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Abstract

To test the relative effectiveness of direct versus indirect interaction with an enriched environment, some rats were housed in groups of 12 in large enriched condition (EC) cages while littermate "observer" (OC) rats were placed singly in small wire-mesh cages within EC. A third group was housed singly in an impoverished condition (IC) where stimulation was minimal. After 30 days, the animals were killed and the brains dissected. In both experiments the usual pattern of EC-IC differences in brain weights appeared, whereas OC showed no significant differences from IC. On measures of exploratory behavior taken during the last 2 days of the second experiment, IC fell significantly below EC, and OC was somewhat below IC. Active contact with an enriched environment appears necessary to development of EC effects.

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This study was designed to test whether brain changes can be induced in rats by allowing them to see, hear and smell other rats in a complex environment or whether direct contact with the enriched conditions (EC) is required. It has already been demonstrated by many investigators that direct experience in EC alters a number of brain measures in rats and other rodents (e.g., Bennett, Diamond, Krech & Rosenzweig, 1964; Ferchmin, Eterović & Caputto, 1970; Geller, Yuwiler & Zolman, 1965; Globus, Rosenzweig, Bennett & Diamond, 1973; Henderson, 1970; La Torre, 1968; Levitan, Mushynski & Ramirez, 1971; Rosenzweig & Bennett, 1969; Rosenzweig, Bennett & Diamond, 1972; Volkmar & Greenough, 1972; Walsh, Budtz-Olsen, Penny & Cummins, 1969; West & Greenough, 1972). Although exposure to the enriched environment in groups produces substantial cerebral effects, exposure of rats individually to EC has only slight effects, unless interaction of the animal with the stimulus objects is facilitated by placing the animal in the environment in the dark under influence of an excitant drug (Rosenzweig & Bennett, 1972). Does the presence of other active rats nearby have a similar "priming" effect on individually caged rats that can observe the complex environment?

Methods

Differential Environments

Three environmental conditions were employed-- (a) Impoverished Condition (IC), (b) Enriched Condition (EC), and (c) Observer Condition (OC). (a) IC in this study conformed to our usual impoverished condition; each animal was assigned to an individual cage, 32 x 20 x 20 cm. Three sides of the cage were solid. The IC cages were placed in a separate quiet room along with IC cages of other experiments. (b) The standard EC cage is 70 x 70 x 46 cm, and about 6 stimulus objects from a large pool of objects are placed in a cage each day. For pictures of the EC and IC situations, see Rosenzweig, Bennett & Diamond (1972). In this experiment, a battery of 4 EC cages was used. Twelve rats were placed in each EC cage, following our usual practice. (c) Each Observer rat was housed individually in a cage 21 x 18 x 16 cm, three OC cages being placed in each of the four EC cages (see Fig. 1). The OC cages

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Insert Fig. 1 about here

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were constructed of hardware cloth with 12 mm spacing so that the rats could readily observe the animals and objects within the EC cage. Four times a day (about 8 a.m., 11 a.m., 2 p.m. and 5 p.m.) the OC cages were removed from the EC cages, placed on the floor briefly, and then moved to the next EC cage. A regular pattern of rotation was followed, so that each OC cage each day was placed in each of the four EC cages and occupied each of four possible positions--suspended from the ceiling, hooked to the right or left wall, placed on the floor.

Assignment of Subjects to Conditions

All subjects were male rats of the Berkeley S_1 line. They came from litters with at least three males, the range of body weights within a litter being restricted to 15%. The rats from each litter were assigned semi-randomly to three groups, the only restriction being that all groups be closely similar in distribution of body weights; the groups were then assigned at random to the experimental conditions.

Rats in all conditions had food and water *ad libitum*. The IC and OC rats were handled only once a week, for weighing.

For the first experiment the rats were assigned to conditions at about 25 days of age and were sacrificed 31 days later. Meanwhile the rats of the second experiment lived in standard colony cages; they were assigned to the experimental conditions at about 65 days of age and were sacrificed 31 days later.

Since there were 4 EC cages and only one EC group, the other 3 cages were each occupied by 12 males of the same age and strain. The same "extra" rats were used in both experiments.

Behavioral Observations

During the second half of the second experiment, observations were made of the OC rats shortly before, during and shortly after the last daily cage change. The behavioral condition of each rat was noted as soon as the experimenter entered the room. The following categories were employed: sleeping, inactive, functional activities (grooming, eating and drinking), sniffing, exploring, rearing, interacting with another rat. After the initial ratings, a second set of ratings was made 2 or 3 min later. Then the OC cages were placed on the floor, and

behavior was again recorded twice. When the OC cages were replaced in the EC cages, three further sets of ratings were made--immediately, 4 or 5 min later, and about 15 min later.

The rats of the second experiment were also tested for exploratory behavior on the day before sacrifice and on the day of sacrifice. This was done in a Greek Cross apparatus (De Nelsky & Denenberg, 1967). This apparatus is constructed of 1/4" masonite and consists of 5 equal compartments arranged in the shape of a cross. The center compartment measures 23 x 23 cm, and each of its walls has an opening, 5 x 5 cm, that connects with a side compartment. The walls of the apparatus are 38 cm high, and the top is open for observation. The floor and walls of the center compartment are painted light gray, 2 opposite side compartments are white, and the other 2 side compartments are black. For a trial, a rat was placed in the center compartment and observed for 5 min. An entry was scored whenever a rat placed at least its head and two front feet through a doorway, and each entry was timed to the nearest hundreth of a minute.

Removal and Weighing of Brain Tissue

At the end of the experiment, the animals were put in a multiple-unit cart bearing code numbers that did not reveal the experimental condition of any rat. The animal was decapitated, and the brain was dissected following our standard procedures (Rosenzweig et al., 1962). We removed standard samples of occipital and somesthetic cortex; remaining dorsal cortex; ventral cortex, including the hippocampus and corpus callosum; cerebellum and medulla; and remaining subcortical brain, including the olfactory bulbs. As soon as each sample was removed it was weighed to the nearest tenth of a milligram on an automatic balance. Measures from all

of the cortical sections could be combined to give total cortex; measures from the two remaining sections could be combined to give rest of brain (or subcortex).

Statistical Tests

Results were evaluated by two-way analyses of variance (litters vs. treatments). Comparisons between different experimental conditions were done by Duncan's multiple-range test.

Results

Effects on Brain Weights

The differences between EC and IC littermates in brain weights corresponded to our usual findings, but the Observer values did not differ significantly from IC values on any of the measures. Table 1 presents some of the main brain weight values separately for experiments 1 and 2, and it gives a fuller set of values based on the two experiments combined. Absolute weights are given for the IC group in each case. As well as brain weights, terminal body weights are also shown. Although 12 litters were run in each experiment, values for experiment 1 are based on 10 litters because 2 rats showed unusually low terminal body weights.

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Insert Table 1 about here

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In comparison with the younger rats in the first experiment, the older rats in the second experiment showed larger values for both brain weights and body weights, and also lower cortical/subcortical weight ratios, in conformity with previous findings (Riege, 1971). In spite

of these differences in absolute weights, the percentage differences between EC and the other groups are closely similar in the two experiments for the brain weight measures. The body weight differences appear to vary somewhat between the experiments, but it should be noted that only one of the body weight differences reached the .05 level of significance, and we have repeatedly observed that body weight is a relatively minor determinant of brain weight. Although the OC rats shared the sights, sounds and smells of their EC littermates and had some contact with them through their wire mesh cage walls, the OC brain weight measures differed significantly from EC but not from those of the IC rats in the separate isolation room. Table 1 shows EC to differ from OC almost as much as from IC. Both experiments thus testify, on the one hand to the effectiveness of direct experience in the enriched condition in altering cerebral weights, and on the other hand to the ineffectiveness of the opportunity to observe the enriched condition.

Behavioral Measures

Measures of activity

Observations made just before the last daily cage change of the OC rats (between 5 and 6 p.m.) showed both them and the EC rats to be quiescent in most cases. Twenty-seven percent of the OC rats were either asleep or inactive (Table 2, based on 16 days of observations). When the OC cages were removed from EC and set next to each other on the floor,

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Insert Table 2 about here

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this aroused the OC rats. Two percent were now sleeping or inactive;

exploring and rearing were the main categories of activity (column 3 of Table 2). In some cases they directed their activity toward OC rats in adjoining cages. Then when the OC cages were placed in EC cages, the EC rats often swarmed over the OC cages. Animals often nosed each other through the wire mesh. The table shows 48 percent interaction immediately after the OC cages were replaced in EC. This kind of interaction was usually short-lived, however, being greatly reduced by the last observation (column 7) 15 min after the OC cages had been repositioned. The percentage of rearing in column 5 is depressed because much interaction took place with OC rats directing themselves toward EC rats on top of OC cages, so most rearing at this time was classed as social interaction. Informal observations indicated that OC rats sustained their interest in EC rats longer than EC did in OC. Nose-to-nose contact between EC and OC was usually brief, with the OC rat continuing to sniff and orient in the direction of the EC rat after the latter stopped reciprocating. OC rats certainly did have more social interaction than IC rats, but, as will be discussed later, previous experiments had already suggested that social interactions contribute little if anything to production of EC-IC brain effects.

Responses in Greek Cross apparatus

In their first session in the Greek Cross apparatus, the EC rats made significantly more entries into the side compartments than did the IC rats ($p < .001$) or the OC rats ($p < .001$). During the second and last session, the performance of the EC rats was similar to that of the previous day, but the IC and OC rats increased their entries (p values of these increases were both significant at beyond the .01 level). On the

second test, EC no longer exceeded IC significantly in entries, but the EC vs. OC difference was still significant ($p < .01$).

Separate tabulations of means entries per animal into the black and white compartments are shown in Figure 2. Overall, 79 percent of all entries were to black. On day 1, only EC made a significant number of

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Insert Figure 2 about here

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white entries. EC habituated somewhat on black entries from day 1 to day 2 but increased their white entries. Both IC and OC increased both black and white entries from day 1 to day 2. It is clear that on this test the behavior of OC rats resembled that of IC more than that of EC rats; in fact, OC seemed to show an exaggeration of IC behavior. That is, the OC rats, although living within the EC cages, showed less behavioral effect of environmental enrichment than did the IC rats living in the separate isolation room.

Discussion

What Aspects of Environment Affect Brain Measures?

This study has yielded further evidence about experiential conditions that can or cannot produce cerebral behavioral EC effects, a subject that we have been investigating for some time. The Observer Condition, although it was not designed to do so, turns out to provide excellent controls for a number of factors that have been supposed at one time or another to be responsible for EC-IC brain differences, and it helps to define and delimit the essential factors required to differentiate EC

from IC. Thus, we originally supposed that at least part of the effects might be due to placing the EC cages in a busy, active laboratory room and the IC cages in a quiet, dimly lighted isolation room. We since found that we could obtain the usual results if IC rats were housed in ordinary colony cages in the same room as the EC rats (Rosenzweig & Bennett, 1972; Bennett, Rosenzweig & Wu, in press). The present experiment demonstrates even more forcefully that the ambient environment has little or no effect, at least on the measures we have employed. A friendly critic suggested, after our initial demonstration of cerebral changes induced by differential experience, that such effects were probably due to the monotony of the IC environment and that isolated rats could probably be given EC brain values just by placing the IC rats once a day in a simple box (Sperry, 1968). We had already tried goal boxes and pretraining alleys as controls for formal maze training--without obtaining cerebral effects. Daily handling and a daily period of stressful experience in another apparatus also failed to produce significant effects on weights, acetylcholinesterase or cholinesterase of brains of IC rats (Riege & Morimoto, 1970). Now rats have been aroused 4 times a day and exposed to 4 cages positions in 4 different EC cages per day--again without effect on brain weights. Results with the OC condition demonstrate conclusively that not any kind of stimulation or arousal or variety suffices to produce the cerebral changes that are characteristic of our experiments.

The failure of the OC condition to produce brain weight effects might be attributed to lack of social stimulation, but the following three reasons lead us to believe that social stimulation is not particularly

important in producing EC effects: (a) Rats placed individually in EC develop typical brain effects if their interaction with the stimulus objects is primed by darkness or excitant drugs (Rosenzweig & Bennett, 1972), so social stimulation is not required. (b) Methamphetamine, which increases the magnitude of EC cerebral effects in rats placed in a group in EC, decreases social contacts among these rats (Bennett, Rosenzweig & Wu, in press). (c) Putting rats by groups of 3 or 12 in an otherwise empty cage produces only minor brain weight differences from values of animals caged alone (Rosenzweig, 1971). We are not denying that rats are sociable; they tend to approach other rats more than inanimate objects. This is particularly true if the introduced stimulus rats can respond to the experimental rats and are not anesthetized or caged (Latane, Joy, Meltzer, Lubell & Cappell, 1972). We conclude only that such social stimulation is not effective in altering cerebral measures in the way that direct experience with varied inanimate objects is effective.

The fact that direct contact with the enriched environment appears to be necessary to produce cerebral and behavioral effects may be related to the distinction between active and passive experience that Held has stressed (Held, 1965; Held & Hein, 1963; Hein, Held & Gower, 1970). Both for original acquisition of sensory-motor coordination in animals and for adaptation to altered sensory input in human beings, sensory feedback from muscular movement was demonstrated by Held to be necessary. The varied inanimate stimuli in the EC cages, which seem to be necessary for development of cerebral differences, were not distant from the OC cages. Nevertheless it is clear that the small extent of locomotion within an OC cage did not permit an OC animal to alter greatly stimulation

from the stimuli within the EC cage--certainly the OC rats had much less movement-produced variation in such stimulation than did the EC rats.

It appears that the necessary and sufficient condition for the production of EC effects is active interaction with varied inanimate stimulus objects. Furthermore, it is likely that no one stimulus modality is essential; typical EC-IC brain differences develop in blind rats (Rosenzweig, Bennett, Diamond, Wu, Slagle & Saffran, 1969) and in anosmic rats (Rosenzweig, Bennett & Wallen, in preparation).

Observation Learning

If the OC rats had the opportunity to engage in learning by observation, does the lack of cerebral differences between OC and IC mean that EC-IC differences cannot be attributed to learning in EC? We believe that lack of OC-IC cerebral effects may simply reflect the fact that little learning occurs in OC, since the literature on observation learning remains rather confused and ambiguous. Whether rats learn by observation without specific rewards being offered has been studied with a variety of experimental designs, including situations in which inanimate stimuli could be observed and situations in which other rats could be observed. Conditions that yield evidence of observation learning and conditions that produce cerebral changes will be described and compared.

Gibson & Walk (1956) reported that when rats had a cutout metal circle and a triangle placed for several weeks on the walls of their cages, they subsequently learned to use these forms as discriminative cues more readily than animals without the prior experience. In a later study, a comparison was made between the use of flat painted forms and cutout forms; the flat painted forms were found to be ineffective (Gibson,

Walk & Tighe, 1959). Meier & McGee (1959) found that later discrimination learning was facilitated by experience with solid objects in the cage, but a group that had visual experience only and no contact with the objects did not differ in performance from a group raised under normal colony conditions.

Observing inanimate visual displays had already been shown not to alter brain weights or brain chemistry in two previous types of experiments in our laboratories. In one set of experiments, conducted by Gilbert Ricard, some rats were given 2-hr slide shows twice a day for 30 days, following the technique of LaVallee (1970). Animals that could watch the slides were found not to differ from controls in brain weights or in activities of brain acetylcholinesterase (AChE) or cholinesterase (ChE). Then Singh, Johnson & Klosterman (1967, 1970) reported that rats whose cages faced a striped wall developed significant differences in AChE activity of the occipital cortex when compared with rats whose cages faced a blank wall. Attempts to replicate this report in our laboratory yielded not even a suggestion of differences between the experimental and control groups (Maki, 1971). In this connection it should be recalled that rats placed individually in EC produced only very small cerebral effects, unless they were primed to interact with the varied stimulus objects; here again, mere visual exposure was not enough to induce brain changes.

Two experiments with stimulus conditions similar to ours were conducted by Hymovitch (1952) and Forgays & Forgays (1952); maze tests after differential experience yielded rather discrepant results. In each

case, some rats were in a "free environment" (a large cage similar to our EC situation), others were confined in small mesh cages placed within the large cage (like our OC rats), and rats of a third group were kept in small cages with solid side walls (like our ICs). In Hymovitch's experiment, rats were placed individually in the mesh cages, and these cages were moved once a day among 8 locations, 6 in the large case and 2 elsewhere in the laboratory. Differential experience was started at 27 days of age and continued until 79 days of age, when preliminary training began. In Forgays and Forgays' study, rats were put in the mesh cages in groups of 3 and the cages were moved only once a week; various mesh-cage groups had different combinations of free-environment (FE) rats and/or objects in the large cages around them. Experience was given from 26 to 90 days of age, when pretraining began. The FE rats were superior in maze scores to the restricted rats in both experiments. Hymovitch found the mesh-cage rats to make almost as few errors as the FE rats and significantly less than the restricted rats. On the contrary, Forgays and Forgays' mesh-cage rats were clearly inferior to the FE rats; three of the specific mesh-cage groups were superior to the restricted group but one was not. Considering the divergent results of mesh-cage groups in the two experiments, Forgays and Forgays conclude, "It would appear that, depending on the [specific] environmental conditions during their rearing, mesh-caged rats may be as superior in their problem-solving ability as free-environmental animals or as inferior as restricted animals" (p. 327). The sources of these discrepancies have not been determined in the ensuing 20 years.

Since some mesh-cage rats did not differ from restricted rats, it is not necessary to conclude that an opportunity for observational learning produces behavioral effects but not cerebral effects. Our experiment is the only one in which both sorts of effects were measured, and the "observers" differed significantly from the EC rats in both brain and behavior.

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Table 1

Comparisons of Brain Weights and Body Weights among Rats in Three Environmental Conditions

		Percentage Differences		
	IC	OC vs.	EC vs.	EC vs.
Experiment 1	Means[a]	IC	IC	OC
N = 12 per group				
Cortex				
Occipital	66.8	3.3	7.0*	3.6
Total	666.6	1.3	5.2***	3.9**
Rest of Brain	885.2	0.2	1.2	1.0
Cortex/Rest	0.750	1.1	4.0**	2.9*
Body Weight	214.2	-1.4	-7.1	-5.7
Experiment 2				
N = 10 per group				
Cortex				
Occipital	71.4	0.2	4.7*	4.5*
Total	689.4	-0.1	3.4**	3.5**
Rest of Brain	962.0	-0.3	0.3	0.6
Cortex/Rest	0.717	0.2	3.1**	2.9**
Body Weight	318.0	-5.2	-1.7	3.7

(Continued)

Table 1 (Cont.)

Experiments 1 and 2				
N = 22 per group				
Cortex				
Occipital	69.3	1.5	5.7**	4.1*
Somesthetic	57.3	-2.6	2.4	5.2**
Rem. dorsal	298.3	0.0	5.3***	5.3***
Ventral	254.0	1.5	2.9	1.4
Total	679.0	0.5	4.2***	3.7***
Rest of Brain	927.1	-0.1	0.7	0.8
Total Brain	1606.1	0.2	2.2**	2.0**
Cortex/Rest	0.733	0.6	3.5***	2.9***
Body Weight	270.8	-3.9	-3.7	0.2

[a] Units are mg for brain weights and gm for body weights.

* $p < .05$, ** $p < .01$, *** $p < .001$.

Table 2

Percentages of Observer Rats Engaging in Various Behaviors

	Before Cage Change		Cages on Floor		Cages repositioned in EC		
Observation period:[a]	1	2	3	4	5	6	7
Behavior							
Sleeping	8	12	0	0	0	0	1
Inactive	19	11	0	2	0	0	5
Functional (mainly grooming)	**26**[b]	**43**	9	**24**	11	**56**	**52**
Sniffing	**29**	**16**	8	6	0	7	12
Exploring	4	5	**44**	**31**	**34**	14	15
Rearing	9	8	**39**	**37**	7	9	5
Interacting	5	5	--	--	**48**	14	10

[a] The timing of the seven observations was described above under Methods, Behavioral Observations.

[b] Bold face [underlined] figures indicate the principal forms of activity in each period.

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Figure Caption

Figure 1. Three small Observer Condition (OC) cages inside a large Enriched Condition (EC) cage.

Figure 2. Comparisons of entries by animals maintained in EC, IC and OC (Observer Condition) for 30 days into the black and white compartments of the Greek Cross apparatus.

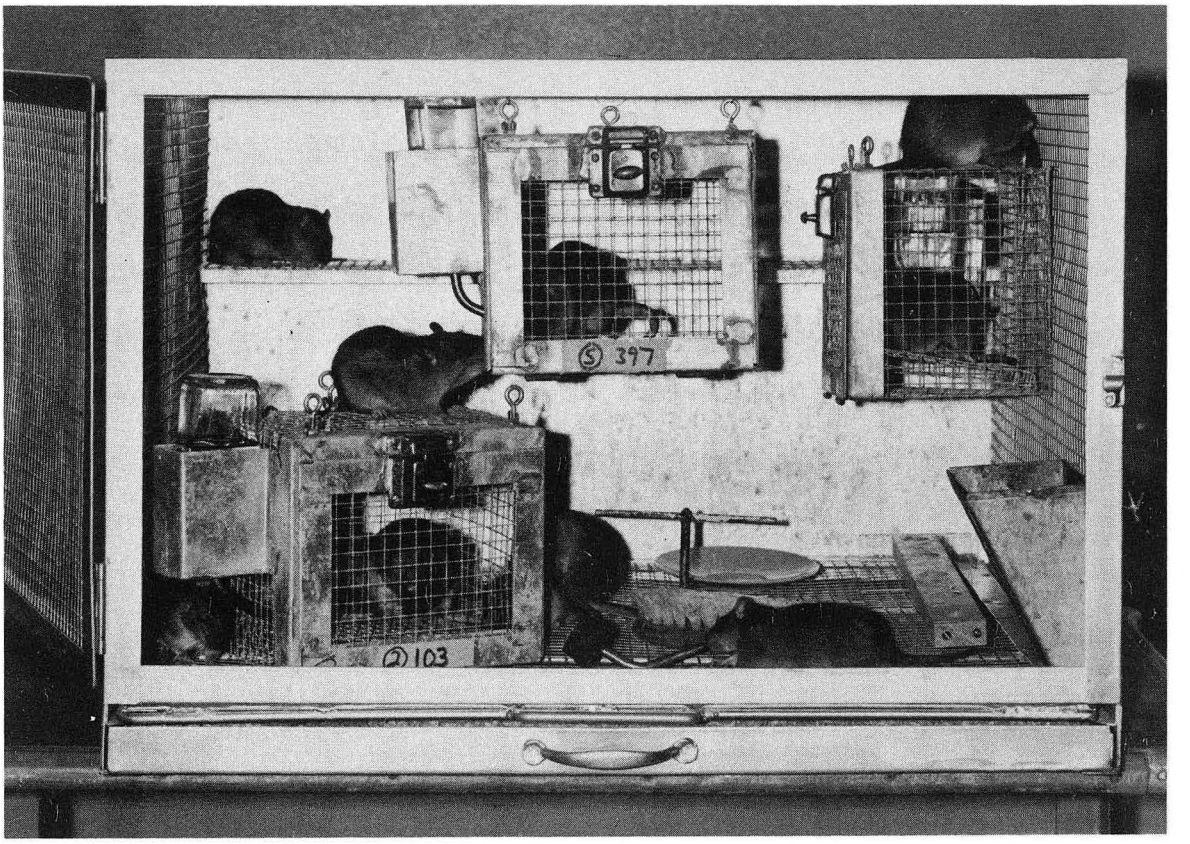

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Fig. 1.

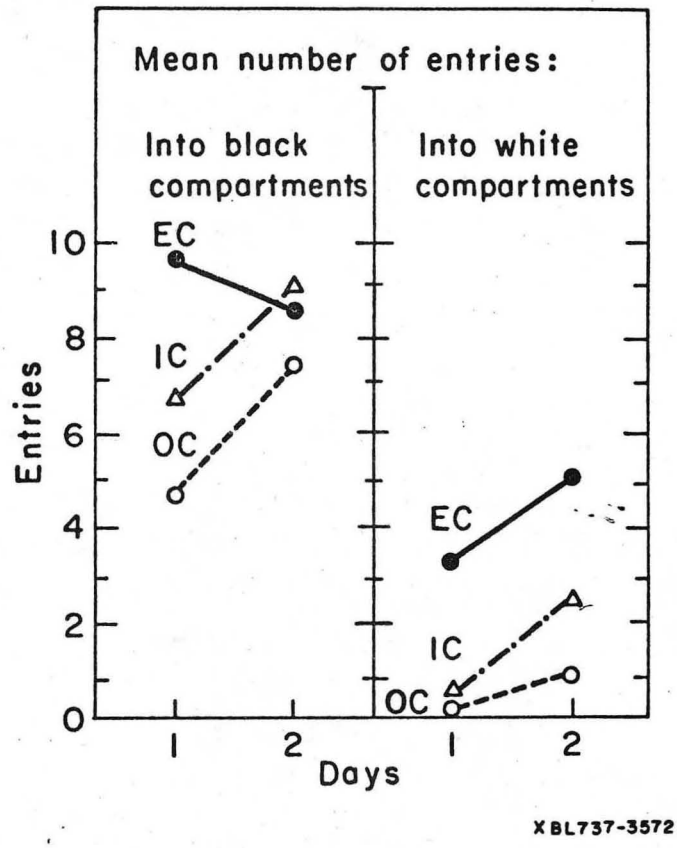
Mean number of entries:
Into black compartments
Into white compartments
EC
IC
OC
EC
IC
OC
Entries
0
2
4
6
8
10
1
2
1
2
Days
XBL737-3572

Fig. 2.

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