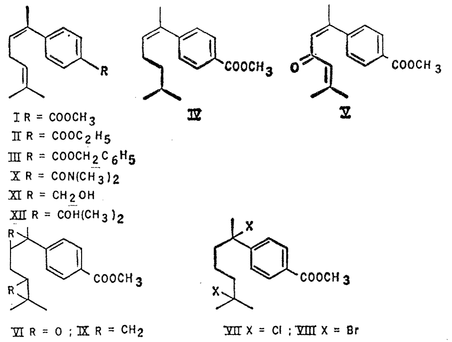

Fig. 1. Structural formulae of synthetic juvenile hormone analogs with specificity for *Dysdercus* spp.

dihalo derivatives VII and VIII, and the compound IX (Table 1). The unit values for the juvenile hormone activity of these compounds range from 0.01 to 0.1 μg per specimen. The least active compounds are X, XI, and XII, in which the carbomethoxy group of the benzene ring is replaced by alcohol or dimethyl amido groups. Their unit values range from 4 to 100 μg per specimen.

There is a close parallel in the juvenile hormone effects of each compound among the species of *Dysdercus* tested. There is less than a tenfold variation in the activity of a given compound from species to species. Variations in activity of different compounds on the same species differ by several orders of magnitude. This indicates that the structural changes of the molecule have much more pronounced effect on the activity than do endogenous factors of species specificity.

The most sensitive species is *D. chaquensis*, and the least sensitive is *D. intermedius*. Their average unit values differ by about 3.7-fold; however, there is about a 2.5-fold difference in size of the last-instar larvae of these species. For this reason we have calculated an average juvenile hormone activity unit on the basis of micrograms of substance per gram of larval weight, and this unit more precisely indicates the sensitivity of individual species (Table 2). Thus, the actual sensitivity of *Dysdercus* species to the juvenile hormone analogs decreases in the following manner: *D. chaquensis*, *D. cingulatus*, *D. discolor*, *D. superstitiosus*, and *D. intermedius*. Small variations in the activity units suggest that there are no profound species-specific differences in the sensitivity of *Dysdercus* bugs to the juvenile hormone analogs tested.

Earlier we determined the juvenile hormone activity of compounds I to IX on *Pyrrhocoris apterus* L. (*4*). The average juvenile hormone unit per gram of larval weight was about ten times larger than those found for the *Dysdercus* species (Table 2). All these compounds have been found inactive when tested on *Graphosoma italicum* Müll. of the family Pentatomidae. Thus, we expect that changes in insect sensitivity to these juvenile hormone analogs are rather insignificant at the species level, becoming more pronounced at the genus level, and extreme at the family level and higher. Similar relationships have also been found with other juvenile hormone analogs, for example farnesenic acid derivatives (*6*).

The compounds with the lowest unit values are potential pesticides with which it would be possible to prevent *Dysdercus* larvae from becoming sexually mature adults, or to sterilize adult females (*1*). So far as we know, these compounds are not toxic to insects in general and are specific for Pyrrhocorid bugs. They show no juvenile hormone activity on some representatives of Lepidoptera, Coleoptera, Diptera, or Hymenoptera. The low differences in their activity on these five *Dysdercus* species suggests that the compounds could be used against any *Dysdercus* species. The high juvenile hormone activity of these materials in topical assays indicates their superiority to the paper or wood extracts used in earlier experiments (*8*).

M. SUCHÝ
Institute of Organic Chemistry and Biochemistry, Czechoslovak Academy of Sciences, Prague

K. SLÁMA
Institute of Entomology, Czechoslovak Academy of Sciences

F. ŠORM
Institute of Organic Chemistry and Biochemistry

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Maintenance of Responding by Fixed-Interval Schedule of Electric Shock Presentation in Squirrel Monkeys

Abstract. *After stabilization of response rates engendered by a free-operant avoidance contingency, the lever-pressing of two squirrel monkeys was maintained for several months by a fixed-interval schedule of electric shock presentation. Initially, response-contingent shocks produced substantial increases in response rates. Continued exposure to the schedule resulted in a reduced overall rate accompanied by a change in the temporal patterning of responses. There was a pause in responding after most shock deliveries; the rate of responding then increased during the interval to reach a terminal value preceding shock presentation. Omission of shocks for part of the daily session led to higher rates of responding; the reintroduction of response-contingent shocks produced a lower overall rate and reinstated the temporal patterning of responding characteristic of the fixed-interval schedule.*

Punishment is usually defined as a procedure in which a noxious stimulus, such as a loud noise (*1*) or an intense electric shock (*2*), is made contingent on the occurrence of a specific response. There is some uncertainty, however, regarding the behavioral effects of a punishing stimulus. Although most experiments show that punishment decreases the future likelihood of a response, others indicate that response suppression is a temporary phenomenon or that a punishing stimulus may sometimes exert the paradoxical effect of maintaining a response which it follows in time (*3*). However, a noxious stimulus has been shown to affect (*4, 5*) patterns of responding differently depending upon the manner in which the stimulus is scheduled to occur and the sort of ongoing behaviors that precede its occurrence.

Responding can be established readily and then maintained indefinitely when each response delays the presentation of an impending electric shock; this contingency is the "avoidance" procedure. We now describe an experiment in which, after extensive avoidance training, the responding of squirrel monkeys was maintained for several months, and the sole consequence of responding was the periodic delivery of a brief, but intense, electric shock.

Two male squirrel monkeys (*Saimiri sciureus*), No. 7 and No. 9, served as subjects; each animal was restrained in a primate chair (*6*) during experimental sessions. Electric shocks were delivered through two brass plates that rested on a shaved section of the monkey's tail; electrode paste (EKG Sol) ensured a low-resistance electrical contact between the electrodes and tail. The shock source was 117 volts a-c at 60 cycle/sec; the current delivered to the electrodes through series resistors was 12 ma for 300 msec (*7*). The operandum was a Lehigh Valley Electronics (Type 1352) rat lever, situated within easy reach of the monkey; each depression of the lever closed a microswitch, and this event defined a response for recording purposes. The restraining chair was located in a ventilated, sound-shielded cubicle illuminated by a houselight; masking noise (75 db) was fed continuously through a speaker within the cubicle for the duration of each session. Experimental arrangements were controlled automatically by relays, stepping switches, and timers located elsewhere; responses and shocks were recorded by digital counters and a Gerbrands cumulative-response recorder.

During the first phase of the experiment, both monkeys were trained to respond by reinforcing successive approximations to the lever-press. Reinforcement consisted of interrupting, for 15 to 20 seconds, brief, inescapable shocks which otherwise occurred every 5 seconds. When both animals had acquired the response, a free-operant avoidance schedule (*8*) with a response-shock (RS) interval of 20 seconds and a shock-shock (SS) interval of 5 seconds was programmed for 72 consecutive sessions for monkey No. 7 and 69 consecutive sessions for monkey No. 9; each session lasted 125 minutes. A 12-ma 300-msec shock was presented at regular 5-second intervals (the SS interval) in the absence of a response; if a response occurred, however, the next shock was delayed for 20 seconds (the RS interval). Each response that was made reset the RS interval, thus permitting the animal to avoid shock presentation indefinitely; lever-holding did not avert shock.

The second part of the experiment began after the last session of avoidance training. The avoidance schedule was replaced by a fixed-interval (FI) schedule of electric-shock presentation. According to this new contingency, the first response to occur after 300 seconds had elapsed, timed from a preceding shock, produced a 300-msec shock (12 ma). If the animal did not emit a response within 15 seconds (after the end of the fixed interval) a shock of identical intensity and duration was presented independently of behavior, and the next interval began. Session length was determined by the number of cycles of the FI schedule to which the monkeys were exposed each day; for the first 55 sessions, each session ended after 20 cycles of the schedule had been completed. Session length was then increased to 30 cycles of the schedule per day for the remainder of the experiment.

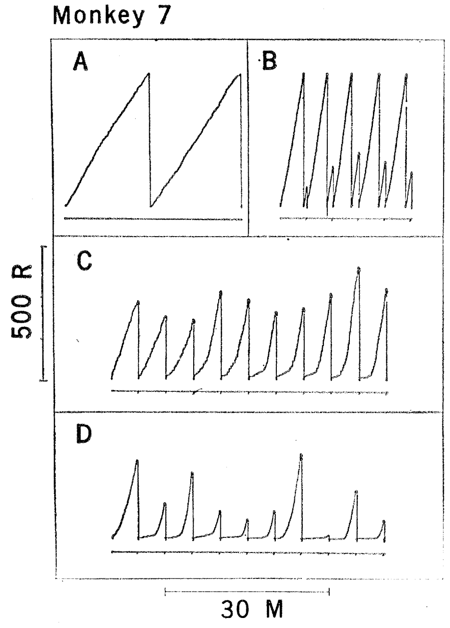

Fig. 1. Representative cumulative-response records at different stages of the experiment for monkey No. 7. (A) Session 70. Free-operant avoidance behavior; overall rate 0.57 response per second. (B) Session 2. Fixed-interval schedule (300-second) of presentation of shock; overall rate 2.02 responses per second. Cumulative response pen resets after 500 responses within any given interval; the pen was also reset at the end of each cycle of the FI schedule. Shocks are shown as diagonal deflections of the event pen beneath the cumulative record. (C) Session 20. Fixed-interval schedule (300-second) of presentation of shock; overall rate 0.77 response per second. (D) Session 70. Fixed-interval schedule (300-second); overall rate 0.38 response per second. After introduction of the FI schedule, high overall rates of responding were observed (B); repeated daily exposure to the schedule resulted in lower rates of responding (C) in which pausing followed shock delivery and a sustained rate usually preceded each shock presentation (D). Abbreviations: *R*, responses; *M*, minutes.

Figure 1 contains representative sections of cumulative-response records obtained from monkey No. 7 at several different stages of the experiment. Record A shows the typical pattern of responding after approximately 145 hours of avoidance conditioning. Shocks occurred infrequently at this stage, averaging 1.3 per session; during the 70th session, part of which is shown (Fig. 1A), one shock occurred, and the overall rate of responding was 0.57 response per second. Record B contains part of the cumulative record obtained during the second session in which monkey No. 7 was exposed to the FI schedule of shock presentation. Substantially higher rates of responding were observed during the initial sessions in which the schedule was first made operative as compared with preceding rates of avoidance responding (Fig. 1A). During session 2, monkey No. 7 responded at an overall rate of 2.02 responses per second; with repeated exposure to the FI contingency, rates of responding diminished gradually from session to session. Record C shows a portion of the cumulative record for the 20th session of conditioning. The overall rate of responding has been reduced considerably (0.77 response per second), and the temporal patterning of responses within each fixed interval has been modified significantly. Except for a brief burst of responses consequent upon shock presentation, the rate is generally low during the earlier part of the interval and then increases as the interval elapses to reach a terminal value preceding shock presentation.

Record D exemplifies the further development of changes in response patterning which occurred with continued exposure to the FI contingency; in most instances, the delivery of shock is followed by a cessation of respond-

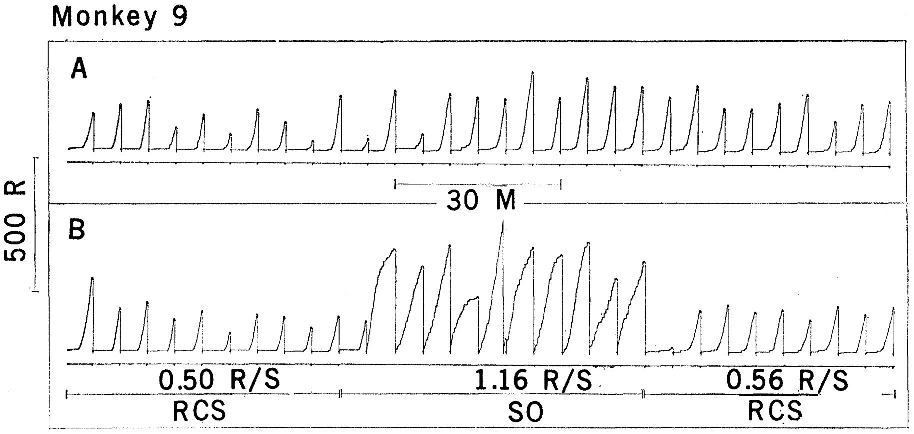

Fig. 2. Cumulative-response records showing performance engendered by the FI schedule of shock presentation and the effects of shock omission for monkey No. 9. (A) Session 93. Fixed-interval schedule; overall rate 0.59 response per second. (B) Session 94: Fixed-interval schedule with shocks scheduled to occur, as before, for the first ten cycles of the session (overall rate, 0.50 response per second). Shock presentations were omitted for cycles 11 through 20 of the schedule (overall rate, 1.16 responses per second) and then reintroduced for the remainder of the session (overall rate, 0.56 response per second). Shock omission produced higher overall rates of responding; the reintroduction of shock presentations reinstated a lower rate and the characteristic pattern of responding. Abbreviations: *M*, minutes; *R*, responses; *R/S*, responses per second; *RCS*, response-contingent shock; *SO*, shock omitted.

ing. When the monkey begins to respond it does so at a low but rapidly increasing rate until a terminal rate is attained preceding shock. The data shown in record D refer to performance during the 70th session of conditioning; the overall rate equaled 0.38 response per second, and, at this stage, rates of responding remained relatively constant although variation in the amount of responding from one interval to the next was a prominent feature of the behavior.

The FI pattern of responding has been consistently maintained in each monkey for 6 months; the development of responding in monkey No. 9 was similar to that for monkey No. 7. Shocks were found to occur only infrequently as a consequence of pauses exceeding 15 seconds at the end of any given interval. Of the total number of shocks delivered during 35 consecutive sessions, monkey No. 7 produced 98.99 percent, and monkey No. 9 produced 99.02 percent, respectively; thus, pauses in responding of sufficient duration to engender the presentation of a shock not contingent on a response were rarely observed. The extent to which responding can be maintained without an inevitable shock, should the animal pause at the end of the interval, has not been determined.

Figure 2 shows the performance of monkey No. 9 for two consecutive sessions of the FI schedule. In record A, the 93rd session, the overall rate was 0.59 response per second; the pattern of responding, maintained by response-contingent shocks, resembles closely that observed in monkey No. 7 (Fig. 1D). Monkey No. 9 produced each shock that was delivered during this session. Record B shows the performance of the same animal the following day. For the middle portion of this session, however, shocks were omitted, that is, for the first ten cycles of the FI schedule, shocks were programmed to occur as before; shock presentations were then omitted for the ensuing 10 intervals (a period approximately 50 minutes long) and were reintroduced subsequently for the remainder of the session. Initially, the overall rate equaled 0.50 response per second. Shock omission led to a substantially higher rate (1.16 responses per second) which was maintained until shock deliveries were reintroduced. In the latter part of the session, after the reintroduction of shock, the overall rate equaled 0.56 response per second, and the characteristic pattern of responding was reestablished. The effects of brief periods of extinction (shock omission) within the experimental session were observed on ten separate occasions (monkey No. 9); in each case, increased rates of responding have accompanied the omission of shocks. (Low overall rates of responding have been observed, however, whenever shock presentation has been omitted for longer periods, that is, an entire session.) A possible explanation for the higher rates of responding, consequent upon shock omission, pertains to the known discriminative properties of shock (*9*) as a stimulus contingent upon responding: to omit shock is to remove a discriminative stimulus customarily associated with the end of one interval and the start of the next. Perhaps the higher rates of responding, after shock omission, can best be understood in terms of the monkey's inability to reinstate the distinctive stimulus conditions which normally prevail during or immediately after shock presentation; this hypothesis calls for further investigation.

Our observations support the view that a noxious stimulus affects patterns of responding differently depending upon the manner in which the stimulus is scheduled to occur and the nature of the ongoing behaviors which precede its occurrence. That a fixed-interval pattern of responding can be maintained by response-contingent electric shocks is not necessarily at variance with other known behavioral effects of electric shock (*5*). For example, Hake, Azrin, and Oxford (*10*) reported an experiment in which responding in squirrel monkeys was maintained by a variable-interval schedule of food presentation. Concurrently, punishment consisting of a brief electric shock followed each response. By gradually increasing the intensity of the punishing stimulus, it was possible to produce response rates that reflected only partial suppression. If comparable intensities of shock were used initially, however, a severe and relatively persistent suppression of responding was observed. This kind of effect exemplifies an important principle—as behavior is modified by a particular stimulus, the effectiveness of that stimulus in producing subsequent modifications of behavior is also altered. The effectiveness of a specific stimulus, such as an intense electric shock, is not invariant but depends upon ongoing patterns of responding; Hebb (*11*) advocated a similar view, in neuropsychological terms, regarding the central effects of painful stimulation.

R. Stretch*
E. R. Orloff*
S. D. Dalrymple†
Department of Psychology, University of Alberta, Edmonton, Canada

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* Present address: Department of Psychology, University of Western Ontario, London, Ontario.

† Present address: Department of Pharmacology, Harvard Medical School, 25 Shattuck Street, Boston, Massachusetts 02115.

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Pineal Gland: Influence on Development of Copulation in Male Rats

Abstract. *Male rats reared in constant darkness, pinealectomized 3 days after birth, and tested for copulation starting at 24 days of age, mounted receptive females more frequently and showed pelvic thrusting at an earlier age than littermate controls.*

Early investigations (*1*) suggesting an inhibitory influence by the mammalian pineal gland on development of the genital system have been subsequently supported. Pinealectomy soon after birth produces an increase in the weights of the ovaries in the maturing female rat (*2*). Long-term administration of small doses of melatonin, a pineal hormone, to immature female rats decreases the weights of the ovaries, diminishes the incidence of estrus as judged by vaginal smears (*3*), and delays vaginal opening (*4*).

The inhibitory influence of environmental darkness on gonadal function in both male and female rodents is somehow mediated by the pineal gland (*5*). Normal development of testes and accessory organs is inhibited in maturing male rats whose eyes are removed, but this effect is blocked in blind subjects pinealectomized at 3 days of age (*6*). These experimental results suggest that, as in genital development, the development of male sex behavior in light-deprived animals might be hastened or accentuated by neonatal pinealectomy.

Male, hooded rats (Royal Victoria Hospital strain), born in total darkness within 14 consecutive days, served in the experiment performed from June to October 1967. Three days after birth, 16 male pups were pinealectomized, and 21 littermate males received sham operations (*6*). Littermates were reared with their mothers until they were weaned at 21 days of age and were then housed two or three males to a cage. All animals were reared in the dark except for short behavioral testing periods under a 15-watt incandescent lamp.

Each subject was observed for 10 minutes in a semicircular Plexiglas box on alternate days beginning at 24 days of age. During a test the male was presented with a behaviorally receptive female (*7*) of comparable age and weight, and the number of mounts by which the male elicited a lordosis response in the female was recorded. The age of the male at initial occurrence of pelvic thrusting without actual intromission of the penis into the female vagina and, subsequently, the age at initial intromission were also recorded. When a male intromitted, the test was terminated before more intromissions occurred. At weaning, nine pinealectomized males and 17 sham-operated males had been randomly chosen for mating tests after initial intromission. These tests (*8*) began 2 days after a male first intromitted with a female and continued on every 4th day, except when a male failed to ejaculate during a test. In the latter case an animal was tested on alternate days until he ejaculated, whereupon the regular 4-day interval between tests was reinstated. Again a receptive female was placed with a male for 10 minutes. If he intromitted during this period, he was allowed 30 additional minutes to ejaculate. A test was stopped after one ejaculation, and animals received approximately 20 mating tests. Both the age at which a male first ejaculated and the age at which an animal first copulated in "adult" fashion (ejaculated after no more than 15 intromissions) were recorded (*8*).

Pinealectomized males between 24 and 42 days of age (Fig. 1) mounted receptive females more frequently than sham-operated males ($F = 5.44$; d.f. $= 1/35$; $P<.05$). In subsequent tests (not shown) the group difference for males not yet intromitting gradually disappeared. Males in both groups mounted more frequently as they grew older. In conjunction with the increased mounting behavior, pinealectomized animals also showed pelvic thrusting toward receptive females at an earlier age than sham-operated controls. Fourteen out of 16 pinealectomized males initially showed the response at a median age of 32 days, whereas 13 out of 21 sham-operated animals showed the response at a median age of 49 days (two-tailed Mann-Whitney, $U = 46$, $P < .05$). Two pinealectomized and eight sham-operated males achieved initial intromission without showing earlier pelvic thrusting. Neonatal pinealectomy seemed to affect early components of the developing sex response in light-deprived males, but

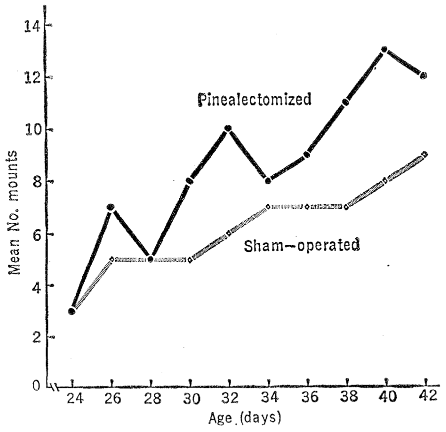

Fig. 1. Frequencies with which 16 pinealectomized and 21 sham-operated male rats mounted receptive females. Observations began when males were 24 days of age and continued on alternate days. Intromissions began to occur at 44 days in some subjects thereby ending this part of the testing for these animals. After 42 days the group difference in mount frequency for males not yet intromitting gradually disappeared (not shown).