was observed. These cells were identified as containing noradrenaline. The second type of glomus cell contains granules smaller in size than the first type and gives a negative reaction with 2 minutes of silver treatment; when treated 15 minutes or longer, it gives a positive reaction (Figs. 1-3). These cells, the most numerous of all, store 5-hydroxytryptamine. The third type of cell, which is very scarce and is characterized by the presence of small, round granules, gives a negative reaction even with more than 30 minutes of treatment with silver. This type contains adrenaline.

These findings explain the results of Costero and Barroso Moguel (15) and Pryse-Davies et al. (16) who found 5hydroxytryptamine in tumors of the carotid body. It is difficult to explain the function of the high amount of 5hydroxytryptamine in the carotid body. Two hypotheses should be considered: either indolamine acts as a transmitter in the initiation of chemoreceptive impulse, or else 5-HT can be discharged into the bloodstream and acts at a distance.

Although it was claimed (17) that 5-hydroxytryptamine increases the discharge of afferents from the carotid body and confirmed (18) that in the dog this effect appears with a short latency, Lever and Lewis (19) refused to consider this substance as a candidate for transmitter. 5-Hydroxytryptamine may, on rare occasions, excite the superfused carotid body (20). Our study shows that the glomus cells in the car-



Fig. 1. Carotid body of cat. Glutaraldehyde-silver technique with 30 minutes of silver treatment (\times 12.000). Figs. 2 and 3. Selected areas of Fig. 1 at higher magnification show a positive reaction in the two types of cells (\times 54,000). The cell on the left, with larger granules, contains noradrenaline; cells on the right with smaller granules contain 5-HT.

otid body of cats contain catechol and indolamines. At the same time, various cells types were identified as containing noradrenaline, adrenaline, and 5-hydroxytryptamine.

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- 5 September 1967

Induction of Coiling in Tendrils by Auxin and Carbon Dioxide

Abstract. Symmetric application of indole-3-acetic acid, CO₂, or, to a lesser extent, ethylene can substitute for the contact stimulus in inducing coiling in the tendrils of Marah fabaceus. In the case of auxin, treatment of the apical few millimeters results in strong, permanent coiling throughout the length of the tendril. The speed of the response to CO_2 is comparable to that to tactile stimuli. A possible mechanism for thigmotropism is outlined.

Accumulated experimental evidence (1) suggests that, when a tendril receives a contact stimulus, the growth rate of the stimulated side falls while that of the opposite side rises sharply.

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Fig. 1. Tendrils of *Marah fabaceus* after floating for 15 hours on water (top) or on IAA at 100 mg/liter (bottom).

While this differential growth would of itself result in coiling, it has recently been proposed (2) that in addition a contractile protein may play a part in the initial phase. The mechanism effecting the differential growth response is unknown. Though it does not appear to have been established that auxin participates, Boresch (3) advanced a theory according to which contact induces a transverse transport of hormone from the stimulated to the opposite side, analogous to the transverse displacement of auxin in phototropism and geotropism.

In the experiments I report, strong coiling of tendrils was induced by symmetric application of indole-3-acetic acid (IAA); auxin can thus replace the contact stimulus. The experimental material was the wild Californian cucumber, *Marah fabaceus* (Naud) Greene (4), which was observed to be more sensitive than peas. In one type of experiment, tendrils excised at their extreme bases were gently floated on



Fig. 2. Tendrils of *Marah fabaceus* 15 hours after placement with tips immersed a few millimeters in water (first and third from left) or in IAA at 150 mg/liter (second and fourth from left). The coiling of the IAA-treated tendrils has caused them to lift high out of the solution.

water in shallow pans. After an interval of at least 30 minutes to check whether or not manipulation had itself caused a response, IAA was added to the pans to a final concentration of from 2 to 150 mg/liter. Responses were detectable in all IAA concentrations after 20 to 30 minutes. With IAA at 20 mg/liter or above, overnight immersion produced tightly coiled spirals, the control tendrils remaining straight (Fig. 1). Even when the control tendrils received a brief contact stimulus before placement in water and consequently curled at first, they were largely uncurled overnight by the straightening reaction that follows the initial response if the contact is not sustained (1). It was immaterial which side of the tendril floated uppermost on the auxin solution. Prolonged immersion in these high concentrations of IAA produced no discernible toxic effects, the tendrils remaining highly turgid; I suggest that their permeability to the auxin is extremely low.

The probable reason why Jaffe and Galston (5) observed only slight effect of symmetrically applied IAA is that they sought the enhancement of a tactile stimulus, whereas in our experiments IAA substituted for the latter.

In a second type of experiment, tendrils, either excised or still attached to their branches, were placed overnight with their tips submerged a few millimeters in either IAA solutions (100 to 200 mg/liter) or water. Extremely strong coiling throughout the length of the IAA-treated tendrils (Fig. 2) indicated basipetal transport of the auxin.

That the effect of IAA did not depend on the low pH of the solutions was shown when the latter were buffered at pH 4.0 or 6.5 with citrate. The pH-4.0 buffer, however, produced slight coiling on its own, the response becoming evident after about 25 minutes in the case of floating tendrils. Gibberellin proved completely ineffective.

Ethylene was slightly effective; CO_2 , extremely so. For experiments with these gases, either excised tendrils or sections of stem with tendrils attached were placed with cut ends in water for several hours, preferably overnight, to achieve a high state of turgor. (It has been observed that turgor plays a very influential role in the thigmotropic response.) In the case of ethylene they were then transferred to closed cham-

Table 1. Time course of coiling of fully turgid tendrils of wild cucumber when gassed with O2 or with CO2.

| Gas | Increase in curvature (deg) after (min): | | | |
|------------------|---|-----------|-------------|-------------|
| | 2.5 | 5 | 7.5 | 10 |
| $\overline{O_2}$ | 0 | 0 | 20 ± 31 | 20 ± 31 |
| \mathbf{CO}_2 | 0 | 75 ± 78 | 405 ± 150 | 555 ± 196 |

bers into which the gas was injected. Ethylene at 10 to 20 parts per million produced slight but definite curling; the weakness of the response, compared with the coiling induced by IAA (Figs. 1 and 2) makes it unlikely that the latter was in fact caused by ethylene produced in vivo under the influence of high concentrations of IAA.

In the experiments with CO_2 the fully turgid tendrils were placed in chambers through which streams of gas (bubbled first through water) were passed. Table 1 shows that, whereas O_2 was almost totally ineffective, CO_2 elicited vigorous curling that started within 5 minutes-close to the average time for response to tactile stimuli. It is likely that this effect of CO_2 is intimately related to its action as a remarkably efficient and quick-acting promoter of extension growth (6).

The strong coiling in response to symmetrically applied IAA and CO₂ reported here argues against Boresch's theory that an asymmetric distribution of auxin, effected by contact, causes the thigmotropic response. [The possibility that CO₂ brings about an asymmetric release of auxin within the tissues may be discounted, since growth induced by CO_2 and by IAA differs widely in susceptibility to inhibitors (6).] I therefore propose that the thigmotropic response is due, not to an asymmetric distribution of auxin, but to an asymmetric response to auxin. The situation may closely parallel that proposed for the various tissues of the pea epicotyl (7). Under the influence of the very low concentrations of auxin present in an unstimulated tendril, the latter grows more or less straight. Higher concentrations, however, produce curvature, either because of differences in the shape of the growth-concentration curves for the tissues on the two sides of the tendril, or because the maximum capacity for growth on the two sides differs.

I suggest the following mechanism for thigmotropism: The contact stimulus gives rise to an action potential 10 NOVEMBER 1967

in the tendril [observed by Umrath (8)]. According to modern theory, this action potential is associated with changed permeability of cell membranes to ions, and a consequent redistribution of ions between, for instance, the vacuole and the cytoplasm. The changed ionic environment brings about an increase in free auxin (by either releasing bound auxin or promoting synthesis) to which the two sides of the tendril respond asymmetrically.

Two of my findings possibly weigh against this proposal: the relatively slow response of the tendrils to external auxin (though this is probably due to slow penetration, as I have noted), and the fact that in its early stages the response to auxin in the floating experiments often did not resemble in form contact coiling. An alternative suggestion is that the auxininduced coiling represents not the primary swift response to touch-which is soon reversed by the straightening reaction (see 1) and which may involve a contractile protein (2)-but the continued curvature under a sustained contact stimulus which leads to a permanent grasp of the support. On the basis of the experiment shown in Fig. 2, I suggest that this permanent grasp (as well as the coiling that subsequently occurs along the entire length of the tendril, bringing the stem closer to the support) involves a supply of auxin translocated basipetally from the point of contact.

It is noteworthy that the effect of CO_2 resembles the tactile response both in form and in speed. Since CO_2 action is comparable to that of IAA in that it produces a decrease in wall pressure (9), this interesting finding appears to favor the first of my two proposals.

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Hydraulic Compression of Mice to 166 Atmospheres

Abstract. Hydraulic uniform compression elicited tremors, uncoordinated limb movements, and tonic convulsions in liquid-breathing mice at pressures ranging from 50 to 100 atmospheres. Such abnormal muscular activity was observed neither in control animals nor in mice caudally to a spinal transection. Uniform compression of isolated preparations of mouse muscle in saline failed to contract at pressures up to 200 atmospheres.

The effects of pressure on marine organisms, isolated organs, and cells have been studied since 1884 (1), and a concise review of pressure physiology has recently been written by Fenn (2). The response to uniform compression of gas-breathing animals may be modified or obscured by the pharmacological properties of compressed gases, and pressure effects in intact mammals have only been postulated thus far on the basis of indirect evidence and extrapolation (3, 4). Since mice with liquid-filled airspaces have been reported to survive submerged in hyperbarically oxygenated salt solutions (5) and in a synthetic liquid equilibrated with oxygen at atmospheric pressure (6), it has become possible to study the effects of increased ambient pressure per se in mammals directly. One can observe the behavior of intact mammals subjected to great hydrostatic pressures and compare it with the behavior of control animals at normal atmospheric pressure under otherwise identical conditions. We report here the preliminary results of a series of such experiments in which adult Swiss mice were used.

The mice were placed in a small (150-ml) pressure chamber consisting of a thick-walled perspex cylinder sealed between two circular aluminum plates which are held together by steel bolts. The mouse enters into the chamber through a hole in the top plate which is then closed by means of a plug incorporating a valve. Gas or