Effect of frontal and parietal lesions on timing behavior in monkeys¹

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Abstract

Timing behavior before and after successive cortical ablations was studied in three monkeys. Frontal lesions profoundly impaired performance while posterior parietal lesions did not. The animals recovered from the impairment following frontal ablation with further training.

Problem

Wilson & Keller (1953) described a behavioral schedule (DRL) in which reinforcement is contingent on a response that follows a period of non-response. For example, a lever-press is reinforced only if 15 seconds have elapsed since the previous lever-press.

In stable performance on such DRL schedules, Ss typically show a normal distribution of inter-response times with a modal peak near the end of the required interval, suggesting an accurate estimation of the passage of time. Since ablation of dorsolateral frontal association cortex in monkeys has been found to disrupt typical per-

formance on at least one other temporal schedule (fixed interval) (1), it seems probable that this area is involved in timing behavior and that DRL performance should be affected as well.

Method

Three pigtail monkeys (*Macaca nemestrina*) were trained to respond on a DRL schedule and then were subjected to sequential ablation of different brain structures in varying order. GRG received a total of three operations; PGG four and DNO two to date.

Since order effects were minimal in these data, we shall present the effects of frontal lesions on DRL performance for the three animals, and, as a control, the effects on these same animals of ablation of a roughly comparable amount of tissue in the posterior parietal cortex.

All of the ablations were performed under aseptic conditions by subpial suction with a metal cannula while Ss were maintained under barbiturate anesthesia.

GRG and PGG were trained on a DRL schedule in which reinforcement was available for an unlimited period after the 15-second interval. DNO was initially trained in this way, but later was shifted to a three-second limited-hold schedule in which reinforcement was available only in the 15-18-second interval following the last response.

Fig. 1. Frequency distributions of inter-response times for each animal five days pre- and postoperative. Frontal and posterior parietal ablations.

Fig. 2. Monkey PGG recovery from frontal ablation. Early middle and late postoperative response distributions and sample cumulative records.

Prior to any ablations, the Ss were placed in primate chairs and were fed one gram CIBA banana pellets daily for four to five days. The Ss were then trained daily in a soundproof chamber which contained a speaker for presentation of white masking noise. Control and recording equipment were housed outside the chamber. Initially, Ss were shaped to press a lever mounted on the primate chair, after which they were trained for two days with continuous reinforcement (CRF). On the third day, 15-second DRL training was started. Ten minutes after the beginning of each day's DRL training session, light and sound were turned on, and the lever was connected to timing and recording devices for the DRL. Each day, Ss were run until they would no longer press the bar or no longer eat the pellets.

Behavioral Results

After frontal ablation, all Ss were markedly impaired in DRL performance. Two Ss (PGG and GRG) had a far higher rate of response and an absence of modal peak near the 15-second interval, while the lever pressing response in DNO appeared to be totally extinguished. This S was retrained to press the lever and then given two days of CRF training before the DRL schedule (in this case with limited-hold) was reinstituted. After the retraining period, DNO showed a response distribution similar to that of PGG and GRG.

Figure 1 shows each S's inter-response time frequency distributions for the DRL schedule for five days before and after each operation. Darker regions indicate reinforced responses. Note that the effects of lesion appear to be independent of the order in which they were made.

Despite initial impairment following frontal ablation, all Ss recovered preoperative levels of performance with further training.

Figure 2 shows PGG's course of recovery. Included are frequency distributions on inter-response time with representative portions of the cumulative record for a day in the early, middle, and late phases of recovery.

Anatomical Results

Histological verification of lesion is available to date for only one animal (GRG). The damage to frontal cortex was as intended and included dorsolateral cortex from the anterior bank of the arcuate sulcus to the frontal pole including banks and depths of sulcus principalis. The posterior association cortex lesion (the control lesion) included the tissue between the intraparietal sulcus and the lunate, including banks and depths of the medial part of the superior temporal fissure. PGG and DNO are being studied after further ablation, and their lesions have not yet been verified.

Discussion

Frontal lesions have been shown in this study to have a disruptive effect on preoperatively acquired DRL performance. The fact that the Ss recovered from such lesions suggests, however, that other neural structures can also mediate efficient timing behavior. Stamm (1963) found similar frontal lesions to have no effect on post-operative acquisition of DRL performance. Thus, alternate structures probably served for acquisition of DRL performance in Stamm's animals.

However, one aspect of Stamm's experiment calls into question the generality of his conclusion about the frontal cortex's role in timing behavior. In his training procedure Stamm presented a two-second white light immediately after each reinforcement. In DRL training the presence of such a light would serve as a consistent S^{Δ} . Thus, in the first two-second interval Stamm was training these animals not to respond in the presence of a light, a procedure which limits any conclusions about timing per se.

References

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