The use of intramaze stimuli in the attenuation of the problem-solving deficit of septal animals

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An attempt was made to ameliorate the deficit in performance shown by septal rats on the Maier three-table task by using either a distinctive visual stimulus insert as a discriminative cue to the route to the daily locus of the food table (Experiment 1) or distinctive visual inserts merely to mark the spatial location of each table and the runway leading to that table from the choice point (Experiment 2). When a single stimulus insert consistently identified the food table and the runway to it, regardless of its location in the room, then septals did not differ from shams, and both septals and shams performed better than comparable animals not given the exploratory experience. When the stimulus inserts merely identified the spatial location of each table and its corresponding runway, then septals still were impaired relative to normals. More importantly, the fact that normals could perform successfully in Experiment 2 only when they had received a prior exploratory experience indicated that highlighting the spatial location of each table and its runway with a distinctive intramaze stimulus marker does not alter the qualitative character of the three-table task as one requiring spatial integration.

A number of neurobehavioral studies (Ellen & Weston, 1983; Herrmann, Black, Anchel, & Ellen, 1978; Herrmann, Black, Doherty, & Ellen, 1980; Rabe & Haddad, 1969; Stahl & Ellen, 1973, 1979) have shown that damage to the septal-hippocampal complex and its interconnections produces profound and long-lasting deficits in performance on the Maier three-table task (Maier, 1932). It will be recalled that on this task animals are required to integrate information concerning the spatial relations existing among the three tables with information concerning the daily locus of food. Each day, the start and food tables are changed so that the animals never learn a particular route to the food or a particular location of the food.

Despite the marked successes that have been achieved with operant tasks in the attenuation of septal-lesion-induced deficits by means of an external cue that indicates when to respond (Braggio & Ellen, 1976; Ellen & Butter, 1969; Kelsey & Grossman, 1971), a comparable improvement in performance has not been achieved when an external cue is used to signal the locus of the food table in the three-table task. Herrmann et al. (1980) have shown that when a cue light was placed on the feeding table during both the feeding experience and the test trial, septal animals were still unable to return directly to the food table on the test trial.

It should be noted that, in the three-table task, the use of the cue light to signal the baited table is

not comparable to that of the operant task. In the operant chamber, the cue light is proximal both to the animal and to the locus of the response. Additionally, in the operant task, the cue light is not continuously present. It signals availability of reinforcement by coming on or off at a particular location or at a particular time. This type of signaling has the potential to be of greater salience and of greater attention value to the animal than a continuously present light located at some distance from the animal or the locus of choice. Specifically, even though the continuously present cue light in the Herrmann et al. (1980) study illuminated the area surrounding the food table, it was still at a considerable distance from the animal when the animal was either at the exit point of the start table or at the intersection of the runways. It would thus appear that, with an elevated-maze type of task, such as the three-table task, septal animals do not react to distal, continuously present stimuli as cues for adaptive behavior.

In contrast to the elevated-maze situation, there is evidence that septal rats do respond to proximal stimuli in an enclosed maze. Ellen and Bate (1970) showed that when septal rats were run on a solid black Dashiell maze, they tended to prefer routes to the goal that followed the outer walls of the maze rather than the inner, zigzag routes. However, when the peripheral routes were painted white and the inner routes black, then both septal and normal animals preferred the inner zigzag routes. This finding suggests that septal rats do indeed respond to external cuing; however, such cuing has to be proximal to the locus of response or choice. In a similar vein, Srebro (1974) reported that the spatial/positional deficit seen following septal lesions on a successive positional re-

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versal task (Srebro & Divac, 1972) could be overcome by using a salient proximal cue consistently associated with the correct side in the reversal task. In short, it would appear that when external cuing is used to ameliorate septal-lesion-induced behavioral alterations, such cuing is effective to the degree that the cuing is proximal to either the animal or the locus of choice.

The above analysis suggests the possibility that by providing septal animals with a stimulus cue that has been associated with the daily feeding table proximal to the locus of choice, that is, the intersection of the runways on the three-table task, the deficit in going directly to the food typically shown by septal animals could be overcome. The first experiment examined this possibility.

EXPERIMENT 1

The purpose of the first experiment was to determine whether rats with septal lesions could perform successfully on the three-table task when the locus and route to the feeding table were cued by a distinctive proximal intramaze visual stimulus insert that was consistently associated with the feeding table each day regardless of the spatial location of the feeding table.

Method

Subjects

Twenty Long-Evans hooded male rats were used in this experiment. The animals ranged in weight from 167 to 326 g 8 days prior to surgery. Ten animals were assigned to the septal lesion group and 10 were assigned to the sham-operate group. Following the surgery, the two groups were further subdivided into an explore and a no-explore group, with an equal number of animals in each group.

Prior to testing, all animals were reduced to 85% of their ad-lib weights. This value was adjusted upward 1.5% each week to reflect the continued growth of the animals.

The animals were individually housed in the colony room, which was maintained on a 16-h-on (0700-2300 h)/8-h-off (2300-0700 h) cycle and kept at 21°C.

Apparatus

A variant of the Maier three-table apparatus was used in this experiment. It consisted of three tables connected by runways elevated 59 cm above the floor and connected at equal angles. Each runway was 61 cm long and 7.5 cm wide. Attached to the front side of each table was a 63 × 49 cm screen with a 10 × 10 cm opening. The purpose of this screen was to obstruct the view of the tables and associated stimuli from other parts of the apparatus.

A distinctive visual stimulus insert was used each day to mark the food table and its associated runway. The two remaining tables and their runways remained solid flat black. It should be stressed that the location of the distinctive stimulus insert varied daily as the location of the baited table varied. A solid gray stimulus was used for half of the animals and a black and gray striped pattern stimulus was used for the others. In each instance, the visual stimulus covered both the surface of the table and runway and the front and back of the obstruction screen.

The entire apparatus was enclosed in a 206 × 174 × 205 cm copper wire enclosure. The enclosure itself was lined with newspaper and covered by black draping material to minimize differ-

ences in the nature of the extramaze stimuli associated with each table. A standard ceiling fluorescent fixture illuminated the enclosed area.

Procedure

Pretraining. Prior to surgery, all animals were trained to run on elevated runways. This training consisted of first placing a board of the same dimensions as the runways of the three-table apparatus between two tables located outside of the experimental space. The animals were placed on these tables and runway and allowed to run between the tables. Any animals that did not run spontaneously were gently prodded. Wet mash was present on both tables. The animals were given 4 days of this type of runway training and then were assigned to one of four groups (septal-explore, septal-no-explore, sham-explore, sham-no-explore). At the end of the pretraining period, surgery was performed on all animals.

Surgery. All animals were injected ip first with .3 cc of atropine sulfate and then with sodium pentobarbital (Nembutal) for anesthesia (40 mg/kg). They were then placed in a Kopf stereotaxic device with the upper incisor bar set at 5.0 mm above the horizontal zero plane. Lidocaine hydrochloride was infiltrated into the scalp as a local anesthetic prior to making a midline incision in the scalp. Bregma was identified, and a single burr-hole was drilled 2 mm anterior to bregma. An insect pin (No. 00), insulated except for .5 mm at the tip, was lowered 5 mm below the surface of the brain on the midline. For half of the operated animals, an anodal (2 mA for 20 sec) current was passed between the electrode in the brain and a cathodal clip attached to the stereotaxic device. For the other half of the operated animals (sham operatees), the electrode was simply lowered and withdrawn without any current being passed. Following the removal of the electrode, the scalp was sutured with silk thread and the animals were given .2 cc of penicillin im.

Test procedure. The animals were handled daily on the 2nd through the 7th postsurgical days. Testing of the animals began 8 days after surgery. At that time, there was no evidence of septal hyperreactivity. Recall that both the septal and sham operatees had been previously divided into two subgroups—one to receive exploration prior to the feeding and test trial and one not to receive the exploratory experience prior to the feeding and test trial.

Experimental testing consisted of three phases. In the first phase, the animals that were to receive the exploration period were placed in groups of five at the intersection of the runways of the three-table apparatus and allowed to run over the tables and runways for 15 min daily. During that period, neither the tables nor the runways were baited. Moreover, during the exploration period, the apparatus was entirely devoid of any distinctive visual stimuli. The animals explored an entirely black complex of tables and runways. It was only during the feeding and testing phase of the experiment that the distinctive visual stimulus insert was placed on the baited table and its associated runway. Following the exploration period, the animals were removed from the apparatus and placed in a group holding cage. The table that was to be that day's food table was baited with a dish of wet mash. One of the other tables was similarly baited, but the food on that table was securely covered with wire mesh, making it unavailable to the animals. A group of five animals was placed on the baited table and allowed to eat for 2 min. Care was taken to ensure that there was always enough food for it never to be totally consumed during the feeding period (Herrmann, Bahr, Bremner, & Ellen, 1982). After this feeding phase, all rats were removed from the apparatus and returned to the holding cage.

Each rat was individually removed from the holding cage and placed on the start table for testing. Guillotine doors were raised on the baited table and on the table containing the wire-enclosed food. Then the guillotine door on the start table was raised, and the animal was allowed 3 min to leave the start table. If an animal did not move within 3 min or reach the baited table within 1 min after having left the start table, the animal was removed from the apparatus and an error was scored. An error was also scored if the animal did not run directly to the food table on its first choice.

Ten animals (five septals, five shams) did not receive the exploration experience prior to the feeding experience. Each day they were merely placed on the baited table and allowed to eat for 2 min. Following this experience, they were removed, placed in the carrying cage, and tested individually in the manner described for the animals that had received the prior exploratory experience.

For the first 14 days of testing, the animals received one trial per day. On the last 10 days of testing, they received three trials per day. Under no circumstance was an animal given an opportunity to correct an error on a given trial.

Histology

At the conclusion of testing, the animals were injected intraperitoneally with a lethal dose of sodium pentobarbital and perfused intracardially with saline followed by a 10% Formalin solution. The brains were removed and stored in Formalin. Frozen sections, 40 μ thick, were taken and stained with cresyl violet for use in identifying location and extent of lesion.

Results and Discussion

Histological

The extent of damage to the septal-explore animals and no-explore animals was comparable (see Figure 1). The most anterior damage started at the origin of the lateral septum and the genu of the corpus callosum. The damage extended posteriorly to the fornix longus and the triangular septal nuclei, the col-

umns of the fornix, and slightly into the hippocampal commissure. The ventral damage extended ventrally into the anterior commissure, and in some of these animals the diagonal band of Broca was invaded.

Behavioral

Three animals (two sham-explore, one septal-no-explore) which never went to the "cued" table were not used in the analysis, inasmuch as such behavior was assumed to reflect an avoidance by the animals of the distinctive features of the cue. Additionally, two animals (one septal-no-explore, one sham-explore) that were inadvertently switched during the exploration period were not used.

The performance of the four groups of animals on the first 14 days of testing is shown in Figure 2A. As can be seen from the figure, there were no significant differences between either of the septal groups and their corresponding sham operatees. This observation was confirmed by a two-way repeated measures ANOVA with lesion and exploration condition as between-group factors and days as the repeated measures factor. The F ratio for lesion was nonsignificant [$F(1,11) = .17, p = .6909$]. In contrast, there was a marked effect for the exploration factor [$F(1,11) =$

Figure 1. Reconstructions of the extent of lesions for the septal-explore and no-explore animals in Experiment 1. The lesion extents are plotted on plates of the Pellegrino and Cushman atlas (1967). For each animal, the lowest numbered plate represents, with slight variations, the posterior extent of the lesion; the highest numbered plate represents the most anterior extent of the lesion; and the middle plate represents the plane with the greatest damage. All planes of damage were anterior to bregma.

Figure 2. Performance of animals during 24 days of testing. During Days 1-14, the animals received one trial per day; during Days 15-24, they received three trials per day. Each point represents the average of 2 consecutive days of data (Block 1 is the average of Days 1 and 2; Block 2 is the average of Days 2 and 3, etc.).

10.73, $p = .0074$). Thus, both septal and normal animals allowed to explore the apparatus prior to a single daily test trial performed significantly better on the test trial than did comparable animals not given the prior exploratory experience. This observation is remarkable in view of the fact that the distinctive visual stimulus was *not* present on the apparatus during the exploratory phase.

In addition to these between-group effects, there was a marked improvement over the course of daily testing for the animals not given the daily exploration experience; this was confirmed by a significant exploration $\times$ days interaction [$F(13,143) = 2.54$, $p = .0036$]. Although the animals (both septal and shams) were improving, the relatively slow rate of improvement prompted us to increase the number of daily test trials to three per day.

The results for the last 10 days of testing, in which the animals received three test trials per day, are illustrated in Figure 2B. As can be seen in the figure, there was a marked improvement in all groups of animals by the end of the 10 days of three-trials-per-day testing. An ANOVA comparing the last 4 days of this period with the last 4 days of one-trial-per-day testing confirmed this impression [$F(1,11) = 9.97$, $p = .0091$].

Finally, it should be stressed that by the last 4 days of training there were no differences among any of the groups on any of the days [$F(3,33) = 1.95$, $p = .1403$]. Thus, it would appear that repeated testing with three trials per day overcame the initial deficit in performance resulting from the lack of exploration prior to the feeding and test trial.

It is clear from the results of Experiment 1 that when septal animals are confronted with a visual

stimulus that consistently signals the pathway to, as well as the location of, the feeding table, they have no more difficulty than sham operatees in going directly to that table on the test trial. This finding, when contrasted with the results of Herrmann et al. (1980), in whose study septal animals could not learn to run to a food table lit by an extramaze cue light visible from the starting table and the intersection of the runways, suggests the possibility that septal animals fail on the traditional three-table task not so much because they do not know the spatial location of the feeding table relative to the start table, but rather because they cannot program an intended series of movements (Vanderwolf, 1971) to get them from the start table to the baited table. It is clear from the results of this experiment that septal animals experience no difficulty in running from the start table to the baited table when they are given the clearly marked path to that table from the choice point.

EXPERIMENT 2

Experiment 1 suggested the possibility that septal rats fail on the three-table task because they cannot plan a series of acts that will bring them to the food table in the most direct manner. Implied in this hypothesis is the assumption that although septal animals have learned the spatial relationships between the tables and the locus of the baited table, they simply are unable to plan the necessary series of movements that will bring them from the start table directly to the food table.

If this is so, then the existence of discriminable routes to the food table should be sufficient to guide the septal animal's performance, even though there

is no longer a single cue that is consistently associated with the locus of food. All that would be required of the animal would be for it to follow the runway from the start table to the choice point and, at the choice point, to follow the path marked by the visual pattern that was present on the table during the feeding experience. The animal would, in this instance, have no need to plan the route to take it from the start table to the food table. Experiment 2 was designed to determine whether rats with septal damage could go directly to the food table when the route to the daily locus of food was clearly indicated to the animal.

Method

Subjects

Twenty Long-Evans hooded male rats were used in this experiment. The animals ranged in weight from 387 to 511 g 2 weeks prior to surgery. Ten animals were assigned to the lesion group and 10 to the sham-operated group. As in Experiment 1, the groups were further subdivided into an explore and a no-explore group with an equal number of animals in each group. One animal in the sham group was rendered immobile for 2-3 min (despite no signs of physical injury) following a fight in the carrying cage. Subsequent to the fight, the animal did not eat during several feeding periods and failed to leave the start table for the duration of testing. Its data were, therefore, not used. As in Experiment 1, the animals were maintained at 85% of their ad-lib weights. Housing conditions were as in Experiment 1.

Apparatus

The apparatus was the same as that used in Experiment 1, with the exception that in this experiment each table and its associated runway were covered with a distinctive visual stimulus insert. As in the first experiment, these stimulus inserts covered not only the surfaces of the tables and runways, but also the fronts and backs of the obstruction screens. One table was covered with a solid gray insert; another was covered with a black and gray striped pattern; the third table was covered with a solid flat black insert.

Surgery and Histology

These procedures were carried out in the manner described for Experiment 1.

Procedure

The preexperimental handling was identical to that used in Experiment 1. There was, however, a major difference in the testing procedures used in this experiment. In this experiment, from the very beginning of testing, the animals were given three trials a day and testing was continued until all animals in the sham-explore group were exhibiting a level of correct performance that could not have occurred by chance more often than 5 times out of 100, according to an expansion of the binomial equation. This level of performance was realized by the 13th day of testing.

Results

Histological

Three of the animals that supposedly sustained septal lesions actually showed no more signs of damage than did the sham-operated animals. Two of these animals were in the septal-explore group, and one was in the septal-no-explore group. Accordingly,

these animals were assigned to the corresponding sham condition.

The extent of septal damage in the animals sustaining septal lesions is shown in Figure 3. In the septal-explore group, damage extended posteriorly from the origin of the lateral septum (3.0 mm anterior to bregma) to the fornix in all animals. There was also slight damage to the diagonal band of Broca and the anterior commissure in these animals.

Damage in the septal-no-explore group was comparable to that of the septal-explore group. In the anteroposterior dimension, damage ranged from a plane located approximately 3.0 mm anterior to bregma in the Pellegrino and Cushman (1967) atlas to a posterior plane approximately 0.6 mm anterior to bregma. In the ventral dimension, damage extended ventrally between 5 and 7.5 mm below the surface of the brain. As a result, in the posterior planes there was encroachment on the stria medullaris and periventricular nuclei ($N=2$), and in the anterior planes there was encroachment on the diagonal band and the bed nucleus of the anterior commissure. In no instance was there encroachment on the caudate nucleus.

Despite the fact that thalamic damage was present in two of septal-no-explore animals, an ANOVA of the behavioral data revealed no differences between these animals and comparable animals not sustaining thalamic damage [$F(1,2)=1.60$, $p=.333$]. Accordingly, the animals with thalamic damage were retained in the septal-no-explore group.

Behavioral

Performance on each of the three daily trials was examined for each group of animals over the 13 days of testing. Table 1 shows the cumulative percent correct for each animal in each group for the 13 test days. The septals averaged 49.5% correct over the 13 days, and the shams averaged 71.2% correct on the first trial. Although shams that explored the apparatus prior to testing performed at a higher level than did shams not given the prior exploratory experience, septal animals, in contrast, did not seem to be affected by whether or not they had received the prior exploratory experience.

On Trial 3, septals averaged 57% correct and shams averaged 75.2% correct. A repeated measures ANOVA with lesion and exploration as the between factors and day of testing and trial within a day as the repeated measures factors confirmed this impression. Septals differed from shams [$F(1,15)=15.87$, $p=.0012$]. More importantly, there was a significant lesion $\times$ exploration interaction [$F(1,15)=8.72$, $p=.0099$]. Thus, the opportunity to explore facilitated performance of the shams but did not affect the performance of the septals. Finally, there was no significant main effect or interactions for the trial factor (all $ps > .4$). There was a significant triple

Figure 3. Reconstruction of extent of lesions for the septal-explore and septal-no-explore animals in Experiment 2. The same designations of the plates were used in this figure as in Figure 1. As in Figure 1, all planes of damage were anterior to bregma.

interaction between lesion, exploration, and days of testing [$F(12,180)=3.36, p=.0002$]; however, examination of the performance of each group over the course of the 3 days revealed no consistent trends (see Figure 4).

Finally, when overall Trial 1 performance of each animal in each group was considered from the perspective of whether their performance was better or worse than would be expected to occur by chance 5% of the time or less, according to an expansion of the binomial equation for 13 test trials with a 50-50 chance

of being correct on any given trial (77% correct), all five animals in the sham-explore, one in the sham-no-explore, and none in the septal groups met this standard. It is thus clear that, despite the addition of salient intramaze stimuli to enhance the identity of each table and runway, septal animals are still deficient.

GENERAL DISCUSSION

The results of Experiment 1 provide clear evidence that septal animals can learn to go to a table that is

Table 1
Cumulative Percent Correct for 13 Days

Sham								Septal							
Explore				No Explore				Explore				No Explore			
Rat No.	1	2	3	Rat No.	1	2	3	Rat No.	1	2	3	Rat No.	1	2	3
ShE1	77	85	85	ShNE1	46	85	77	SE1	55	46	54	SNE1	31	46	69
ShE2	85	38	85	ShNE2	54	15	62	SE2	46	46	62	SNE2	54	36	48
ShE3	85	92	100	ShNE3	46	62	69	SE4	46	54	46	SNE4	54	69	46
ShE4	85	62	62	ShNE4	38	77	46					SNE5	62	62	85
ShE5	100	85	85	ShNE5	62	62	77								
ShE6	100	85	85	ShNE6	77	54	69								
Mean	88	74	84		54	59	67		49	49	54		50	56	60

Figure 4. Performance of animals during 13 days of testing. Each point represents the average of 2 consecutive days of data (Block 1 is the average of Days 1 and 2; Block 2 is the average of Days 2 and 3, etc.).

baited with food provided that the route to that table is clearly marked by an intramaze stimulus. Moreover, the fact that the success of septal and sham animals on this task was not determined by whether or not the animals were given the opportunity to explore the apparatus prior to feeding and testing provides clear evidence that the procedures of Experiment 1, in which the baited table was marked by the same salient intramaze stimulus regardless of its spatial location, provided the animals with a more or less difficult visual discrimination task. The difficulty of the task would seem to have derived from the lack of an opportunity to explore. With exploration, both septals and shams learned significantly faster than did comparable animals not given exploration.

What is most interesting about the findings of Experiment 1 is that septal animals can profit from an exploratory experience as well as follow a route—a point to which we shall return below.

Turning now to the results of Experiment 2, we found that when the distinctive intramaze stimuli merely marked the spatial location of the three tables and their associated runways rather than consistently marking the food table, septal animals showed the typical impairment seen on this task when there are no distinctive intramaze stimuli (Herrmann et al., 1978; Herrmann et al., 1980; Stahl & Ellen 1973, 1979). Similar findings were obtained by Beatty and Carbone (1980) using a radial-arm maze. More importantly, the results of Experiment 2 also indicate that the failure of septal animals on the three-table task does not derive from their inability to program the required route to the baited table as suggested by the results of Experiment 1; rather, it would seem that the addition of the salient visual inserts in Ex-

periment 2 did not alter the basic character of the three-table task. The fact that the sham-no-explore animals were unsuccessful provides clear evidence that despite the addition of salient intramaze stimuli, the three-table task still required the formation of a spatial representation as well as knowledge of the location of the food. Thus, it would appear that the deficit shown by septal animals in Experiment 2 is the result of a failure to learn the spatial relationships existing among the tables. To the extent that the septal animals given a prior exploratory experience on the integration task did not do better than those not given this experience, we have support for the view that septal animals do not form a spatial representation of the environment.

Although the preceding conclusion is consistent with that drawn by Ellen and Weston (1983), who showed that the sector entry behavior of septal animals during a 15-min exploratory period failed to habituate each day, as it did in the case of normal animals, it is inconsistent with the observations of the present Experiment 1, which show that both septal animals and shams profit from exploration.

One solution to this apparent contradiction is that several effects result from an animal's locomoting through an environment, and habituation is indicative of only one of these effects. Specifically, it has been proposed that habituation occurs only when an animal has acquired a cognitive representation of the environment (Halliday, 1968; O'Keefe & Nadel, 1978). What, then, are the other effects of exploration? What did the animals of Experiment 1 acquire during exploration that facilitated their cue learning? If we assume that exploration allows animals to familiarize themselves with the test environment, then

the animals given the opportunity to explore the black apparatus were familiar with the apparatus when the distinctive visual insert was introduced. The insertion of the visual pattern during the feeding experience provided a stimulus that could command attention simply because of its novelty. In contrast, the introduction of the visual pattern did not command preferential attention relative to the other stimuli present in the test environment for those animals that had never explored the test environment.

Taking this approach, it would appear that exploration has two effects. First, as suggested by the results of Experiment 1, it simply allows animals to attend to the various objects and features of the environment, and, to the extent that these features and objects remain constant, they rapidly become familiar. Septal-explore animals did not differ from comparable shams with respect to this effect of exploration.

Second, during exploration, the animals learn about the spatial relationship that exists among the tables. The Ellen and Weston (1983) study suggests that septals are deficient with respect to this latter effect of exploration and hence fail to decrease their activity during the exploratory period.

The basis for this latter deficit most likely derives from an absence of septally driven theta (Winson, 1978). The role of the septum in the pacing of theta activity is well established (Petsche, Stumpf, & Gogolak, 1962). Consistent with this role of the septum is the proposition that the inability of septal animals to learn the spatial relationship that exists between objects in the environment most likely derives from an absence of septally driven theta which provides the mechanism whereby the distances and directions between objects in the environment are specified (O'Keefe & Nadel, 1978). The results of Experiment 2 of the present study suggest that such a function cannot be readily substituted for by the use of salient intramaze stimuli that mark the route to the baited table.

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