

taste quality reaction time (16). In addition, when humans are presented NaCl or sucrose solutions for 700 to 800 msec, they receive enough information to quantitatively estimate concentration (17).

Most neurophysiological models of taste quality categorization and of gustatory receptor kinetics (2, 7) have not systematically utilized the activity from the early phasic response period. It is well known in other sensory systems that the transient or phasic portions of activity are most important, and incorporation of these behaviorally relevant temporal properties of gustatory response into such models may produce an improved understanding of taste and other sensory systems.

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10. The observed rapid cessation of licking is thought to depend on gustatory afferent input for several reasons. First, complete absence of licking during a presentation occurred less than 8 percent of the time, and was found equally often for water and the NaCl solutions. Thus, contact of the tongue with the liquid was necessary for further licking to be withheld. Second, duration of an initial licking burst to an aversive solution never exceeded 800 msec, but the latency of a vertebrate olfactory primary neuron response is 1 to 2.8 seconds. Thus, olfactory afferent input would not occur until several hundred milliseconds, or more, after the licking burst had ended [R. J. O'Connell and M. M. Mozell, *J. Neurophysiol.* **32**, 51 (1969)]. Third, the general vapor phase environment of the drinking tubes was made relatively homogeneous by locating the tubes close to each other.
11. Licking was done by extending the snout through a single opening 1 cm in diameter. The two stainless steel drinking tubes were alternately positioned 2 mm outside this opening by an automatic mechanism. The tubes were fixed so that the nonpresented tube was 2.2 cm above or below the presented tube at all times. Between presentations, access was prevented by an automatic shutter. The lickometer circuits were Grason-Stadler E4690A-Z1 Rev. O, which passed less than 1 μ A through the animal.
12. Each animal must consume at least 80 percent as much water at each presentation as it consumed on the day prior to conditioning. Its PCS consumption must be less than 15 percent of water consumption for each of the six consecutive water-PCS presentation pairs. Radiation-induced gustatory avoidance of NaCl (140 mM) has previously been reported [N. W. Perry, Jr., *Radiat. Res.* **20**, 471 (1963)].
13. The first licking burst of each period was considered ended when an interlick interval of 200 msec, or of twice the median interlick interval of the first five licks with intervals less than 200 msec, whichever was greater, occurred. A "pause" in 10-minute licking periods, in which the interlick interval was 150 ± 15 msec (mean \pm standard deviation), has been defined as 200 msec [J. D. Corbit and E. S. Luschel, *J. Comp. Physiol. Psychol.* **69**, 119 (1969)].
14. The volume of individual licks was measured by dividing the total number of licks into the total volume consumed. A value of 5 ml had been previously reported [E. Stellar and J. H. Hill, *J. Comp. Physiol. Psychol.* **45**, 96 (1952)].
15. The latency for rat chorda tympani single unit responses to gustatory stimulation with sucrose has been reported to be as long as 300 msec (3) or as short as 90 msec [M. S. Nejad, "Factors involved in the mechanism of stimulation of gustatory receptors and bare nerve endings of the tongue of the rat," Ph.D. thesis, Florida State University (1961)]. Experiments using a digitalized summator with 10 msec integrating intervals to discretely analyze chorda tympani population responses, and a calibrated reflection phototransistor to determine liquid contact with the tongue, indicate a latency of 60 msec; J. R. Faull and B. P. Halpern, in preparation. For digitalized summator, see A. D. Brush and B. P. Halpern, *Physiol. Behav.* **5**, 743 (1970); for calibrated phototransistor, see (4). Visual stimulus presentations of 50 msec are still being processed 100 msec or more later. See U. Neisser, *Cognitive Psychology* (Appleton-Century-Crofts, New York, 1967), pp. 15–27.
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Melatonin: Effect on Punished and Nonpunished Operant Behavior of the Pigeon

Abstract. Intramuscular injections of melatonin had a dose-dependent, rate-increasing effect on responding maintained by a fixed-interval schedule of positive reinforcement. When a punishment contingency was added to the fixed-interval schedule, the overall rates were not increased although responding was increased during the initial part of each interval.

Melatonin, a major constituent of the pineal gland (1), has effects on many endocrine systems (2, 3). In addition, systemic or intracerebral administration of melatonin to cats or systemic administration to young chickens produces sleep and corresponding changes in the electroencephalogram (4). A slight decrease in motor activity occurs after administration of low doses to rats (5). In a study of the central metabolic effects of melatonin (6), both increased and decreased levels of serotonin were found after intraperitoneal injection. The direction of the change was dependent upon the brain region sampled. This finding and the experimental work implicating serotonin in the mechanism underlying sleep production (7) have led to the suggestion that serotonin derivatives found in the pineal gland readily gain access to the central nervous system where they modify the function of serotonin-containing neurons (3).

In the following experiments I have studied the effect of melatonin on punished and nonpunished key-pecking behavior of the pigeon. It has thus been possible to determine the behavioral effects of melatonin in situations in which a wide variety of compounds has

been studied (8). The present study also makes possible a comparison of the behavioral effects of melatonin with those of agents presumed to alter the function of central neurons containing serotonin, since punished and nonpunished schedules of reinforcement have been previously utilized to study the behavioral effects of serotonin agonist and antagonist drugs (9).

Eight adult, male, White Carneaux pigeons were housed in individual cages and maintained at 80 percent of their free-feeding weights. All birds had been previously trained and used in drug experiments. Four birds were trained on a multiple fixed-interval 5-minute fixed-ratio 30-response schedule (multiple FI 5 FR 30) and the other birds were trained on a concurrent fixed-interval 5-minute (food) fixed-ratio 30 (shock) schedule (concurrent FI 5 FR 30).

The experimental chamber was similar to that described by Ferster and Skinner (10). A translucent key, 2 cm in diameter, was mounted in the partition wall of the chamber facing the animal compartment. The key could be transilluminated with lights of different colors. The minimum force required to operate the key was about 15 g. A rectangular opening below the response

key gave occasional access to the feeder. The animal compartment was illuminated by a 25-watt bulb in series with a resistance of 300 ohms. White noise was continually present.

The multiple FI FR schedule has been described in detail elsewhere (10). When the response key was transilluminated with a red light, the first peck after 5 minutes was reinforced with 3 seconds of access to the food magazine (FI 5). In the presence of a blue light the 30th response was reinforced (FR 30). If no response occurred within 60 seconds of the end of a 5-minute interval or if 30 responses did not occur during 60 seconds under the FR 30 schedule (1-minute limited hold), the schedule automatically switched to the next component. The FI and FR components alternated. After a sequence of one FI and one FR a time-out period of 0.5 minute occurred during which both the key and house lights were off and responses had no programmed consequences. Each session ended automatically after 20 cycles.

The concurrent FI FR schedule employed in the present experiments has been described by Wuttke and Kelleher (11). In the presence of a white key light the pigeons responded under a FI 5 schedule of food presentation as described above. In addition, every 30th response produced an electric shock (3 ma for 200 msec, 650 volts, 60 hertz) administered through gold wire electrodes implanted around the pubic bones. The electrodes were attached to a permanent leather harness (12). During the experimental session a jack was attached to a plug in the harness. The jack was connected to a swivel mounted in one of the side walls of the chamber by means of flexible electric wire, permitting the bird to move freely inside the experimental box. A 1-minute limited hold terminated the FI 5 automatically when the pigeon did not respond after the 5-minute period. A 0.5-minute time-out (TO) period occurred after each FI. The experimental session was composed of a sequence of 20 cycles (FI 5 TO 0.5).

The experiments were conducted daily from Monday through Friday. Melatonin (Regis Chemical Co., Chicago) was dissolved in warm distilled water (13) and administered (intramuscularly) immediately before the daily session on Tuesday and Friday. The Thursday session was used for control data.

The pattern of responding generated by the multiple FI FR schedule was

Table 1. Effect of melatonin on punished responding during first and last half of each fixed interval.

Dose (mg/kg)	Number of key pecks			N*
	First halves of intervals	Last halves of intervals	Total	
Control	35 (30-40)†	306 (280-334)†	341 (310-374)†	6
1	117	218	335	3
3	140	234	374	3
10	78	93	171	3

* Number of observations. † Mean number of responses (and range).

typical of these schedules (10). During the FI component responding was very low in the initial part of the interval and then rapidly accelerated to a high rate that was sustained until reinforcement. In the FR component a short initial pause of a few seconds' duration was followed by responding at a high constant rate (Fig. 1).

The administration of 0.1 to 3.0 mg of melatonin per kilogram produced an increase in the response rate during the FI component, most noticeable in the initial portion of each interval (Fig. 1). It should be noted that even after a 0.01 mg/kg dose a tendency for responding to be elevated during the first few intervals of each session was observed, but, owing to the brief duration of this effect, the overall rate was not

elevated above the control range. This may be because of the short half-life of melatonin in the blood (14). No change in the response rate during the FR component was observed until after the highest dose of melatonin (10 mg/kg). At this point both FI responding and FR responding were decreased. The effect of melatonin on multiple FI FR performance is similar to the effect of the serotonin antagonists previously studied (9) in that these compounds also produced dose-dependent increases in the FI response rate and then decreased responding in both components at higher doses. With the serotonin antagonists, however, a slight increase in FR responding was also noted.

In contrast to its effect on the FI component of the multiple schedule,

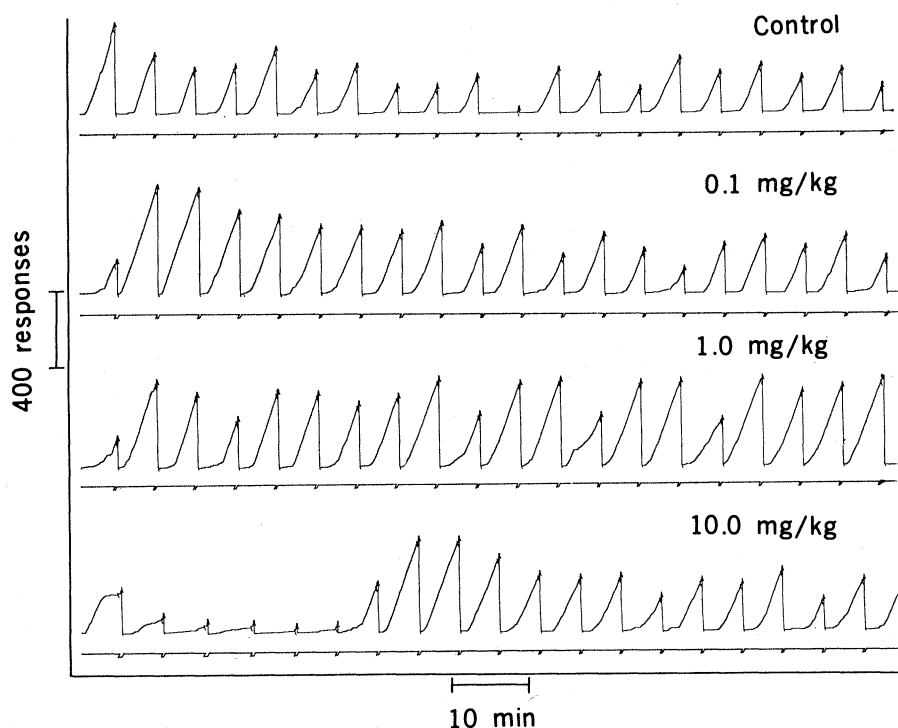


Fig. 1. Representative cumulative records of performance of one pigeon (No. 176) on the multiple FI 5 FR 30 schedule during control session and after various doses of melatonin (intramuscularly) immediately before the session. Key-pecking responses were cumulatively recorded by upward movements of the recording pen; resetting to base line occurred after completion of the FR component. Vertical deflection of the recording pen indicates food reinforcement. Vertical deflection of the event pen indicates duration of the FR component. Note shorter initial pause in FI components after melatonin.

melatonin did not increase the overall rate of responding during the punished FI (Table 1). Again, however, there was a noticeable increase in responding during the beginning of each interval (Table 1) even though responding was slightly suppressed at the end of each interval.

The behavioral effects of melatonin differ from those of other compounds whose effects on punished and nonpunished behavior have been studied. Several drugs which can produce sleep, including barbiturates and benzodiazepines, are able to increase both nonpunished and punished FI response rates (8, 11). It is not inconsistent that melatonin administration, which has been reported to induce sleep, should be followed by increased responding on a nonpunished FI schedule. Since melatonin did not increase the overall rate of responding during the punished FI, it can be distinguished from these sedative drugs. Imipramine, *d*-amphetamine, and phenothiazine derivatives can also increase nonpunished responding, but appear only to enhance the suppressant effect of punishment (11, 15).

A comparison of the effects of melatonin on key-pecking behavior with those, previously reported (9), of the two serotonin antagonists, methysergide and bromolysergic acid, and those of the serotonin agonist, alpha-methyl-tryptamine, further indicates the uniqueness of melatonin. The two antagonists increased the overall rate of responding during both punished and nonpunished schedules, while the agonist had only rate-decreasing effects. It would appear that the behavioral effects of melatonin are not simply due to its mimicking or antagonizing the action of serotonin.

The present study demonstrates that the peripheral administration of melatonin produces effects on behavior which vary with the schedule of reinforcement. These results are consistent with the proposal that serotonin derivatives found in the pineal gland can modify central nervous system function and support a role for the pineal in the modulation of behavior.

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Maternally Derived Transferrin in Pigeon Squabs

Abstract. *With the use of genetically marked transferrin, a major portion of circulating transferrin from a newly hatched squab was found to be derived from the mother through the egg. The transfer is not through the parental crop milk. The squab does not accumulate enough transferrin of its own making to be detectable until it is about 8 days old. The maternally derived protein remains detectable until 14 days after hatching. The squab actively synthesizes a portion its own transferrin from hatching onward.*

Transferrin is a nonheme iron-binding protein (1) that is widely distributed throughout the chordates from lamprey to man (2). One of its principal functions is the transport of iron to reticulocytes for incorporation into hemoglobin (3). It may be important in nonspecific resistance to disease, as well as for its iron transport function. Transferrin has been found to be polymorphic in most species, the products of different alleles usually differing in electrophoretic mobility (4).

Although the development of transferrin has been studied in several mammalian species, including mouse, rabbit, and man (5), I am not aware of any reports on developmental studies of transferrin in birds. In mammals, there is very little transport of transferrin to the developing fetus (6); in this, transferrin differs from certain immunoglobulins, which are known to be transported intact to the embryo.

Pigeons have been shown to be polymorphic at a transferrin locus, and have only two reported variants, Tf^A and Tf^B (7). The alleles are inherited as autosomal codominants, and in populations so far examined they are present in nearly equal frequency. Transferrin is found in the pigeon blood, egg white, egg yolk, crop milk, and probably in the semen. In all these fluids it is under the control of the same gene. In pigeons,

which differ in this respect from chickens (8), the electrophoretic mobility of transferrin in all these fluids is identical. In this report, therefore, transferrin derived from egg white will not be distinguished by the specific term ovotransferrin, which is often used.

Pigeons (*Columba livia*) were maintained in the laboratory in mating cages (1 pair per cage) or in large fly-pens. Eggs were checked daily and the day of hatching was designated as day 0.

For adults and squabs over 4 days old, when more than 0.5 ml of blood was to be removed, the birds were bled from the brachial vein by syringe and needle. The blood was allowed to clot and the serum was collected. For younger birds, blood was collected directly onto filter paper for electrophoresis. In order to determine whether this would give consistent serum patterns, several squabs were killed by exsanguination and their serums were collected. The results for collection by filter paper and by syringe were identical.

Transferrin typing was carried out on horizontal starch gels by the use of tris-citric acid buffer (pH 7.5) in the gel and borate buffer (pH 8.7) as electrolyte (9). An ice pack was placed on top of the gel to prevent excessive heating; the gels were stained with Coomassie blue.

Antibodies to pigeon transferrin were