Table 2. Photosynthetic yields under completely natural conditions compared with yields computed from light- and dark-bottle data (see *13*).

Time interval	Rate of photosynthesis ($mm/m^2/day$)*		
	Under natural conditions		Computed from bottle data
	Net	Gross	Gross
17 June–18 July	225	450	187
19 July–22 August	288	576	242

* The difference between 225 and 288 is not statistically significant with the number of samples used (14 in each period), but the differences between 450 and 187, 576, and 242 are significant beyond the 1 percent level.

photosynthetic rate by doubling the observed diurnal net rate, for the respiration rate indicated by the nocturnal CO_2 gain must continue throughout the daylight hours.

Table 2 shows the average daily CO_2 uptake, net and gross, computed in this way and compared with daily gross yields estimated from light- and dark-bottle data. Note that the diurnal net yields exceed the gross yields computed from the bottle data. It is evident that enclosing the aquatic community in bottles reduces photosynthetic activity to less than half that maintained under natural conditions (*8*). One factor which may contribute importantly to the reduced rates in bottles is the greatly reduced turbulence. Eddy diffusivities in western Lake Erie in summer are of the order of 25 cm^2/sec; this must be at least 10^4 times greater than the values for unagitated bottles.

Photosynthetic rates for terrestrial plant leaves have usually been measured by determining CO_2 absorption from an air stream passing through a leaf chamber. The highest rates of air flow routinely used have been about 2.5 lit. of air per square centimeter of leaf per hour (*9*). Heinicke and Hoffman (*9*) state that they chose a flow rate of 2.5 lit./cm^2 hr because they observed that a hydroxide surface when exposed to such a flow rate absorbed CO_2 at the same rate as did a hydroxide surface standing open in the room. Such a flow rate, therefore, represents conditions of air turbulence much quieter than those prevailing outdoors.

Heinicke and Hoffman observed an increase in photosynthetic rate (in apple) from 22.1 to 30.8 mg of CO_2 per square decimeter per hour when they increased the rate of air flow from 2.5 to 7.5 lit./cm^2 hr, although the CO_2 content of air at this flow rate did not fall below 80 percent of that in normal air. More recently Burnside (*10*) observed that increasing the flow rate from 1 to 6 lit./cm^2 hr increased the photosynthetic rate (in cotton, and sunflower) from 20 to 37 mg/dm^2 hr. Most of the maximum yields in Rabinowitch's (*11*) Table 28.VI are less than 20. The rates reported by Russian workers represent notable exceptions. Kursanov's rate for *Pyrus malus* is 35, closely similar to the rate obtained by Heinicke and Hoffman with their high flow rate. Perhaps the higher yields reported by Russian workers reflect higher turbulence in their leaf chambers. A relation of photosynthetic rates to eddy diffusivity in leaf chambers might contribute to our understanding of the problem. Verduin (*12*) has published some computations of probable CO_2 concentrations within leaf chambers, but we have found no quantitative study of eddy diffusivity in leaf chambers.

It seems likely that most of the maximal terrestrial photosynthetic rates appearing in the literature are considerably lower than the maximal rates attained under completely natural conditions; the reduced turbulence of the medium in the experimental apparatus may be primarily responsible for the reduced rates.

JACOB VERDUIN
E. ELOISE WHITWER
BRUCE C. COWELL

Biology Department,
Bowling Green State University,
Bowling Green, Ohio

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7. This computation is made as follows:

$$\underset{(cm/sec)}{2 \times 10^{-3}} \times \underset{\text{Concn. difference across boundary layers}}{13 \times 10^{-6}} \times \underset{\text{Partition coeff.}}{0.8} \times 10^4\ (cm^2/m^2) \times 4.3 \times 10^4\ sec/12\ hr$$

8. J. H. Ryther, C. S. Yentsch, E. M. Hulburt, R. F. Vaccaro, *Biol. Bull.* 115, 257 (1958). This study represents only 2 days' work. On both days the diurnal net rate under completely natural conditions exceeded the rate observed in bottles. This finding suggests that diurnal respiration rates may exceed the nocturnal rates.
9. A. J. Heinicke and M. B. Hoffman, *Cornell Univ. Agr. Expt. Sta. Bull. No. 577* (1933).
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13. A sample computation from bottle data is as follows:

$$\underset{\substack{(mm/m^2/hr)\\ \text{Optimal light}}}{4.8} \times \underset{\substack{\text{Ratio of optimal value to av. in euphotic zone}}}{0.65} \times \underset{\substack{(m)\\ \text{Depth of euphotic zone}}}{5} \times \underset{\text{Hours of daylight}}{12}$$

26 February 1959

Magnitude of Reinforcement and Consummatory Behavior

Abstract. The rates at which white rats licked saline, sucrose, and saccharin solutions, respectively, were measured by cumulative recording of tongue contacts with the solution in question. The local rate of licking was constant for all solutions, but differences in the distribution of sustained periods of licking were related to the type and concentration of the fluid consumed.

In place of Hull's (*1*) original associative interpretation, Spence (*2*) has recently argued for a motivational theory of the effects on behavior of different reward magnitudes. Spence bases part of his argument upon empirical data collected in his own and other laboratories. But greater attention is given to indirect evidence derived from a theoretical analysis of runway behavior. According to this theory, part of an animal's consummatory behavior in a goal box becomes conditioned to stimuli in that goal box, and ultimately, through generalization, anticipatory goal responses (r_g) are elicited by stimuli in the runway. When s_g represents feedback stimulation from the response r_g, the mechanism r_g-s_g is said to maintain running in the alley. In particular, this r_g-s_g mechanism is assumed to possess motivational properties "that vary with the magnitude or vigor with which it occurs" (*2*, p. 135).

Whether or not this assumption is necessary is not certain (see *3*), but it is inadequate as stated, owing to the ambiguity of the term *vigor*. The vigor of a response might, for instance, refer to the magnitude, or strength, of the response —that is, the amount of effort that goes into a single occurrence of that response; it might refer to the rate at which that response occurs (when it does occur); or it might refer to the persistence of that response in competition with other responses. Thus, *vigor* might refer to the intension, tempo, or perseveration of a response, or to any combination of these and other response dimensions (*4*). Only the first and second of these dimensions appear to have been considered by Spence—that is, he questions whether different magnitudes of reward produce different r_g's in terms of strength or intension (*3*, p. 137) or whether the effect is on the tempo of a single r_g (*2*, p. 147), and, with some reservations, he concludes that the second alternative is correct—on the basis of experiments reported by Guttman (*5*) and by Sheffield, Roby, and Campbell (*6*). However, neither of these studies is pertinent, because although they show that different reward conditions lead to different operant and consumption rates, there is no indication whether these were due to the tempo, perseveration, or latency of the consummatory behavior. That is, the consummatory response may have oc-

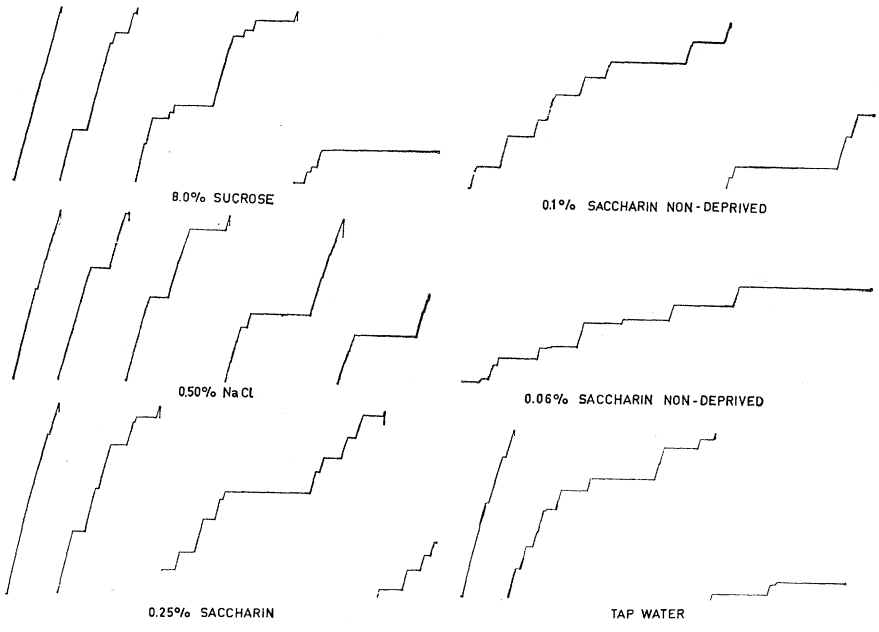

Fig. 1. Cumulative curves of the response of one animal given access to the six fluids indicated. Unless otherwise indicated the animal had been deprived of water for 23½ hours prior to the test. Each full excursion of the pen represents 1000 licks, and each graph represents 30 minutes of drinking. Thus, for example, when the deprived animal was offered 0.50-percent NaCl, it made approximately 4500 tongue laps in a 30-minute period.

curred more slowly (when it did occur) with smaller rewards rather than larger ones; it may have occurred at the same tempo but less often in the sense that more, or longer, pauses intervened between sequences of consummatory responses; or it may have begun at different latencies after the reinforcing solutions became available.

Despite Spence's contention to the contrary (*2*, p. 144), it is possible to measure consummatory behavior directly in a Skinner-box situation. This method, first employed by Kappauf and later by Stellar and Hill (*7*), has been utilized by one of us to record the drinking behavior of white rats when presented with various concentrations of sucrose, saccharin, and sodium chloride in distilled water solutions.

The apparatus was a 15- by 6- by 6-in. compartment wired so that a small current (less than 1 μa) flowed each time the animal's tongue made contact with the fluid under test. This current was amplified sufficiently to operate a relay which activated a Gerbrands-type cumulative recorder. Each lick of the fluid from a drinking tube with a 3-mm opening, which protruded into the cage, advanced the pen one step across the recording paper, with the result that a curve directly reflecting the rate of consumption of the fluid in the tube was automatically produced. The apparatus was installed in a large darkened and sound-shielded room. None of the noises of the apparatus were audible to the human ear from inside the room.

Each one of four rats of the Sprague-Dawley strain was tested with all of the solutions used in the experiment. The animals were first adapted for 10 days to a 23½-hour drinking rhythm, with access to tap water for ½ hour out of each 24 hours. The sodium chloride tests were then run for ½-hour sessions, with 2-day intervals between the test sessions. For the 2 days following each test day the animals were given only tap water to drink, so as to equalize as far as possible the degree of water deficit prior to the tests. If, for example, on a test day a large quantity of the proffered fluid was consumed, the tap-water intake on the following day was reduced. It has been observed, however, that by the third day following a large intake the amount of tap water consumed is about the same as that normally consumed by a rat that has been deprived of water for 23½ hours. The concentrations of the sodium chloride solutions employed were 0.50, 0.86, 2.0, and 3.0 percent, respectively. All the solutions used were percentage (weight/volume) preparations in distilled water. At the end of the sodium chloride tests the same procedure was followed with saccharine and sucrose solutions, in that order. After the licking rates for these solutions for water-deprived rats had been determined, the saccharin series was repeated when the animals had been sated with food and water.

The results in all cases were clear-cut; the local rate of drinking an acceptable solution was constant for each animal. If an animal drank all, it drank at a constant rate, regardless of its state of deprivation and the concentration of the solution under test. Figure 1 presents typical examples of all the records collected and shows some of the licking curves for one of the animals given access to tap water, 0.50-percent sodium chloride, 0.25-percent saccharin, and 8.0-percent sucrose, respectively, when water-deprived and to 0.6-percent and 0.10-percent saccharin when satiated. The curves that were produced by the other three animals are identical with respect to the major characeristic performance.

Although Gilbert (*4*) reports individual differences in tempo of bar pressing, no such differences in licking rates were observed in these studies. The local rates of responding remained between five and six licks per second for all animals under all conditions. Variations in the total amount of intake were a function solely of the duration of the pauses and the lengths of the sustained drinking periods. That is, differences in quantities of liquid consumed per unit of time represent not, as Spence (*2*) appears to believe, differences in the tempo of the consummatory response but differences in the perseveration of that response.

It seems clear, then, that the tempo, although not necessarily the intension (*4*), of the consummatory response must be ruled out as a determiner of instrumental performance with different reinforcing stimuli. If some characteristic of the consummatory act itself is to be used to account for these differences, perseveration seems the most likely, in our current state of knowledge (*7*). Although the local rate of licking is a constant, independent of individual subject differences and the chemical composition of the fluids investigated in this study, other dimensions of the licking operant are not. Latency, perseveration, and duration of the operant may all vary with differing test fluids, as Gilbert (*4*) has demonstrated with another operant. An investigation of the dimensions of the consummatory operant would appear to be necessary before an adequate explanation of the effect of the quantity or quality of a reinforcing substance on instrumental behavior can be given. Clearly the amount of reward substance consumed per unit of time is too coarse a measure. It does not describe how the substance is consumed. It tells nothing about the temporal distribution of pauses, about the duration of sustained periods of drinking, or about the rate of drinking when it occurs (*8*).

JOHN D. DAVIS
J. D. KEEHN
Department of Psychology,
American University of Beirut,
Beirut, Lebanon

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6 March 1959

Control of Oöcyte Development in Cockroaches

Abstract. Development of ovarian eggs and secretory activity of colleterial glands are inhibited by the oötheca in the oöthecal chamber of *Blattella germanica* (L.) and by the oötheca in the uterus of *Pycnoscelus surinamensis* (L.). The inhibition is due to nervous stimuli from pressure of the oötheca. Removing the oötheca or severing the ventral nerve cord eliminates inhibition of the *corpora allata* and results in premature development of the oöcytes and resumption of activity of the colleterial glands.

Oöthecal eggs in the uterus of the cockroach *Leucophaea maderae* (Fab.) are said to release a substance which causes the brain to inhibit secretion of the *corpora allata* and, thus, maturation of oöcytes (*1*). Differences in ovipositing behavior among various species of cockroaches (*2*) indicate that this mechanism would operate only in species carrying their oöthecae internally throughout embryogenesis.

Blattella germanica carries its oötheca externally during embryogenesis, and the oötheca inhibits development of the oöcytes and secretion of the colleterial glands. Removal of the egg case from the female results in an increase in the rate of oötheca production (*3*). The oötheca is carried an average of 30 days (*4*). During this time the oöcytes increase in length only slightly, from 0.34 to 0.52 mm. Ten days after the first oötheca is dropped the oöcytes have grown to an average length of 2.55 mm, and a second oötheca is formed. The *corpora allata* were shown to be necessary for development of the oöcytes of *B. germanica*; allatectomized adult females did not oviposit. Implantation of *corpora allata* into allatectomized females resulted in oviposition within 2 weeks. An allatectomized female with four implanted *corpora allata* produced three oöthecae in 61 days; another produced four in 58 days. When imitation wax "oöthecae" were inserted into the oöthecal chamber of adult females 1 day old or less, the oöcytes remained undeveloped. When the ventral nerve cord was severed in a female carrying an oötheca, the oöcytes grew rapidly and colleterial glands accumulated secretion in spite of the presence of an attached oötheca [Fig. 1 (1 and 2)]. Nineteen females from which oöthecae were removed 3 to 5 days after oviposition formed new oöthecae in 19.8 ± 0.5 days (*5*). Similarly, 11 females whose nerve cords were cut 3 to 5 days after oviposition formed new oöthecae in 19.5 ± 0.5 days. The original oötheca may adhere to the new one, as shown in Fig. 2. One female with a severed nerve cord formed four oöthecae over a period of 82 days, essentially doubling the rate of oöthecal production.

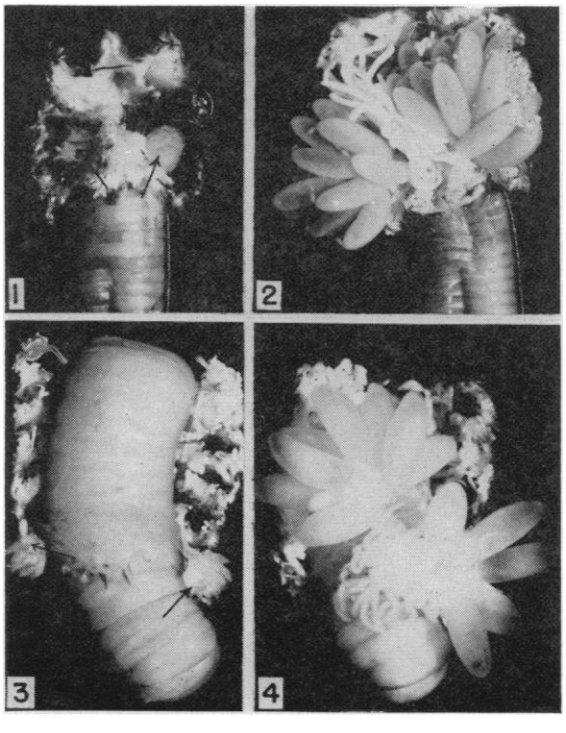

Fig. 1. (1, 2) Reproductive tracts of *B. germanica* females that carried oöthecae for 26 days. (about × 4.8). (1) Unoperated female; the ovaries (arrows) are undeveloped and the colleterial glands lack secretion; (2) female whose ventral nerve cord was severed 6 days after oviposition; the basal oöcytes are almost mature, and the colleterial glands are full of secretion. (3, 4) Reproductive tracts of *P. surinamensis* females that have oöthecae in their brood sacs. (about × 4.1). (3) Unoperated female 37 days after oviposition; the ovaries (arrows) are small, and the colleterial glands lack secretion; (4) female whose ventral nerve cord was severed just after oviposition; 29 days later the basal oöcytes have matured and the colleterial glands are full of secretion.

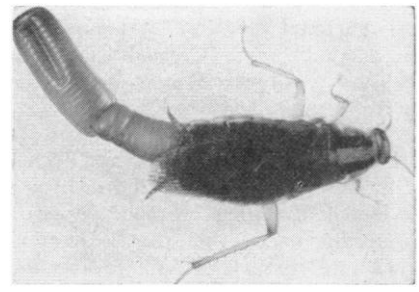

Fig. 2. *Blattella germanica* whose ventral nerve cord was severed 4 days after oviposition; 19 days after the operation it had formed a second oötheca, to which the first adhered. (× 2.4). [E. R. Willis]

Pycnoscelus surinamensis incubates its eggs in a uterus, like *Leucophaea maderae* (*2*). During gestation, which averaged 55.5 days in our parthenogenetic strain of *Pycnoscelus* (*4*), the oöcytes increased slightly in length, from 0.56 to 0.75 mm. About 2 weeks after parturition, oviposition again occurs, when the oöcytes average 3.2 mm in length. Usually about 70 days elapse between the formation of the first and second oöthecae. Allatectomized adult females failed to oviposit, but when *corpora allata* were implanted, these females oviposited 2 or more weeks later. The presence of an oötheca in the uterus inhibited ovarian development; the interval between the production of successive oöthecae was decreased from about 70 to 27 days when oöthecae were removed between 1 and 7 days after oviposition. The presence of parts of oöthecae implanted into the body cavity of adult females 1 day old or less failed to inhibit development of the oöcytes. Parts of young oöthecae were implanted into the body cavities of six females 1 day old or less; after 11 days the oöcytes of these six females were 2.91 ± 0.06 mm long—a length similar to that (2.93 ± 0.06 mm) of oöcytes of normal 11-day-old females.

The oötheca was removed from the uterus of each of ten females 1 to 16 days after oviposition, and one half of each oötheca was implanted into the body cavity of the donor female. Twenty-three days after the operation the oöcytes averaged 2.70 ± 0.10 mm in length. However, substitution of a wax oötheca for a real oötheca in the uterus inhibited oöcyte development. Ten females whose nerve cords were cut either 0, < 1, or 4 days after oviposition had well-developed oöcytes 2.74 ± 0.18 mm long and