was identical to that described in normal secretory endometrium (*9*), comprising an amorphous matrix, dense granules, and a series of tubular channels. The NCS connected the perinuclear space with channels of endoplasmic reticulum, providing a means for direct nucleocytoplasmic exchange. Additional, less obvious postovulatory characteristics were found in the experimental proliferative specimens.

Secretory endometria showed histologic and ultrastructural evidence of a premature decidual reaction. In about 25 percent of specimens taken after ovulation a perivascular cuff of stromal cells and an unusually well-developed endoplasmic reticulum were found by day 19 or 20 (Figs. 4–6). In a few specimens a pattern of broad cellular contact between stromal cells, similar to that in the decidua, was found as early as the late proliferative phase, particularly in association with prominence of the NCS's. In the experimental series, large mitochondria were more common at the end of the proliferative phase and shortly after ovulation, but no consistent change was observed in Golgi bodies or microtubules or in the distribution of secretory granules. All alterations in endometrial pattern suggested that there was premature maturation; the ultrastructure of the experimental specimens was similar to that of normal controls from several days later in the cycle. These ultrastructural changes affected the entire endometrium of the corpus, except for the portion in contact with the device, where direct results of pressure were obvious. The asynchrony, furthermore, often affected stroma more than epithelium, creating a pattern resembling that produced by certain oral progestational agents.

Although the relation of ovarian steroids to the development of the NCS, which presumably accompanies synthesis of nucleic acids, is ill-defined, the interaction of hormones, nucleic acids, and proteins in uterine metabolism is under intensive study (*10*). Upon which of these factors the IUD exerts a primary effect is not yet clear, but the premature and asynchronous maturation of the human endometrium must affect the precise correlation with ovular development. In macaques, furthermore, the intrauterine device increased the rapidity of tubal transfer of ova in animals treated with gonadotropins to induce superovulation (*11*). The premature appearance of ova in the endometrial cavity is another factor that may disturb the precise synchrony required for normal implantation.

These electron microscopic studies suggest that the IUD creates an environment unfavorable for blastocystic attachment. The mechanism of action, which is primarily contraceptive rather than abortifacient, makes the device a more generally acceptable means of control of fertility.

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Temperature Compensation in Short-Duration Time-Measurement by an Intertidal Amphipod

Abstract. *The duration of the swimming response of an intertidal amphipod to increases in hydrostatic pressure apparently serves to measure the timing of wave uprush on the beach. Experiments have demonstrated that this response to a standard pressure-increase stimulus varies in duration only slightly with temperature over the range from 10° to 28°C, with estimated* Q_{10} *values of 1.3 to 1.5. Relative insensitivity to temperature, such as here described, seems to be an essential component of biological time-measuring systems (including endogenous circadian, tidal, and lunar rhythms) that are ecologically keyed to the timing of temperature-independent environmental factors.*

One of the most unusual properties of circadian rhythms, and a feature that has been extensively studied experimentally, is the relative insensitivity of these time-measuring systems to environmental temperature. While Q_{10} values (*1*) ranging between 2 and 3 are very commonly observed in other biological systems at cellular, tissue, and whole-organism levels, the Q_{10}'s of steady-state, free-running circadian rhythms of both plants and poikilothermous animals usually differ very little from 1.0, with extreme values from different organisms lying between about 0.9 and 1.2.

As Pittendrigh has emphasized (*2*), this relative independence of temperature is of obvious selective advantage; if the internal rhythmicity is to serve the organism as a time-measuring system in an ecologically useful way, relative insensitivity to temperature must be achieved in some manner. This requirement, that a physiological time-measuring system must correspond over a wide range of temperatures to geophysical, temperature-independent time-measurement, applies not only to circadian rhythms but also to endogenous tidal rhythms, as well as to lunar rhythms with fortnightly and monthly recurrence. At time scales appreciably shorter than these long-period endogenous rhythms (biological time-measurement on the order of milliseconds to minutes), however, there is usually far less reason to expect temperature compensation of the time-measuring process because there is seldom direct ecological significance to the absolute duration of time measured.

A clear exception to this generalization is the response of the intertidal amphipod *Synchelidium* sp. to the small increases in hydrostatic pressure associated with waves on the beach. The duration of the animals' intense swim-

Table 1. Estimates of Q_{10} based on measurements of response durations by four observers.

Observer	Temp. range (°C)	Estimated Q_{10} (± S.D.)
J.E.	10–25	1.30±0.025
R.H.	14–28	1.28± .035
M.L.	13–27	1.53± .052
T.S.	14–26	1.42± .046
	Average	
		1.38± .058*

* Standard error of the mean of the four separate estimates.

ming responses, measured at room temperature, varies from about 5 to 15 seconds during rising tides, depending on the magnitude of the increase in pressure (and so on wave height). This response appears to be keyed in its duration to the timing of waves on the beach, permitting the animals to be swept landward by an advancing wave front in the uprush zone, and then (after 5 to 15 seconds) to rebury in the sand at or near the peak of the uprush (*3*); thus they migrate up the beach during the rising tide (*4*).

This interpretation of the pressure-change responses implies, then, that duration of the response represents absolute time-measurement. The ecological usefulness of the response seems to require that the duration of pressure-change responses not show a "normal" Q_{10}, but instead be relatively independent of temperature, as is the case with circadian rhythms. Furthermore, adjustment of the response duration to temperature could not be adequately accomplished by seasonal or other long-term acclimatization, since changes of temperature of more than 10°C within a few minutes, due to inundation of the sun-warmed beach by cold waves, are common in the animals' environment. Adjustment of response times to different temperatures would have to be very rapid in order to be fully useful. My experiments were conducted to test the validity of this interpretation and hypothesis.

Several hundred freshly collected *Synchelidium* sp. (*5*) were divided into three approximately equal groups, which were then assigned at random to 125-ml erlenmeyer flasks of sea water at different temperatures selected to cover the normal ecological range. The experiments began about 15 minutes later. Temperature within each flask was held constant within 1°C. The standard pressure-increase stimulus of 120 mb was produced by placing a weight atop the plunger of a water-filled 50-ml syringe, which was connected by small-diameter tubing to the stoppered flask containing the animals. With no air in the closed system, this procedure results in a rapid increase in pressure, with slight overshoot; the new equilibrium pressure level is essentially stable after about 0.5 second.

The initial response of the amphipods to such a stimulus consists of a sudden onset of rapid swimming and scurrying activity on the bottom of the flask; thereafter, the intensity of activity decays, apparently exponentially, to the original background level (*3*). The duration of response can be determined precisely from quantitative analyses of films of the behavior, an extremely tedious and time-consuming procedure (*3*, figs. 2–5). With a little experience, one can also estimate visually the end of significant, above-background, swimming activity of a population of animals, and the duration of the response can then be approximated with a stopwatch. I used this latter method of measurement in the present experiments. Larger numbers of replicate measurements can compensate for the greater variation inherent in such visual estimates, and comparisons of measurements by different observers indicate the probable magnitude of an observer's error and/or bias.

The measurements were made in blocks of five repetitions at each temperature, with a pause of about 30 seconds between repetitions; measurements at other temperatures intervened between blocks. Twenty-five measurements (in one case, 16) were made at each temperature. Four observers participated, with different animals. All observations were made at approximately the same stage of the rising tide: 1300 to 1500 hours, 3 February; 1600 to 1800 hours, 6 February; 1500 to 1700 hours, 20 February; and 1530 to 1700 hours, 21 February 1967.

Analyses of variance within temperatures indicate that time-trends during an experimental series (due, for example, to accommodation) were generally negligible. In only two of 12 instances was the between-blocks *F* value significant ($p < .05$). The most extreme departure was a block average that differed by 1.6 seconds from the general mean at this temperature; in the other case of a significant *F* value, block averages were all within 1 second of the general mean. The blocks of values were therefore pooled.

The results (Fig. 1) indicate a clearly significant dependence of duration of response on temperature, with somewhat longer responses at colder temperatures. The results of the four ex-

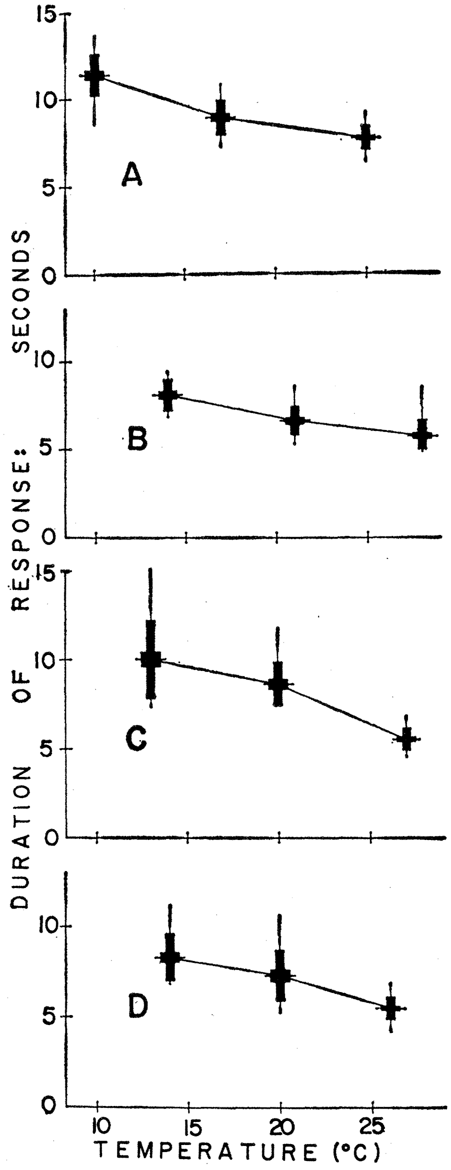

Fig. 1. Summary of durations of response by *Synchelidium* sp. to rapid pressure increases of 120 mb, as a function of temperature; duration measured from application of stimulus to end of significant, above-background activity. Horizontal lines are mean values ($N = 16$ at 14°C in B; $N = 25$ at all other temperatures); vertical lines include entire ranges of measurements; narrow vertical bars are drawn to ± 1 S.D., wide vertical bars to ± 1 S.E. of the mean. All measurements made during rising tide. Measurements by observer J.E. on 3 February (A), by R.H. on 6 February (B), by M.L. on 20 February (C), and by T.S. on 21 February 1967 (D).

perimental series are treated separately, since the response durations recorded at comparable temperatures in the separate experimental series often differed appreciably. These differences probably reflect nonuniformity in criteria of the four observers in deciding that significant population response had ended, but conceivably also include real differences between the organisms from the separate collections. In any case, calculation of Q_{10} values is meaningful only in comparisons within an experimental series, where the prehistories of the animals were the same and where observer bias, if any, was constant; such values with their standard errors (*1*) appear in Table 1.

The real durations of response, measured from onset of significant activity rather than from application of the stimulus, would be even less temperature-dependent than these values seem to indicate. A major portion of the apparent difference in Fig. 1 is accounted for by the fact that the latent interval between application of the stimulus and attainment of full, maximum response was 2 to 4 seconds at 10° to 15°C against ≤ 1 second at the warmer temperatures. No allowance was made for this factor in the Q_{10} estimates, although it probably operates on the beach in a manner tending to produce greater uniformity in the distance that an animal is carried by a wave before it reburies, since the factor implies a more uniform duration of real transport than is indicated in Fig. 1.

The Q_{10} values, as calculated, are much smaller than those seen in most behavioral and physiological responses, but are nonetheless appreciably larger than those common in circadian rhythms. Since the times of passage of ocean waves in the uprush zone, to which this response is apparently keyed, are much more irregular than the timing of the daily or the tidal cycle, it is perhaps not surprising that the response is not as thoroughly buffered against environmental temperature as are the longer-period time-measuring systems. The sensitivity to temperature, evident in these data, is still so small that the response duration at all temperatures overlaps most of the ecologically appropriate values.

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References and Notes

1. The term Q_{10} is defined as the ratio between a reaction rate of one temperature, r_T, and the rate at a temperature 10°C lower, r_{T-10}. On the basis of measurements at any two temperatures, $T1$ and $T2$ ($T1 > T2$), an average Q_{10} over the interval can be calculated as the ratio $r_{T1} : r_{T2}$ raised to the power of $10/(T1 - T2)$. When measurements, at different temperatures, of the times required for a reaction to reach a given end point (t_{T1} and t_{T2}) are available, rather than reaction rates themselves, the average Q_{10} can be calculated as the ratio $t_{T2} : t_{T1}$ raised to the power of $10/(T1 - T2)$. Standard deviations of the individually calculated Q_{10} values were estimated as $(c/a^2)(b/a)^{c-1}(a^2 s_b{}^2 + b^2 s_a{}^2)^{\frac{1}{2}}$, in which a is the average duration of response at the higher temperature, b is the average duration of response at the lower temperature, $s_a{}^2$ and $s_b{}^2$ are the variances of the mean durations at these temperatures, and c is the absolute value of the difference in temperatures, divided into 10.0.
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4. Other components of behavior are involved in the subsequent seaward migration with the ebbing tide. These include an endogenous rhythm of activity synchronized by the tides; and, in conjunction with this rhythm, a different response, of much longer duration, to pressure increases (*3*, for details).
5. For a morphological characterization of this unnamed species, see ref. 7 of J. T. Enright, *Science* **133**, 758 (1961).
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Nonhormonal Basis of Maternal Behavior in the Rat

Abstract. *Rats were tested for induction of maternal behavior by exposing them to young pups continuously for 10 to 15 days. Nonpregnant intact, ovariectomized, and hypophysectomized females were studied, as well as intact and castrated males. Nearly all the animals exhibited the four main items of maternal behavior and there were only minor differences in the latencies for the onset of maternal behavior among the various groups. It is concluded that all rats have a basic level of maternal responsiveness which is independent of hormonal stimulation.*

From the earliest studies, maternal behavior in the rat has been considered to be dependent upon hormones. It appears during a particular phase of the endocrine reproductive cycle (namely, postparturition), and its onset is closely associated with the onset of lactation, which is known to be under hormonal control. After parturition nearly all females show maternal behavior upon being exposed to pups, but in the single study in which a large number of animals were tested, even after 4 days of continuous exposure, maternal behavior appeared in only 30 percent of nonpregnant females (*1*).

In several mammalian species [mouse (*2*), hamster (*3*), wolf (*4*), monkey (*5*), and human beings] young elicit maternal behavior in nonpregnant females, as well as at the usual time after parturition. This is particularly striking in the mouse. Maternal behavior appears in nonpregnant mice and, since hypophysectomy does not prevent it, it is clearly not based upon hormones (*2*).

We exposed nonpregnant female rats to pups for 10 to 15 days and tested daily for the appearance of maternal behavior. Lengthening the period of exposure to pups proved highly successful in eliciting maternal behavior, and the study was extended to include males, gonadectomized females and males, and hypophysectomized females.

Three groups of nulliparous females of the Charles River strain, 80 to 120 days old, were used: intact ($N = 14$), ovariectomized ($N = 12$), and hypophysectomized ($N = 11$). The hypophysectomized females, which were obtained commercially, were examined by means of daily vaginal smears to confirm the absence of estrous cycling. The operations were performed approximately 2 weeks before the start of testing. In addition two groups of males of the same strain and age-range were used: intact ($N = 13$) and castrated ($N = 12$). Each animal was housed in a large rectangular cage, 45.7 by 50.8 by 41.9 cm, with transparent plexiglass walls, a grid floor, wall feeder, water bottle, and two bins containing hay and coarse wood shavings for nesting ma-

Table 1. Percentage of animals displaying each of the four items of maternal behavior. Number in each group is in parentheses.

Group	Retrieve	Crouch	Lick	Build nest
	Females			
Intact (14)*	93	100	100	100
Ovariectomized (12)	92	83	100	92
Hypophysectomized (11)	100	100	100	100
	Males			
Intact (13)	77	77	85	46
Castrated (12)	83	75	83	67

*Observations made inadveretntly on only 10 of the 14 females of this group.