Table 3. Effect of high amino acid feedings on brain serotonin concentration, after the five groups of rats had been on their particular diets for 14 days.

Diet	Brain serotonin (mμg/g)	Control (%)
B alone	485	100
B + Phe	430 ($P < .05$)	89
B + Leu	420 ($P < .05$)	87
B + Try	685 ($P < .05$)	141
B + Phe + Try	550 ($P < .05$)	133

"auxiliary phenomenon." However, as they pointed out, monoamine oxidase inhibitors also increase the brain levels of other centrally active amines, such as dopamine and norepinephrine. L-Tryptophan, on the other hand, increases the brain content of serotonin *without* simultaneously increasing the levels of catecholamines.

Perry (*15*) has also expressed doubt as to the importance of serotonin in cerebral development after observing that 7 days of subcutaneous phenylalanine administration, begun shortly after birth, lowered cerebral serotonin during this 7-day period of rapid development but left no residual deficits in "visual discrimination" when the rats were tested 5 to 7 weeks later. The absence of a behavioral alteration may be related to the duration of treatment or to the test instrument used, since Schalock and Klopfer (*16*), using different testing procedures, report permanent performance deficits when L-phenylalanine (3 g/kg) was administered daily by gavage (from birth to 60 days of age). Those investigators (*16*) and Hess *et al.* (*17*) suggest that certain behavioral assays may be more sensitive to impairments of the central nervous system in experimental phenylketonuria than other assays.

The work of Woolley and van der Hoeven (*18, 19*), which proposes a major role for serotonin in cerebral development, has received considerable attention. The major shortcoming in their studies relates to the absence of specific information on blood or tissue levels of phenylalanine or phenylketones, which prevents comparison of their biochemical conditions with those of other "phenylketonuric" preparations. These authors describe an irreversible "mental defect" in infant mice associated with poor T-maze performance and poor shock avoidance, which could be prevented by the administration of serotonin congeners (*18*). They could find no such "defect" in weanling mice fed diets containing 3 percent DL-phenylalanine and 3½ percent L-tyrosine. No blood phenylalanine values are given in either study and there is small likelihood that the concentrations of dietary phenylalanine used could have produced more than a transient rise in circulating L-phenylalanine levels.

In summary, diets high in phenylalanine or leucine are associated with poor water-maze performance and lowered brain serotonin, whereas diets high in tryptophan produce superior maze performance and supranormal levels of cerebral serotonin. Furthermore, the serotonin depletion and maze performance deficit associated with phenylketonuric rats can be more than compensated by adding 5 percent tryptophan to the phenylketogenic diet. This is compatible with a role for disturbed indole metabolism in the behavioral defect observed in phenylketonuric rats.

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Modulation of Elicited Behavior by a Fixed-Interval Schedule of Electric Shock Presentation

Abstract. *Responding elicited in the squirrel monkey by electric shocks presented every 60 seconds was gradually altered in temporal patterning, especially when the shock was also produced by responses under a 30-second fixed-interval schedule. The initially elicited pattern of maximal responding just after each shock was altered by the recurrent shock and by the added fixed-interval schedule to a pattern of maximal responding just before each shock. Most shocks were produced by responses and the response pattern was maintained for several months, but little responding occurred when shocks were omitted.*

A noxious stimulus, such as an intense electric shock, influences the behavior of animals differently, depending upon how the noxious stimulus is scheduled and the nature of the behavior preceding it. Responding can be engendered and maintained under conditions in which responses terminate or postpone electric shocks ("escape" or avoidance); ongoing responding can be suppressed under conditions in which responses are followed by electric shocks (punishment). We here describe the maintenance of responding, initially elicited by electric shock in a situation in which the only programmed consequence of responding was the scheduled delivery of electric shocks.

Typically, presenting a reinforcer after infrequently occurring responses will increase the rate of responding (*1*). When a known reinforcer follows specified responses that occur frequently, responding may be modulated more than changed in absolute level (*2*). Frequently occurring responses can also be modulated and maintained by the recurring presentation of reinforcers, such as food or electric shocks, without reference to behavior (adventitious reinforcement) (*3*). The effects of adventitious reinforcement depend critically upon the nature of the ongoing behavior. In the present experiments, responding was first elicited by electric shocks, then adventitiously modulated by the recurrent presentation of electric shock, and later maintained by a fixed-interval schedule of presentation of electric shock.

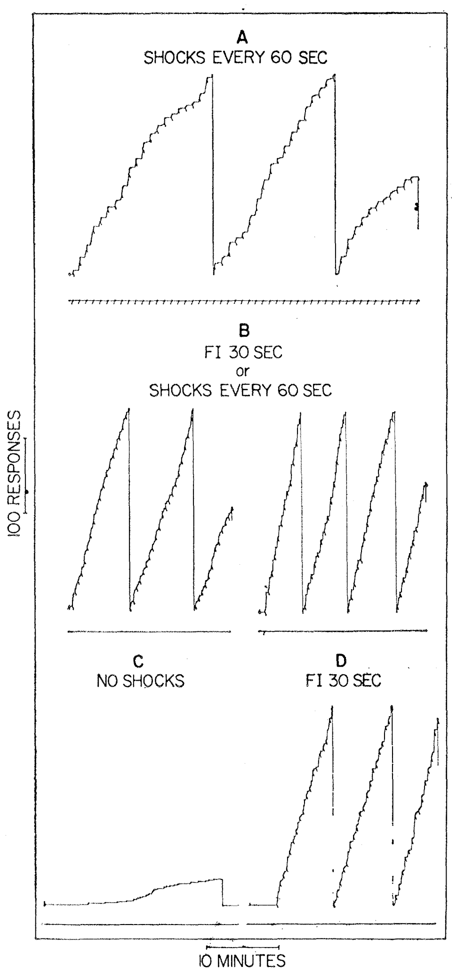

Fig. 1 (Monkey S-41). Response patterns under different experimental conditions. Ordinate, cumulative number of responses; abscissa, time. A: Session nine, electric shocks scheduled to occur every 60 seconds. B: Sessions 31 and 79, shocks scheduled to occur every 60 seconds or following the first response 30 seconds after last shock (FI 30 seconds). C: Session 83, no shocks scheduled (extinction). D: Session 93, FI 30 seconds alone. The diagonal strokes on the cumulative records indicate the delivery of electric shocks; the diagonal strokes on the event record indicate the delivery of shocks (without a response) after 60 seconds. In A responding occurs predominantly after shocks, producing patterns of deceleration. After the introduction of the fixed-interval contingency (B and D) sustained responding usually occurred before the shock. When shocks were omitted (C), few responses occurred.

Brief electric shocks can elicit stereotyped patterns of behavior (*4*). When electric shock is delivered to a rat or squirrel monkey, the animal will attack other members of the same species or certain other nearby objects. This elicited behavior can be so prepotent in an untrained monkey that it prevents the occurrence of other responses that terminate the electric shock, such as pressing a response key. In previous experiments with the squirrel monkey in a restraining chair, we noticed during initial training that electric shocks delivered to the monkey's tail caused the monkey to persistently pull and bite a leash attached to his collar (*5*). When the leash was fastened to a lever mounted at the top of the front panel of the chair, biting and pulling on the leash resulted in repeated closures of a precision switch attached to the lever. We studied this elicited response.

Three adult male squirrel monkeys (*Saimiri sciureus*) were studied individually while restrained in a primate chair (*6*). Electric shock was delivered through two metal plates that rested lightly on a shaved portion of the monkey's tail; a noncorrosive electrode paste (EKG Sol) insured a low resistance electrical contact between the plates and the tail. The electric shock source was 110 volts a-c at 60 cycle/sec; the current delivered to the plates through a series resistor was 7 ma for 250 msec. The monkey's leash was attached to a lever-operated switch located about 20 cm above its head; each closure of the switch was recorded as a response. A 6-watt red bulb was mounted behind a transparent Plexiglas wall in front of the monkey and was illuminated during each experimental session. The chair unit was enclosed in a ventilated soundproof chamber illuminated by a 25-watt overhead light.

Two monkeys (S-55 and S-41) had previously been deprived of food. Each had been trained to press a response key with its hand; this response had been maintained by the termination of electric shock and, under other conditions, by the presentation of food. In the present experiments, the monkeys were allowed to feed freely and the response key was removed from the front panel of the chair. Initially they were studied under a schedule in which the 7-ma electric shock was presented every 60 seconds. After ten sessions for one monkey and 20 sessions for the other, the schedule was changed so that the first closure of the switch 30 seconds after a shock produced the next shock. If no switch closure occurred between 30 seconds and 60 seconds, the shock was delivered as before, 60 seconds after the previous shock. At this time, experiments began on an untrained monkey (S-58). From the start, shocks were delivered following a closure of the switch 30 seconds after a previous shock or at 60-second intervals if no switch closure occurred.

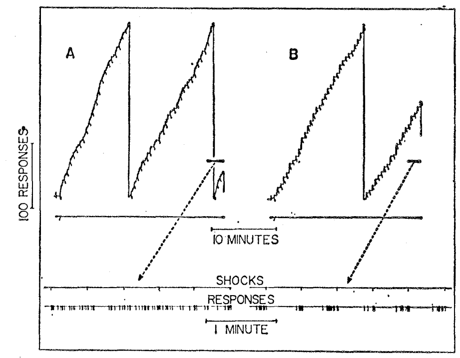

Fig. 2 (Monkey S-58). Response patterns under the schedule in which shocks occur every 60 seconds or following the first response 30 seconds after the last shock (FI 30 seconds). A: Session 5; B: Session 26. Cumulative response records recorded as in Fig. 1. Responses and shocks during the terminal part of the session are shown as recorded on a faster speed paper tape. The heavy horizontal line on the cumulative record indicates the intervals corresponding to those shown on the paper tape. The deceleration in responding following shock in session 5 has changed to an acceleration in responding before shock in session 26.

Initially, each shock elicited a burst of switch closures, which were the result of pulling and biting of the leash, but the relations of the switch closures to the latter behaviors were not studied explicitly. When the shock was scheduled to occur following a switch closure after 30 seconds (FI 30 seconds), the closure of the switch could be identified as a response, defined by its relation to the shock. This response initially occurred predominantly after a shock, but subsequently occurred predominantly before shocks.

Figure 1 shows representative performances of monkey S-41 under the various procedures. Record A shows the terminal performance under the initial procedure in which electric shock was delivered every 60 seconds. Usually the shock initiated a high rate of responding that abruptly decreased; further responding often occurred just before the next shock was delivered. The relative increase in responding during the latter part of many cycles developed with continued exposure to the recurrent shock. During initial sessions under the added FI 30-second schedule the high rates of responding which started immediately after each shock had decreased only slightly in 30 seconds. In the session shown at the left of Fig. 1B, every shock was produced by a response. With further exposure to the FI 30-second schedule (right of Fig. 1B), high rates of responding still occurred following most electric shocks, and sometimes responding decreased just before shock was delivered. Nevertheless, in most intervals after the initial responding there was a brief period without responses followed by a high rate of responding preceding the shock. When shocks were omitted (Fig. 1C), the rate of responding was low. Figure 1D shows that the performance of S-41 was maintained under the FI 30-second schedule alone; that is, electric shock was presented only when response produced it.

For monkey S-55, which had a lower rate of responding than S-41, the development of responding during the latter part of each cycle was more pronounced. Under the initial procedure when shocks were delivered every 60 seconds, the shock usually initiated a high rate of responding that ceased abruptly after a few seconds; a few more responses often occurred just before the next shock. As the session proceeded, the number of responses following shock tended to decrease while the number occurring just before shock tended to increase. After exposure to the added FI 30-second schedule, responding declined soon after an electric shock was delivered and then increased until the first response after 30 seconds produced the next shock. In most sessions, only the first electric shock of the session was delivered without a response. Again when shocks were omitted, little responding occurred. Under the FI 30-second schedule alone some responding was maintained, but the rates of responding were relatively low.

The performance of monkey S-58, trained from the beginning with the added FI 30-second schedule, is shown in Fig. 2. During initial exposure (Fig. 2A), responding was either sustained at a relatively high rate throughout each 30-second interval or occurred at a high rate following shock delivery and then at a relatively low rate until a response produced the next shock. Details of representative response patterns at the end of a session are shown in the paper tape record in Fig. 2A. With further exposure to the FI 30-second schedule, monkey S-58 tended to stop responding soon after shock and then to respond frequently just before a response produced the next shock at 30 seconds. This pattern of responding can be seen in detail in the paper tape record in Fig. 2B. Whereas responding always occurred after shocks in the earlier session, responding often did not occur after shock in the later session.

The present experiments question the need for a response to precede an event in order to be reinforced by that event. In the reinforcement of an operant, the reinforcer changes the subsequent occurrence of responses of the class that preceded the reinforcer. But in this situation, initially at least, the shock preceded the response. Is it not possible that a response or a pattern of responding elicited by an event, or occurring in close temporal proximity following the event, can also be strengthened as an operant?

The typical behavior in the situation in which a subject terminates a recurring shock by a response such as running or pressing a lever could be viewed in this way. For example, when a shock is scheduled to occur every 30 seconds and to continue until terminated by a response, the response that occurred after the onset of the shock will subsequently tend to occur preceding the shock. It is commonly arranged that the response preceding the shock then postpones the next scheduled shock (avoidance), thereby introducing further consequences that obscure the basic relationship; when responses have followed recurrent shock they tend to occur before the shock.

In this study, the first response occurring after 30 seconds was followed by an electric shock; responses during this 30-second interval had no programmed consequences. This schedule of shock presentation is formally comparable to fixed-interval schedules of food or water presentation (*7*). The fixed-interval patterns that developed in this study differed from fixed-interval patterns engendered in the squirrel monkey by the presentation of food or the termination of a schedule complex (*5*), especially in the rapid loss of responding in the absence of shocks. Though the performances were developed and maintained by the shock, two of the monkeys usually did not begin responding until a shock occurred. It has been reported that some elicited responses are not easily modified by consequent events (*8*), but in the present experiment the recorded response was changed in its temporal patterning by the fixed-interval schedule. Perhaps the change came about because the temporal patterning of responses is easier to change than their topographical characteristics, or because the pulling and biting following the shock have characteristics intermediate between elicited and operant behavior.

That electric shock can maintain responding when the only programmed consequence of responding is the scheduled presentation of electric shock is not incompatible with other known behavioral effects of electric shock. When an event following some response increases or decreases the subsequent occurrence of that response, it does not mean that the same event consequent on other behavior or presented under another schedule would necessarily modify the other behavior in the same way. Both the quantitative properties of the response preceding an event and the schedule under which the event is presented determine the effects of that event in further modifying behavior. Under other conditions, the electric shock used in the present study could maintain responding that terminated the shock or postponed its occurrence.

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