a number to the loudness of the second rf sound with reference to the first rf sound. The reference rf sound was selected as being approximately in the middle loudness range. A brief dim light signaled the subject that a trial would begin. After a variable period of up to 5 seconds, the reference rf sound was presented for 2 seconds. A silent period of approximately 5 seconds followed, and then the rf sound of variable loudness was presented for 2 seconds. The subject would then indicate with the hand switch the number he assigned to the loudness. On some occasions, in order to account for the possibility of false positives, no rf sound was presented at the time that the variable rf sound should have been presented. Before starting a session, the subject was given two warm-up trials. Each test condition (Table 1) is defined by a specific peak power, average power, pulse width, and pulse repetition rate. We randomized the order of presentation of these sets of rf parameter by using a table of random numbers. There were three randomized repetitions of the series.

The results are presented in Fig. 1. The point plotted for each test condition number represents the median of all subjects and all repetitions. The graph shown in Fig. 1A was derived from the results of a test series in which we studied the effect of varying the peak power while holding the average power constant, as specified in Table 1. The average power was held constant by varying the pulse width. The graph shown in Fig. 1B was derived from the results obtained in a series of tests in which the average power was allowed to vary while the peak power was held constant, as specified in Table 1. The data obtained were reliable, as is typical from trained subjects in psychophysical experiments. The curves fitted to the data are estimations and are intended only as a guide for the reader's eye. The precise shape or slope of the curves will require many more studies for definition because of the sensitivity of judgments of sensory magnitude to details of experimental procedure (*9*).

Once a minimum pulse width is used, perceived loudness is a function of peak power (Fig. 1, A and B). The location of the point for test condition 6 is inconsistent with what would be expected. The data represented by this point were obtained when a 10-μsec pulse width was used. Since a consideration of all the data shown in Fig. 1 indicates that this pulse width is outside the optimal band for loudness, we tested the possibility that the apparent inconsistency was due to the use of a nonoptimal pulse width. We therefore presented to the subjects the same peak power, but with a pulse width within the optimal band, that is, 40 μsec. The average of the data so obtained is represented by the square labeled *a* in Fig. 1A. Its location indicates that the apparent decrease in perceived loudness at test condition 6 is due more to the pulse width being less than optimal than to an actual decrease in perceived loudness at the high peak power level. The data plotted in Fig. 1B indicate that, in addition to an apparent minimum pulse width, there may be a maximum pulse width defining an optimal band of pulse widths for perceived loudness. It appears that average power does not determine loudness except when it is incidentally involved in producing a minimum pulse width for optimal effect.

In one test series, we varied the average power by changing the pulse repetition rate while holding the pulse width constant. We found that the quality of the sound is in part determined by the repetition rate. The subjects reported sounds that had pitch as well as timbre characteristics. This confused subjects who were instructed to judge loudness.

The data do not support the hypothesis of radiation pressure against the skin conveyed by bone conduction to the ear; the energy available is far below the threshold for bone conduction. Nor do the data support a mechanism involving radiation pressure against the tympanic membrane, external auditory meatus, or round window. For example, there are no significant effects of changing head orientation as would be expected if radiation pressure was an important factor. Moreover, a series in which the Gellé test (*10*) was used with plastic air tubes yielded negative results for rf sound and positive results for acoustic sound.

In summary, the perceived loudness of the rf sound as judged by the magnitude estimation technique, and within the limitation of the rf parameters investigated here, is a function of peak power rather than average power. Calculations from the data presented indicate that in this particular experiment, the peak power required for perception is somewhat less than 80 mw/cm^2. A band of optimal pulse widths seems to exist for the effect. There are also rf modulation parameters that cause subjects to report hearing "sounds" with definite pitch and timbre characteristics.

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8. Peak power is equal to the average power divided by the duty cycle.
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10. The Gellé test procedure is dependent on the fact that any force exerting sudden inward pressure on the stapes pushes the ossicles further into the oval window. This increases intralabyrinthine pressure and reduces sound perception, irrespective of whether the sound wave has reached the tympanum by air conduction or by bone conduction.
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Thermoperiodic Control of Diapause in an Insect: Theory of Internal Coincidence

Abstract. *Females of the parasitic wasp* Nasonia vitripennis *raised from the egg stage in the total absence of light but subjected to daily temperature cycles (13° to 23°C), are able to distinguish a "short-day" thermoperiod (< 13 hours at 23°C per day) from a "long-day" thermoperiod (> 13 hours at 23°C per day) and produce diapausing or developing progeny accordingly.*

Many insect species develop continuously during the summer when days are long, but enter diapause in the autumn when the hours of light fall below the number necessary for a well-defined critical daylength (*1–3*). There is now substantial experimental evidence that photoperiodic induction of this nature—

at least in some species—is a function of the circadian system (*4*). For example, in the parasitic wasp *Nasonia vitripennis* and its flesh-fly host, *Sarcophaga argyrostoma*, "resonance" experiments (*5*) have shown that the amount of diapause induced varies rhythmically with the length of the environmental light cycle (T), and that the rhythm thus revealed has a period close to 24 hours (*6*).

Of the current models devised to explain such seasonal switches in metabolism, two have received the most attention. In one, a circadian rhythm, the exact nature of which is unknown, is phase set by the light cycle in such a way that a light-sensitive or photoinducible phase is illuminated, or not illuminated, according to the length of the photoperiod (*7*). Since this model depends on the interaction of a light-sensitive phase point and the environmental light cycle, it has been referred to as an "external coincidence model" (*8*). In the second class of model, the photoperiodic clock is envisaged as a two- or multioscillator system (*9*, *10*), in which one (or some) of the oscillators are phase set by dawn and the second (or others) by dusk. In Tyshchenko's (*10*) more explicit version of this model, diapause occurs when "active" phase points of the two oscillators are held out-of-phase (as at short daylength), but development occurs when the "active" phase points coincide (as at long daylengths, or very short daylengths). Resonance experiments with *N. vitripennis* have already indicated the existence of "dawn" and "dusk" oscillators, and that photoperiodic induction depends on the phase angle between the two (*6*). Since the environmental light cycle plays no direct part in the inductive process, this class of model has been called "internal coincidence" (*8*).

My experiments were designed to discriminate between these two possible models, according to suggestions by Pittendrigh (*8*) and on the grounds that temperature pulses and cycles are known to entrain circadian rhythms as well as light pulses (*11*). Since I now show that the clock controlling diapause induction in *N. vitripennis* responds to daily temperature cycles (in continuous darkness) in a manner almost identical to its response to light, a model in which environmental light plays an inductive role—in addition to its role in entrainment—must be ruled out.

Cultures of *N. vitripennis* were raised from the egg stage at 23°C and in continuous darkness. On the day they emerged as adults (as judged from a parallel series examined daily in the light), groups of wasps were placed in small glass jars containing 20 to 30 puparia of *Sarcophaga argyrostoma* as hosts. These jars were closed with perforated lids and placed within larger vessels (Kilner jars) made to exclude light with the use of black cellulose paint and aluminum foil. The Kilner jars also contained a layer of about 1 cm of a saturated solution of sodium chloride to provide a relative humidity of about 70 percent. When fully assembled, the Kilner jars were placed in Gallenkamp cooled incubators (which were sealed to exclude light) maintained in a darkened room.

A daily temperature cycle was obtained by transferring the inner glass jars from one incubator (at 13°C) to another (at 23°C), always in the dark. Control groups of wasps were maintained, in the dark, at 13° and 18°C. Fresh puparia of *S. argyrostoma* were provided for the wasps 6 and 12 days after the start of the experiment.

On day 15 the surviving females were placed singly in glass vials (50 by 12 mm) together with two host puparia. Two days later these puparia, now parasitized, were removed from the vials and incubated at 25°C for 10 days more before being opened to ascertain whether the contained parasites (the progeny of the experimental wasps) were developing pupae or diapausing larvae. Separation of the adult wasps and the removal of the host puparia on days 15 and 17, respectively, were performed in the light. However, earlier results (*12*) have shown that progeny

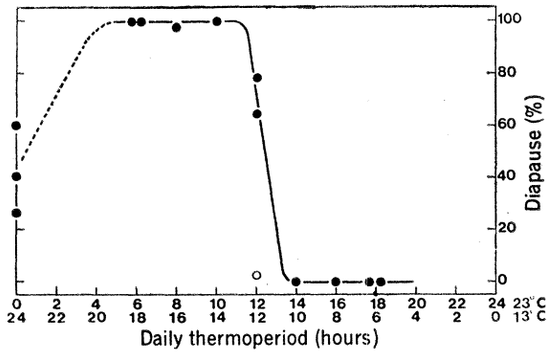

Fig. 1. The effect of a daily temperature cycle (23°C/13°C) on the induction of larval diapause in *Nasonia vitripennis* kept in continuous darkness, showing the sharp discontinuity (critical thermoperiod) between short and long thermoperiods. The ordinate shows the proportion of female wasps producing diapausing broods during the test period (days 15 to 17 of adult life). The open circle shows the proportion producing diapause larvae in the dark at 18°C; this is considered to be the most meaningful control for the group maintained for 12 hours at 23°C and 12 hours at 13°C (mean temperature, 18°C).

Table 1. The thermoperiodic control of diapause induction in *Nasonia vitripennis*, with a 13° to 23°C temperature cycle in continuous darkness.

T (hr)	HL ratio*	Females (No.)	Progeny produced on days 15 to 17			Percent diapause
			Developing	Diapause	None†	
			Control			
	13°C	118	32	25	61	43.9
	18°C	56	40	1	15	2.4
			Experimental			
24	6 : 18	110	0	83	27	100.0
24	8 : 16	59	1	43	15	97.7
24	10 : 14	40	0	22	18	100.0
24	12 : 12	95	10	26	59	72.2
24	14 : 10	11	8	0	3	0.0
24	16 : 8	31	17	0	14	0.0
24	18 : 6	43	24	0	19	0.0
36	12 : 24	57	26	14	17	35.0
48	12 : 36	49	17	13	19	43.3
60	12 : 48	47	14	8	25	36.4
72	12 : 60	12	1	5	6	83.3

* HL ratio (in hours) of high temperature (23°C) to low temperature (13°C) in thermoperiodic cycle. † The number of experimental females of *N. vitripennis* that failed to lay eggs during the test period (day 15 to 17 of adult life); hence the empty host puparia.

type is fully determined by day 15, and any reversal takes 5 to 10 days more. The type of progeny produced during the test period (days 15 to 17), therefore, must be a consequence of the preceding thermoperiodic treatment.

The results of this experiment (Fig. 1 and Table 1) show that females of *N. vitripennis* produce nearly all of their progeny as diapause larvae when the warm period of the "day" is less than about 13 hours, but that diapause is absent when the warm period is more protracted. Females of *N. vitripennis*, therefore, are able to distinguish a 'short-day" thermoperiod from a "long-day" thermoperiod and produce diapausing or nondiapausing progeny accordingly. The critical thermoperiod in these experiments was about 13 hours out of 24, whereas the critical photoperiod measured earlier (*12*) was 15¼ hours out of 24. However, little importance is attached to this difference; it is almost certainly associated with the slow rate of cooling and warming consequent upon the manner of transfer from one incubator to the other. More abrupt temperature transitions would undoubtedly produce a critical thermoperiod closer to that for light.

A resonance experiment, in which 12 hours at 23°C was coupled with 12, 24, 36, 48, and 60 hours at 13°C (Table 1), failed to show that diapause induction was a rhythmic function of the length of the temperature cycle (T), presumably because of the weakness of temperature as an entraining agent in cycles longer than 24 hours.

In a 24-hour cycle, the proportion of wasps producing diapause broods when the warm period lasted 12 hours was significantly greater than that for control females kept at 18°C throughout ($\chi^2 = 26.72$; $P < .001$). Similar results have been described by others for the moths *Ostrinia nubilalis* (*13*) and *Pectinophora gossypiella* (*14*), although in both cases the effects were weaker than those for 12 hours of light. Similarly, discrimination between a short and a long thermoperiod, described for *O. nubilalis* (*15*) and *Acronycta rumicis* (*16*), was, for both species, considerably weaker than the corresponding photoperiodic effect. My data for *N. vitripennis*, however, show that thermoperiod and photoperiod are equally effective in 24-hour cycles; indeed both are considered to be manifestations of the same phenomenon. Furthermore, since the switch in metabolism can be controlled by thermoperiod in the absence of light, any model for the *Nasonia* clock in which light plays a part in induction ("external coincidence") must be ruled out. Since a specific temperature-sensitive phase seems unlikely, the most probable explanation for this phenomenon is a model of the "internal coincidence" type, involving the mutual interaction of the "dawn" and "dusk" oscillators.

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4. In at least one species, the aphid *Megoura viciae*, there is good evidence that night length is measured by a noncircadian or hourglass mechanism (*3*, pp. 47–137).
5. In "resonance" experiments a short light period (usually 8 to 12 hours) is coupled with different periods of dark to provide environmental light cycles (T) up to 72 hours or more in length. If the photoperiodic clock incorporates a circadian oscillation (that is, with an endogenous periodicity, τ, close to 24 hours), the product of photoperiodic induction (for example, diapause) is observed to be high when T is close to τ or modulo τ (that is, the two oscillating systems resonate), or low when T is not close to modulo τ (that is, the two oscillating systems do not resonate).
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Visual Effects on Alpha Feedback Training

Abstract. *Presenting an audible indication of subjects' electroencephalographic alpha activity under conditions of dim ambient illumination led to systematic increases in alpha density, while in total darkness the same procedure did not. These results support the view that feedback training can be clearly demonstrated only when factors leading to a suppression of alpha activity are present in the environment.*

Much of the current interest in electroencephalographic (EEG) alpha activity centers around the apparent ability of individuals to learn volitional augmentation of alpha densities in their EEG. Kamiya (*1*) and Mulholland (*2*) have independently demonstrated that providing a subject with feedback concerning the presence or absence of his own EEG alpha activity makes it possible for him to alter the amount of such activity seen in the record. In addition, it has been suggested that volitional increases in alpha density lead to changes in subjective mood (*3*, *4*), and it has even been proposed that feedback techniques may be useful as a means of "mapping the subjective space of consciousness" (*5*).

The effects of feedback training usually have been demonstrated in one of two ways, both of which contain inherent methodological shortcomings. The first procedure involves comparing periods during which subjects are instructed to maximize alpha density with similar periods when they are instructed to minimize density. Although it is easy to demonstrate differences between periods when subjects are instructed to produce alpha activity and periods when they are instructed to block it, such differences rarely reflect symmetrical increases and decreases. Usually subjects learn to block alpha activity volitionally within one or two trials, and impressive differences with this procedure tend to be the result of unidirectional rather than bidirectional control.

The second procedure involves comparing initial baseline levels with the higher densities seen after training. Such a comparison more appropriately addresses the question whether individuals can learn to augment their level of alpha activity significantly. It then, however, becomes crucial to specify the nature of the baseline level from which increases can be measured. Novelty and apprehension are known to depress the subject's initial alpha density