findings of Clouet and Ratner (*13*) who found little evidence of tolerance to increased synthesis of catecholamines during long-term morphine administration. Also, our failure to demonstrate tolerance to the threshold-lowering effect of morphine parallels the report of Roffman *et al.* (*14*) who found tolerance to morphine induced changes in the concentration of MHPG (*15*) in a variety of brain areas with the exception of the hypothalamus.

We believe that the threshold-lowering effect of morphine may be related to the euphoria-producing and the reinforcing properties of the opiates in man. In this context a study of Mirin *et al.* (*16*) is of interest. In an effort to understand the continued working for, and self-administration of heroin in human subjects who had acquired tolerance to the drug and showed marked clinical and social deterioration, these workers measured changes in mood during the period of peak drug effect, 30 minutes after each injection. Using the Osgood semantic differential scale they found significant alterations in mood following the intravenous administration of heroin. Their subjects reported feeling more carefree, relaxed, calm, clear, and elated. These effects were sustained over the entire course of the addiction cycle with no significant decrement in the drug's ability to produce such mood alterations. To the extent that our threshold-lowering effect may be related to these mood alterations, we think that we have demonstrated a mechanism of primary importance to the sustained reinforcing and addictive properties of the opiates.

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Experimental Separation of Sensory and Motor Functions in Pea Tendrils

Abstract. *When illuminated pea tendrils from light-grown plants are rubbed on their abaxial side, they rapidly coil in a spiral fashion. If similar tendrils are held in the dark for 3 days and then rubbed, however, they will not coil until they are subsequently illuminated. They can remain uncoiled in the dark for as long as 2 hours after stimulation, and will still coil immediately when they are illuminated. Tendrils that are rubbed and held at 25°C will coil, but those treated at 5° or 10°C will not. However, tendrils rubbed at 25°C and kept from coiling for an hour at 5°C, will immediately coil when restored to the higher temperature. These observations are interpreted to imply separation of sensory and motor functions.*

Tendrils are thin, hairlike organs by means of which some weak-stemmed plants anchor themselves upright to supporting structures. They do so by slowly rotating through space by the process of circumnutation (*1*) until they touch a potential support, at which time they cease to circumnutate and begin to coil around the support (*2*). This latter movement, called contact coiling (*3*), is quite rapid, and the tendril can throw more than one complete coil around its support in less than 1 hour (*3*). A conceptual model has been proposed (*4*) which links the sensory function (absorption of stimulus energy) with the motor function (motile response) by one or more transduction steps. Although many correlations of contact coiling with both physiological and biochemical events have been reported (*4*), no one has been able to discern if they were part of the sensory or the motor function. For example, the utilization of adenosine triphosphate has been shown to be necessary for contact coiling (*5*), but it is not known whether this occurs during absorption of the mechanical stimulus, or afterward, during the actual coiling itself.

Therefore, a technique was sought which would permit experimental separation of the motor function from the sensory function. The first experiment shows that tendrils can store sensory information and retrieve it and respond at

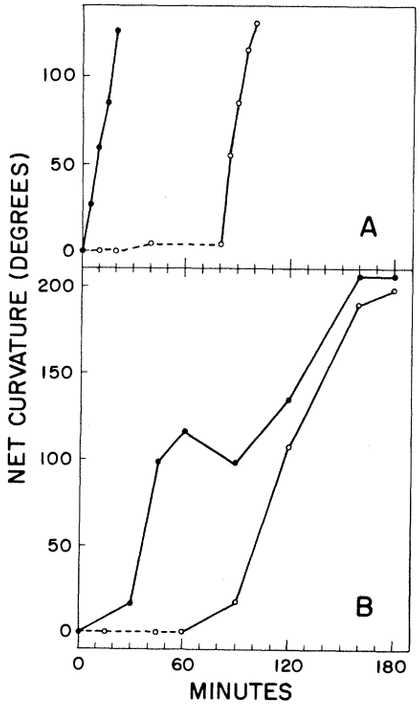

Fig. 1. The effect of low temperature (A) and prolonged darkness (B) on both the sensory and motor functions of contact-stimulated pea tendrils. For the temperature experiment (A), tendrils were excised at the base into petri dishes containing 0.01 percent Tween-20 in 0.05*M* phosphates buffer, *p*H 6.4. After floating for 1 hour to recover from excision, they were stimulated and either held at 25°C (•——•) or at 5°C (o-----o) for 80 minutes and then at 25°C (o——o). For the light experiment (B), preparations were made by excising material at the base of the petiole, and standing the petiole in a jar of wet vermiculite for 3 days in the dark at 26°C. The tendrils were then stimulated and immediately brought out into the light (•——•), or held in the dark for 60 minutes more (o-----o), and then brought out into the light (o——o).

a later time. The second experiment confirms this finding and operationally separates the sensory function from the motor function. Young plants of the Alaska pea (*Pisum sativum* L.) were grown in a growth chamber in vermiculite. Single tendrils from the fifth node were used for the explants in the dark-adaptation study and triply branched tendrils from the seventh node were excised for the cold-break experiments (*3*, *6*). The tendrils were mechanically stimulated by stroking each one ten times acropetally on the abaxial side with the tip of a Pasteur pipette. The details of experimental protocol are given in Table 1 and the figure legends.

Observations of suppression of a response during a cold period have been reported in geotropism in beans, thigmonasty in pea tendrils and in the sensitive plant *Mimosa pudica*, and photomorphogenesis in the fungus *Phycomyces blakesleeanus* (*6*, *7*). When tendrils were excised and stimulated at 25°C, and then immediately chilled by being floated on cold water, they did not coil until they were warmed to the higher temperature (*6*). This suggests that the information signaled by the stimulus was retained during the cold break. If the poststimulation cold break is 10°C, a small amount of coiling occurs at that temperature, but if it is 5°C, there is no coiling. Figure 1A shows that both the amplitude and rate of coiling following an 80-minute cold break do not differ from coiling that occurs in control tendrils experiencing no cold break. Coiling is thus suppressed during the duration of the cold break, but there is retention of absorbed sensory information, so that coiling proceeds as soon as the tendril warms up. At this time it is not known how the cold break effects this phenomenon, although preliminary experiments using colchicine and electron microscopy indicate that microtubules might somehow be involved (*8*). Because the low temperature suppresses absorption of the stimulus, as well as the coiling response (Table 1), this technique cannot be used to separate the motor and sensory functions. However, the following series of experiments describes a method which is able to separate them.

It had previously been shown that an overnight dark period reduces the amount of contact coiling (*5*). In an extension of this observation, it was found that when preparations, each consisting of a tendril subtended by flanking leaves and a petiole, were explanted in wet vermiculite for longer dark periods (48 to 72 hours) and then stimulated, the tendrils would not coil while they remained in the dark. As soon as the tendrils were illuminated, however, they proceeded to coil (Table 1). The light requirement is site specific, for when the light is applied as a small spot, 1 mm in diameter, the tendril begins to coil at the point illuminated (Fig. 2). Contact coiling occurs if the mechanical stimulus is applied either immediately before or immediately after illumination, so it is difficult to determine from the above if the prolonged dark treatment is blocking the sensory or the motor function, or both. However, the following experiment is able to discriminate between the two. Figure 1B shows that although a dark-adapted tendril will not coil if it is stimulated in the dark, it will retain the absorbed sensory information derived from the stimulus for as long as 1 or 2 hours in the dark, and proceed to coil as soon as it is illuminated. All the sensory information is capable of being stored during dark incubation, for the subsequent amount of coiling as well as the rate are comparable to those of the controls (Fig. 1B). Thus, dark adaptation enables the sensory function to proceed, but successfully blocks the motor function. It is not known at this time how it does so, but one possibility is that some necessary requirement for the motor function is used up during dark adaptation, and is quickly replenished during subsequent illumination. Adenosine triphosphate has been shown to substitute for light in tendrils held in the dark for short periods of time and has been shown to be used up in coiling tendrils (*5*). It is possible, therefore, that adenosine triphosphate becomes used up during dark adaptation, and is restored during illumination by the process of photosynthesis. It is also possible that a coiling inhibitor accumulates during dark adaptation, and that it is quickly removed during illumination. Although this question requires further research, it is of interest that the technique of dark adaptation will now permit an operational isolation of the sensory function, allowing its mechanism to be studied free of confusion with the motor function.

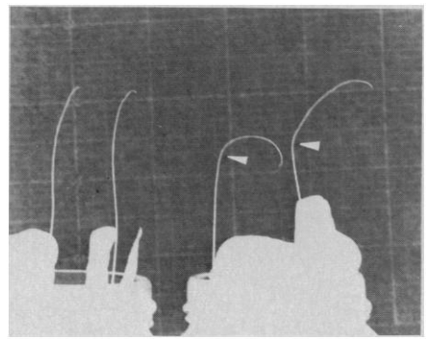

Fig. 2. Light-induced coiling of dark-adapted, stimulated tendrils. After 3 days of dark adaptation, the two tendrils on the right were mechanically stimulated and held in the dark for 15 minutes. They were then illuminated with a spot of light 1 mm in diameter at the locations indicated by the arrows. The two tendrils on the left were not stimulated. The photograph was taken 15 minutes after the beginning of spot illumination.

Table 1. The ability of pea tendrils to undergo contact coiling after stimulation given during a period of low temperature or darkness. For the light experiment, excision was made at the base of the petiole containing a single tendril flanked by two leaves. This was stood in wet vermiculite in a small jar for 3 days in the dark. The tendrils were stimulated once each day during the 3 days. In the low-temperature experiment, the tendrils were excised at their base into a petri dish containing 0.01 percent Tween-20 in 0.05 phosphates buffer, *p*H 6.4. They were allowed to recover for 1 hour from the trauma of being cut before the experiment was performed. Values are means ± standard errors.

Treatment	Net curvature (degrees)
Stimulated at 25°C and measured after incubation at 25°C for 21 minutes	144 ± 7
Stimulated at 25°C. Held for 6 minutes at 5°C. Incubated for 21 minutes at 25°C and then measured	126 ± 5
Held at 10°C and then stimulated while still at 10°C. Then transferred to 25°C, incubated for 21 minutes, and then measured	9 ± 4
Held in the dark for 72 hours at 26°C, stimulated in the dark, incubated in the dark for 30 minutes, and then measured	2 ± 1
Held in the dark for 72 hours at 26°C, stimulated in the dark, brought out into the light for 30 minutes, and then measured	148 ± 6

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