/\, [\text{blade area} \times \text{air density} \times (\text{sinking speed})^2]$$

better measures the aerodynamic success of the design, and is proportional to the area over which a wind of varying strength and direction sows the samaras. (The length and breadth of the area are each proportional to the time the samara takes to descend, hence inversely proportional to the sinking speed.)

Lift and drag coefficients are the aerodynamic forces transverse to and parallel to the model's path, respectively, divided by half the product of air density, blade area, and the speed squared. Ailanthus has 2.62 times the lift coefficient of zanonia, at the expense of 13.3 times the drag coefficient.

Zanonia and ailanthus can add gliding distance to wind drift, but only if they fly straight. Most ailanthus seeds spiral in a helix a meter or less in diameter in one hand or the other, but some fly straighter and may serve out of proportion to their number in dispersing the species. Zanonia samaras are said to circle (*1*, p. 59), but again, a minority that flew straight could be biologically essential.

Since zanonia sinks slowest and glides farthest, why are more samaras built on the other plans? Perhaps because the others are more stable in turbulent air (the ash-tulip system being the stablest) and give performance that is less degraded by variations in shape. Ash and tulip fly in windy temperate woodlands; zanonia glides in the sheltered interior of tropical rain forests.

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5. The Reynolds number for any set of objects of geometrically similar shape supported by fluid dynamic lift is proportional to [weight/(lift coefficient)]$^{1/2}$ and independent of the area of the lifting surface. Increasing the area reduces the airspeed in the same proportion, leaving the Reynolds number unchanged.
6. I thank A. Terry for help with the experiments.

11 January 1977; revised 4 March 1977

A Developmental Theory of Environmental Enrichment

Abstract. *The differential brain development induced by sensory enrichment or deprivation is most apparent in rats with low brain weights. These differences are hypothesized to represent the retarded development of environment-dependent neurons in the isolated animals.*

If animals are separated at weaning into enriched and deprived sensory environments, the enriched animals acquire larger and more complex cortices than their isolated counterparts. This enhanced cortical development includes increased cortex depth (*1*), dendritic branching (*2*), and number of glial cells (*3*).

We have recently proposed (*4*) that the mechanism responsible for this enhanced development is experience of the arousal response; such arousal is caused by both social interactions and object exploration, which provide nonspecific stimulation of cortical elements, which is, in turn, transduced into biosynthetic activity. In the following studies, we extend this concept by hypothesizing that during ontogeny, the development of some neurons can be described as environment-dependent; that is, these neurons will fully develop only in the presence of adequate amounts of sensory stimulation. The consequence is that the enrichment-isolation differences represent the extent to which normal neural development has been retarded by sensory deprivation.

Of the following nine separate studies, the first eight (groups 18, 30a, 30b, 40, 60, 80, 90, and 120) were conducted between 1968 and 1974 at the University of Queensland. The subjects were male,

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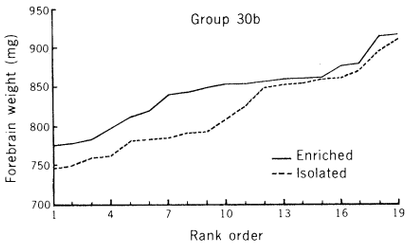

Fig. 1. Forebrain weights for enriched and isolated animals of group 30b. Weights from each environmental treatment are rank-ordered from lowest to highest.

random-bred Wistar rats. The final study (group 30c), designed as a replication, was conducted in 1976 at the University of Western Australia with random-bred albino rats. All nine studies will be reported together.

For each study, male rats were separated at weaning into one of two groups. In the enriched condition, the rats lived in social groups of between 6 and 12 animals in large open-mesh cages supplied daily with a variety of "toys." In the isolated condition, the rats were confined to small, individual, solid-walled cages with mesh floors and ceilings. The duration of exposure to these differential rearing conditions is given by the group number, from which it can be seen that the range was from 18 to 120 days.

At the end of this rearing period the animals were killed and weighed, and their brains were removed. After fixation in formol saline, the olfactory bulbs were removed and the brain was sectioned coronally immediately behind the posterior pole of the cerebrum. The resulting anterior brain component, which included all of the forebrain and most of the midbrain (forebrain sample) was subsequently weighed.

The distribution of brain weights within each study was examined by rank-ordering the animals, in terms of forebrain weight, for each environmental treatment (for example, Fig. 1). The enrichment-isolation difference is apparent only between the animals ranked low in brain weight. This relationship was found in seven of the nine studies, but in groups 30a and 30c the effect was not present.

Included in our investigation of the determinants of intragroup variance was an examination of the correlation between forebrain weight and body weight. In groups 30a and 30c, there was a significant correlation ($r = .54$, $P < .001$; $r = .37$, $P < .05$, respectively), whereas in the other seven groups, the correlation was not significant ($r = .22$ to $r = .02$). Having thus identified a significant confounding variable for forebrain weight in groups 30a and 30c, its influence was removed by forming a ratio of forebrain weight to body weight. When this ratio was used in the ranking procedure, groups 30a and 30c now showed the largest enrichment-isolation effect between the animals ranked low in brain weight (Table 1).

Two observations can be made on the data from Table 1. (i) The greatest high-ranks versus low-ranks differences tended to occur between 30 and 60 days of differential rearing. This duration has been reported to be the most effective in eliciting the enrichment-isolation effect for some cortical weight changes (*5*, *6*). (ii) Most important for our purpose, in all nine experiments, the low ranks showed a larger enrichment-isolation effect than the high ranks.

We propose a developmental model to explain this significant interaction between brain size and the magnitude of the enrichment-isolation difference (Fig. 2). The essential feature of this model is that there exists an element of neural development associated with cells that fully mature only in response to sensory stimulation. The extent of this development is represented by a percentage scale, 100 percent representing a genetically determined ceiling beyond which the development cannot proceed.

The optimal amount of sensory stimulation is not known. However, it is probably comparable to that experienced by the feral rat, since it is to suit this environment that the rat brain evolved to its present form. Thus, the enriched environment, while no doubt deprived by feral standards, must represent a closer approximation to optimal sensory conditions than isolation does. As such, the

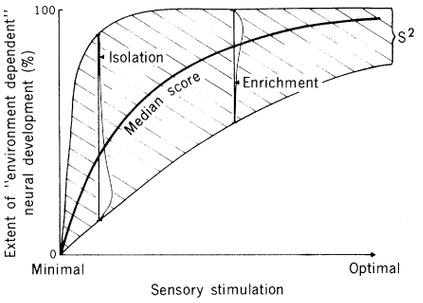

Fig. 2. Developmental model for environmental enrichment. The asymptotic curve represents the median value for environmentally dependent development at any level of sensory stimulation, and the shaded region depicts the variance distribution around this curve. Hypothetical frequency distributions are shown for the two environmental groups, isolated and enriched.

enriched animals will achieve a higher level of environment-dependent neural development than their isolated counterparts.

From this model, our finding of a greater enrichment-isolation effect in animals of low brain weight can be explained. Within each group (the enriched and the isolated), there will be marked individual differences in the extent to which any given amount of stimulation will induce development. Thus, for some of the isolates, the relatively low level of stimulation may be adequate to produce development comparable to that achieved by others in the enriched environment; these isolates could thus approach the developmental ceiling. However, although all animals in the enriched group would be expected to show some upward shift and most would show a relatively substantial increase in brain weight as a result of the exposure, many

Table 1. The rank-order effect for forebrain weight (FB) between enriched (EC) and isolated (IC) animals for the nine experimental studies. In groups 30a and 30c, FB was divided by body weight (B) as described in the text. Forebrain weights were separated into high or low ranks with respect to the group median. "High-ranks %" means the difference between enriched and isolated animals in the high-ranking half of the sample expressed as a percentage. Each difference probability value was calculated with a one-tailed *t*-test. The proportion of the overall difference contributed by the low ranks was calculated from the percentage differences between the enriched and isolated animals by dividing the low-ranks percent by the sum of the low- and high-ranks percentage. Abbreviation: N.S., not significant.

Group	Parameter	Animals (No.)	Forebrain weights				Low-ranks contribution (proportion)
			High ranks		Low ranks		
			%	EC > IC ($P<$)	%	EC > IC ($P<$)	
18	FB	32	4.8	.01	7.7	.01	.62
30a	FB/B	36	12.2	.05	26.8	.001	.69
30b	FB	40	1.1	N.S.	4.8	.01	.82
30c	FB/B	38	0.0	N.S.	6.7	.05	1.00
40	FB	30	0.6	N.S.	2.5	N.S.	.81
60	FB	32	0.0	N.S.	2.7	.05	1.00
80	FB	26	1.7	N.S.	2.5	.05	.60
90	FB	30	3.7	.05	4.9	.01	.57
120	FB	34	6.5	.01	7.2	.001	.53

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of those in the isolated group would show comparatively little added development.

If the median of the groups is used as the dividing line for low- and high-ranking brain weights, the isolation-enrichment differences would be most apparent between the low-ranking brain weights from each group. This is so because although all animals in the enriched group, both low-ranking and high-ranking in terms of the genetic brain weight component, would show an upward shift as a result of their experience, the low-ranking animals in the isolated group would be more likely to be those which had received little or no benefit from the limited stimulation they had received. Those isolated animals that would have ranked low on the basis of the genetic component alone but had shown some additional environment-dependent development would be likely to move above the median displacing somewhat higher-ranking animals that had exhibited little response to the limited stimulation.

Two predictions can be made on the basis of this model. (i) The amount of intragroup variance among the isolated animals will exceed that among the enriched. Such a prediction results from the presence of a genetically determined developmental ceiling against which the enriched animals will be pushed, combined with the increased probability that enrichment will lift all animals from the base line. This comparison was performed by computing the coefficient of variation for each of the enriched and isolated groups. In eight of the nine studies the variance of each isolated group exceeded that of its enriched counterpart, and in the remaining study (group 80) they were equal.

The second prediction is based on the assumption that the two groups fall on opposite sides of the midpoint of the asymptotic curve. (ii) Since there exists both an effective ceiling to development and a base line from which such development commences, the variance distribution on either side of the median should be opposite for the two environmental groups. Within the enriched groups, the variance between the brain weights lying below the group median should exceed the variance of those above; the opposite should be the case for the isolated groups. This prediction was tested by using a Fisher exact probability test ($P < .05$).

We conclude that the data support the hypothesis that sensory stimuli act by inducing environment-dependent neural development in accordance with the model (Fig. 2). The nature of this stimulation has been the subject of a previous paper (*4*) wherein we argued that the basic mechanism is that of nonspecific activation of the cortex during arousal. In this regard, the rank-ordering effect decreased after 60 days of differential rearing. This may be explained if progressive habituation of the sensitization derived from arousal-inducing aspects of the environment occurs in the enriched animals, while spontaneous recovery of habituated sensitization occurs in the isolates as a result of the absence of such arousal-inducing (sensitizing) stimuli (*7*). The net effect of these alterations in the arousal threshold would be that the arousal potential of both types of living environment would become more similar to their respective inhabitants with increasing duration of exposure.

There remains, however, an additional consideration. While, in accordance with our prediction of sensitization during isolation, there was an inverse relationship between the magnitude of the rank-ordering effect and the duration of isolation, an overall enrichment-isolation difference was present at both 90 and 120 days (4.5 percent, $P < .01$, and 6.8 percent, $P < .001$, respectively). In groups 90 and 120, the forebrains of the enriched animals were consistently heavier than those of the isolates for all brain-weight ranks. Other reports have also indicated that, under some conditions, enrichment-isolation differences in cortex weight have been observed beyond 80 days of differential rearing (*6*, *8*). Thus, it appears likely that sensitization of the isolated animals does not fully compensate for the reduced stimulus levels, and that development stabilizes at a suboptimal level.

Finally, we suggest that environmental enrichment has been greatly overemphasized as the causative agent for enrichment-isolation brain changes. The degree of sensory deprivation suffered by the isolated animals is likely to be the critical factor, since the stringency of this condition determines the proportion of subjects retarded in their environment-dependent neural development.

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Disruption of Sex Pheromone Communication in a Nematode

Abstract. *Males of* Nippostrongylus brasiliensis, *an intestinal parasite of rodents, were maintained in an environment permeated with pheromone produced by females of the species. After the males were removed from that environment, their subsequent ability to orient to a gradient of the pheromone emanating from living females was greatly reduced for periods up to 2 hours. This phenomenon might serve as the basis for a new, selective antihelminthic technique in which the premating communication between males and females is disrupted.*

The first report concerning the use of chemical signals in premating communication between the sexes of a nematode was published in 1964 (*1*). Since that time, it has rapidly become apparent that sex pheromones are the primary communicative signals that bring together the sexes of many plant-parasitic, free-living, and animal-parasitic nematode species. We propose that a necessity for distance communication by pheromones prior to mating may constitute a "weak link" in the life cycle of certain pestiferous species, wherein man might manipulate the chemical signals to his advantage and to the disadvantage of the nematodes.

Entomologists have recognized for some time that pheromone communication is an essential component of the premating behavior of a number of pest insect species and are now advancing rapidly toward environmentally safe insect-control strategies based on manipulation

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