Avoidance learning after simultaneous versus serial telencephalic ablations in the goldfish

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The effects of simultaneous and serial bilateral ablation of the goldfish telencephalon on the retention of an avoidance response was studied. On the basis of research in mammals, it was expected that the serial procedure would produce significant savings in the retention of avoidance learning, which is otherwise significantly impaired after simultaneous bilateral ablations of the telencephalon. The retention of the avoidance task learned prior to the ablations was unaffected by the serial procedure.

The study of the relationship between teleost telencephalon function and acquired and species-typical behavior has been carried out mainly through the use of ablation procedures (de Bruin, 1980; Hollis & Overmier, 1978; Savage, 1980). Typically, the ablation is performed simultaneously on both hemispheres, and behavioral changes are determined by appropriate comparisons with sham-operated animals.

The effects of simultaneous bilateral ablations of the telencephalon on acquired responses have, to a great extent, depended upon the tasks designed to detect such deficits. For example, forebrainless fish have shown no deficits on classical conditioning experiments (Farr & Savage, 1978; Overmier & Curnow, 1969; Overmier & Savage, 1974) and on relatively simple instrumental tasks (Savage, 1969a). However, telencephalon ablation produced detectable deficits on habituation of the cardiac arousal response (Laming & McKee, 1981), food-reinforced responses (Overmier & Patten, 1982; Savage, 1969a), and complex maze performance (Warren, 1961). Avoidance behaviors have been dramatically disrupted by such ablations (Hainsworth, Overmier, & Snowdon, 1967; Kaplan & Aronson, 1967; Overmier & Flood, 1969; Overmier & Gross, 1974; Savage, 1969b).

The effect of telencephalon ablation on avoidance learning has received comparatively more attention from researchers interested in the functions of teleost telencephalon, in part due to its magnitude and reliability under a wide variety of conditions. Although the ablation was found to exert its influence on both de novo acquisition

and retention, avoidance behaviors seem to recover and reach an unstable but relatively high level (Hainsworth et al., 1967; Savage, 1969b). The present research is an attempt to identify some of the factors affecting behavioral recovery after damage to the telencephalon in the goldfish.

A different, although complementary, approach to the phenomenon of behavioral recovery would be to ask whether different types of ablation procedures would allow the behavior to be recovered faster and to a higher level. From research on mammals, it is known that the serial ablation procedure has, in general, facilitating effects on behavioral recovery from brain damage (Finger, Walbran, & Stein, 1973). Various kinds of behavior have been shown to be spared after sequential lesions, as opposed to simultaneous lesions of similar extent. This "serial lesion effect" has been found in learning situations including discriminative avoidance in rats after lesions in the occipital neocortex (Glendenning, 1972; Petrionovich & Bliss, 1966; Petrionovich & Carew, 1969; Thompson, 1960) and two-way shuttle avoidance after lesions in the lateral septal area in the rat (Kouba & Bussey, 1973).

The experiment reported in the present paper attempted to characterize the retention of instrumental avoidance behavior in fish that had been submitted to serial, simultaneous, and sham ablations of the telencephalon. The experiment was a partial replication of another (Overmier & Papini, *in press*); it used a higher level of shock intensity in the avoidance training because level of "arousal" was known to be important in postoperative retention.

METHOD

The subjects were 18 goldfish (*Carassius auratus*) 8-12 cm long, housed individually in 20-liter aquaria at 21° C and pH 7.3. The fish were assigned to three groups of equal size.

Avoidance training took place in a 46.5-cm shuttlebox divided into two equal chambers by a 7.5-cm barrier. Water depth was 9-cm. The device was modeled after that of Horner, Longo, and Bitterman (1961).

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The chambers were illuminated by white light during the intertrial interval. The warning signal was a change to red illumination throughout. The shock to be avoided was 10 V ac pulsed (105 msec on, 320 msec off) delivered through longitudinal electrode walls. The interval between the onset of the warning signal and the scheduled onset of the shock was 10 sec. The warning stimulus overlapped the shock, which lasted up to 2 sec. A response terminated the trial by ending the warning signal and the shock (escape) or ending the warning signal and preventing the shock if shock had not yet come on (avoidance). The intertrial interval averaged 92.4 sec. Each daily session consisted of 10 trials.

First, all fish were adapted to the apparatus for two sessions, and spontaneous crossings were recorded. Then avoidance training began and continued until the subjects had met a mastery criterion of six consecutive sessions in which the percentage avoidance equalled or exceeded 70% on at least five of the sessions. Upon reaching criterion, the fish began to receive different surgical treatments.

For surgery, the fish were anesthetized with tricaine methanesulfonate (.5 mg/ml) and mounted in a special sponge clamp holder. Gills were continuously bathed while the fish was in the holder. A rectangular flap about 4 mm² was reflected over the anterior portion of the brain, and the fatty superficial tissue was aspirated in all fish. In addition, some fish had one (unilateral) or both (bilateral) hemispheres of the telencephalon aspirated. The wound was then filled with Gelfoam, and the flap was closed and secured with dental cement. The fish were then returned to their compartments for 48 h before any further treatments.

Postexperimental verification of the ablations revealed that one fish in Group S+S (see below) received a small lesion in the dorsal telencephalon. This fish was therefore excluded from the experiment. The ablations were quite uniform in achieving removal of the telencephalic hemispheres with no detected damage to the optic tectum or to the preoptic nucleus area. Representative brains from each group are shown in Figure 1.

There were three treatment groups. Group U+U received a unilateral ablation of the telencephalon followed (after 48 h) by 10 daily sessions of interoperative training (IOT) on the avoidance task and then a second unilateral hemispherectomy. Group S+B received a sham operation followed (after 48 h) by 10 sessions of IOT and then bilateral ablation of the telencephalon. Group S+S received a sham operation followed by 10 sessions of IOT and then a second sham operation.

Forty-eight hours after the second operation, all groups were tested for retention of the avoidance task for two sessions. The avoidance performance of the three groups during acquisition and retention sessions constitute the data of most interest.

RESULTS

Individual subjects' avoidance scores were computed on the basis of performance in blocks of two sessions and were subjected to analyses of variance for each phase of the experiment. These data for the acquisition and retention behavioral phases of the experiment are shown in Figure 2.

During adaptation, there was little spontaneous crossing of the barrier on the blank trials. Analysis of Variance detected no between-groups differences.

The original training on the avoidance task was carried out until each fish had reached the criterion of mastery, and all groups were averaging between 78% and 88% avoidance by the end of original training. The subjects reached criterion in an average of 7.7 session. Analysis of variance (groups $\times$ 2 session blocks, unequal ns) of avoidance performances of the criterion run detected no significant differences among groups, but did detect an effect of blocks of training [$F(2,28) = 15.62, p < .01$].

The next behavioral phase of the experiment involved

Figure 1. Representative brains from each group and a metric scale. Brains are from Groups S+S (above), U+U (center), and S+B (below).

the 10 days of IOT for Groups S+S, S+B, and U+U. Performance for all groups was relatively high: It did not fall below 80% and, hence, exceeded criterion throughout. Only for Group U+U do the data potentially reflect the effect of a lesion. An analysis of variance detected a numerically small, but significant, effect of groups [$F(2,14) = 7.36, p < .01$]. Follow-up pairwise comparison between the unilaterally ablated group and the two shams was significant [$t(14) = 3.51, p < .01$]. Additional analysis showed the intertrial activity level of the unilateral group to be less; pairwise comparisons showed Group U+U differed from both Groups S+S and S+B [$ts(14) \geq 3.5, p < .01$].

Following the second behavioral phase, which consisted of IOT, all subjects received a sham (Group S+S), unilateral (Group U+U), and bilateral (Group S+B) ablation, and then, 48 h after the last surgical procedure, were tested for retention of the avoidance task using the training procedures. These are the data of central interest.

The group subjected to two sham operations 12 days apart, Group S+S, continued to perform at a very high level. The story was quite different for the ablated animals, which showed substantial deficits in retention. Analysis of variance indicated an effect of groups [$F(2,14) = 9.7, p < .01$]. Pairwise comparison confirmed that the two ablated groups differed from Group S+S [$ts(14) \geq 2.1, p < .05$], but not from each other. This difference in avoidance was paralleled by similar differences in intertrial activity: Both Groups U+U and S+B differed

Figure 2. Percent avoidance responses for Groups S+S, S+B, and U+U during each training phase.

from Group S+S [$t(14) \geq 8.7$, $p < .01$], but not from each other. Group U+U, which had been only mildly insensitive to the first unilateral operation, showed a marked decrement in performance after the second unilateral ablation. Finally, the deficits seen in Group S+B were not greater than those seen in Group U+U, which suggested that two-stage serial ablation of the teleost telencephalon results in functionally similar deficits in retention of a shuttlebox avoidance behavior, as does one-stage bilateral ablation.

DISCUSSION

Reviews of the literature (e.g., Finger et al., 1973) confirm the serial lesion effect in mice, rats, cats, dogs, monkeys, and man subjected to a wide variety of lesions on a wide variety of brain loci and tested in a variety of tasks. Yet no evidence for a serial lesion effect was found in these telencephalon-ablated fish. On occasion, others have failed to find a serial lesion effect in mammals (e.g., Kircher, Braun, Meyer, & Meyer, 1970), but such failure may be attributable to lack of IOT. Absence of a serial lesion effect in this experiment cannot be attributed to a failure to provide task-relevant interoperative experience because the serial ablation group received 10 days of training on the avoidance task between the two unilateral ablations.

The absence of a serial lesion effect is somewhat surprising in the historical context. Moreover, the design used in the present experiment could be inferred to have a slight bias in favor of the serial group because the time to recover following the initial invasion of the brain was longer for the serial group (see Kassel & Davis, 1977; Meyer et al., 1958); nevertheless, no serial lesion effect was observed.

This experiment essentially replicated the results of an earlier experiment that used lower shock levels—4 V ac (Overmier & Papini, in press). Although absolute levels of performance were somewhat higher here, the patterns of effects among sham, simultaneous, and serial ablation groups were the same. In particular, in retention tests both ablated groups were inferior to the sham group, but these ablated groups did not differ from each other significantly. Using a different level of motivating stimulus did not alter the pattern of results. The serial procedure did not enhance retention of the preoperatively trained avoidance even when the interoperative training was given.

Even though the serial ablation procedure is often conceived as a means

of sparing a specific learning process that has begun before ablation or damage to the central nervous system (Bodart, Hata, Meyer, & Meyer, 1980; Meyer & Meyer, 1977), one could also speculate that behavioral sparing might be rather nonspecific with respect to the task already learned by the animal. In other words, the serial procedure could facilitate nonspecific learning capabilities by leaving the rest of the nervous system in a, so to speak, more plastic state. Following this reasoning, it might be wise to include a task that demanded the learning of a somewhat new feature of the environment, such as a "reversal" learning phase, as a relatively simple way to test this basic idea (see LeVere & Morelock, 1973).

Intertrial activity was included as a measure because it might provide an assessment of general effects of telencephalic manipulations separate from specific discriminated avoidance behavior. Ablations decreased both avoidance performance and "spontaneous" intertrial crossings of the barrier. This consideration would suggest that the telencephalon of the goldfish is not exclusively involved in memory or cued response evocation but may well involve general arousal functions, as others have suggested (Aronson & Kaplan, 1968).

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