

cally, with the root oriented perpendicular to the direction of gravity. The initial pattern of coloration was the same as that in vertically mounted roots, that is, yellow in the elongation zone and purple elsewhere (Fig. 2A). After the root had been held in the horizontal position for about 10 to 20 minutes, this pattern began to change; the yellow zone on the upper surface of the root intensified and extended further toward the tip while, on the lower surface of the root, the purple region of the tip began to encroach on the yellow region of the elongation zone, reducing its length and intensity (Fig. 2B). Shortly thereafter the root began to curve downward, showing typical positive geotropic curvature as the yellow zone on the upper surface increased in intensity (Fig. 2C). Time-lapse movies of these events clearly show the sequence of shifts in color patterns preceding the initiation of curvature.

These data are relevant to the acid efflux hypothesis of growth regulation since they show that (i) the region of acid efflux coincides with the region of cell elongation in an undisturbed intact organ (ii) hormonal inhibition of growth in the elongation zone of roots is correlated with hormonal reversal of H^+ efflux from these cells, and (iii) predictable changes in H^+ efflux patterns accompany geotropically induced shifts in growth patterns. Thus the H^+ efflux patterns are closely tied to the growth of the organ (7) rather than to some other physiological function such as ion uptake.

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3. The medium consists of a 4-mm-thick plate of 0.6 percent agar containing 0.71 mM bromocresol purple plus the following inorganic nutrients: 1.5 mM $Ca(NO_3)_2$; 1 mM each of $MgSO_4$, KH_2PO_4 , and KNO_3 ; 20 μM H_3BO_3 ; 3.8 μM $ZnCl_2$; 0.18 μM MoO_3 ; and 0.14 μM $CuCl_2$. The primary root is pressed lightly into the medium so that about half of the cylindrical root is embedded. Under these conditions the roots grow at a normal rate (1.5 to 2.5 mm per hour) during the entire course of the experiment (up to 48 hours).
4. The region of cell elongation is determined by marking the root surface with India ink at 1-mm intervals and observing the displacement of the marks during elongation. This method shows that the elongation zone extends from a point 2 to 3 mm from the tip to about 10 mm from the tip, the most vigorous elongation being in the region extending from about 2 to 7 mm from the tip. As the root grows along the agar-dye medium it leaves a yellow trail, which is caused by acid efflux from the elongation zone. There is also a region of acidity adjacent to the root hair zone. This accounts for the second yellow zone in some of the figures, for example in Figs. 1A and 2C; IAA appears not to affect H^+ efflux from the root hair zone.
5. By this method we measure only pH change and cannot distinguish between effects caused by H^+

- uptake and OH^- efflux. However, Weissenel *et al.* (2) measured pH shifts and electrical currents in barley roots and concluded that the observed electrical currents were due primarily to flow of H^+ ; they reported that the direction of H^+ efflux is into the elongation zone of barley roots, the opposite of what we report for corn roots. We have examined acidification patterns in barley roots and find the same pattern of coloration as that reported by Weissenel *et al.*: purple at the tip and yellow farther back. However, we find that the zone of active elongation is in the yellow (most acidic) region, not near the purple (less acidic) tip.
6. Experiments showing apparent acidification and auxin reversal of acidification in the elongation zone of growing roots were done at least 200

times. Experiments showing unilateral acid efflux during geotropism in growing roots were done 80 times.

7. Unilateral hydrogen ion efflux also accompanies positive geotropism in shoots (preferential acid efflux on the lower side of geostimulated corn coleoptiles) as well as positive phototropism (preferential acid efflux on the dark side of unilaterally illuminated sunflower hypocotyls). This indicates that differential hydrogen ion efflux may be generally involved as a mediator of tropic responses in plant organs.
8. Supported by NSF grant PCM 780581. We thank K. Kuzmanoff for technical assistance and advice.

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Meprobamate Reduces Accuracy of Physiological Detection of Deception

Abstract. Normal male subjects attempted to deceive an experimenter recording electrodermal, respiratory, and cardiovascular activity. Those who had ingested a placebo or nothing were detected with statistically significant frequency on the basis of their phasic electrodermal responses, which clearly distinguished them from truthful suspects. That was not the case with deceptive subjects who had ingested 400 milligrams of meprobamate, nor did the examiner detect which subjects had received the drug.

The psychophysiological detection of deception depends upon the subject's having larger physiological reactions to questions associated with deception than to control questions (1). Despite both laboratory support for the basic premises underlying the procedure and its widespread use in police investigations and personnel screening, the validity and reliability of the polygraph test have yet to be established and remain a subject of controversy (2, 3).

We have investigated the detection of deception both as a practical problem and as a model for studying social stress (1). One question that is important for both purposes is whether a tranquilizer selectively reduces the physiological response to social stress—in this instance, the stress of attempting to deceive. Professional polygraphers have assumed that tranquilizers might reduce the physiological response to all test questions as part of a general reduction in tonic arousal levels but that the difference in reactivity to critical and control items would be unaffected (4, 5). Clinical and pharmacological views of tranquilizers, however, suggest otherwise (6); that is, the effect of a tranquilizer might be precisely to reduce the physiological correlates of fear or anxiety concerning the critical questions.

Empirical evidence for either view is sparse (7, 8). Antianxiety drugs have been shown to reduce the electrodermal response (EDR) to some stressful stimuli, such as anticipation of shock, "emotional" words, or riding a Ferris wheel (9), but their effects on the EDR to more

common and natural social stressors such as interpersonal conflict have not been investigated.

We report here a double-blind test of the effects of a tranquilizer, meprobamate, on polygraph test results (10). It was hypothesized that the EDR would accurately discriminate between truthful subjects and deceptive subjects who had not ingested a tranquilizer, as in previous studies (1); that deceptive subjects who had taken a placebo would also be accurately discriminated from truthful subjects and would not differ from deceptive subjects who had taken no drug; and that deceptive subjects who had ingested a tranquilizer would not be discriminated from truthful subjects by their EDR's but would be discriminated from no-drug and placebo-treated deceptive subjects. We also tested whether the experimenter could judge which subjects had ingested a tranquilizer, because it has been suggested (4, 5) that a tranquilizer would produce overt effects that would be readily discernible to the experienced examiner.

Each subject (11) was randomly assigned to either guilty ($N = 33$) or innocent ($N = 11$) conditions (12). Guilty subjects completed an overlearning task that ensured their sensitization to six common words and were told it would later be their task to convince a polygraph operator that they had not memorized any words. Guilty subjects were randomly assigned on a double-blind basis to one of three groups. Subjects who ingested a pill were told that they were being given a tranquilizer that would

Table 1. Number of subjects classified as "deception indicated" (DI) or "no deception indicated" (NDI) for each physiological measure, and examiner's judgment of subjects as tranquilized (T) or not tranquilized (NT).

Group	Electro-dermal		Cardio-vascular		Respira-tory		Examiner's judgment	
	DI	NDI	DI	NDI	DI	NDI	T	NT
Innocent	0	11	1	10	1	10	2	9
Guilty: no pill	9	2	0	11	4	7	5	6
Guilty: placebo	8	3	2	9	3	8	3	8
Guilty: meprobamate	3	8	0	11	5	6	0	11

help them avoid detection; 11 of these subjects were given 400 mg of meprobamate orally, the typical minimum clinical dose (6), and the other 11 were given a placebo. The remaining guilty subjects and the innocent subjects were given nothing.

Thirty minutes later (13) experimenter 2, who did not know the subject's assignment, attached him to the polygraph (14) and began the test, using the "guilty knowledge" technique (15). The question list consisted of 24 words, four in each of the six semantic categories, one of the four being a word the guilty subjects had memorized. The subject was asked whether any of the 24 were words he had learned. The interstimulus interval was 10 seconds. The list was prefaced with a dummy word so that the typically large initial response would not be to any of the test items. After the test the examiner completed a rating scale indicating whether the subject appeared to have taken a tranquilizer (16).

Amplitude of the EDR, smallest inspiration, and change in relative blood pressure following each stimulus were scored in millimeters, by research assistants who had no opportunity to observe the subject, and number of lies detected was scored separately for each channel (17). There are several ways to evaluate such data statistically. We report the analysis that provided the most accurate discrimination between truthful and deceptive subjects. Each guilty subject knew six critical items of information, one from each of six semantic categories, and the list was presented twice, so that each guilty subject lied 12 times. The probability of a subject's reacting more to a critical item than to any of the three control items purely by chance is .25. Thus, even an innocent subject might be expected to give as many as three responses indicating deception purely by chance. For a final classification of "deception indicated" (Table 1), we adopted a conservative criterion of five items with responses indicative of deception.

The EDR identified most guilty subjects in the no-pill and placebo groups;

the differences between those groups and the innocent group are statistically significant, $P < .005$ and $P < .005$, respectively, by Fisher's exact probability test (18). Most meprobamate subjects, however, were mistakenly classified as truthful; and the discrimination between meprobamate and innocent groups was not statistically significant. The meprobamate group differed significantly from both the no-pill and the placebo groups, $P < .01$ and $P < .04$, respectively, by Fisher's exact probability test.

These results were not due to lack of electrodermal responsiveness among drug subjects; there were no differences among the four groups in the mean number of critical words ($\bar{X} = 10$ for all subjects) that evoked a measurable EDR. Thus, although all subjects responded electrodermally throughout the test, the drug subjects did not respond more strongly when lying than when telling the truth, whereas the guilty no-pill and placebo subjects did (19). The groups did not differ in the mean amplitude of the EDR to all questions, but there was a tendency for the meprobamate subjects to give smaller EDR's as the test progressed; comparison of the mean EDR to the first presentation of the word list with the mean EDR to the second showed the effect to be most striking with the drug subjects ($t = 2.37$, d.f. = 10, $P < .05$). For the other groups the decline in amplitude was not statistically significant ($t = 0.27$, d.f. = 10 for the innocent subjects; $t = 0.34$, d.f. = 10 for no-pill subjects; and $t = 0.27$, d.f. = 10 for placebo subjects).

The respiratory and cardiovascular measures did not discriminate between guilty and innocent subjects. The superior detection with the EDR is consistent with other studies in which detection was scored blindly and separately for each channel (20, 21).

The examiner's judgments of whether a subject had received a tranquilizer did not approach significant accuracy. In clinical studies ratings of patients do discriminate between placebo and tranquilizer conditions (22), but patients in

such studies have typically been observed over a considerable period of time under both drug and placebo conditions. The field polygraph examiner has, as in the present study, little or no previous experience with the subject to provide a baseline for the judgment. Other studies suggest that clinical doses of minor tranquilizers do not cause overt impairment of behavior or performance (23).

It is possible that meprobamate is effective in the experimental laboratory but would be ineffective in the field lie-detection laboratory, where fear of detection is presumably greater. It should be noted, however, that 400-mg doses of meprobamate are effective in reducing the anxiety of psychiatric patients (24). It is also possible that substantially higher doses than we used here could be used unobtrusively to defeat the field test; several studies (23) show no evidence of observable behavioral impairment with single doses of 800 mg. Finally, it may be that meprobamate would be ineffective with the "control question" test more commonly used in the field. Since for guilty subjects there is little difference in principle between the two types of test, the differences arising mainly for innocent subjects (15), the present results may well generalize to the control question test. On the other hand, the more arousing circumstances surrounding a field test and the more intrusive questioning practiced by field examiners might overcome any effects of a tranquilizer.

Nonetheless, the results reported here are consistent with the hypothesis, based on clinical observations, that minor tranquilizers such as meprobamate selectively reduce the phasic physiological response to disturbing social stimuli rather than simply lower tonic levels of arousal.

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 10. In field polygraph testing the actual guilt or innocence of subjects usually does not become established for a long time, if at all. More serious for the purpose of scientific investigation is that the ultimate disposition of the case cannot be considered to be independent of the polygraph test outcome; suspects who appear truthful may not be examined as thoroughly as those who appear deceptive. Finally, it is not typically feasible to introduce experimental treatments, such as tranquilizers, into field polygraph tests. Consequently, we must depend upon laboratory experiments. The experimental subject cannot be expected to suffer the same degree of apprehension as the field subject. Although this must be kept in mind, it would be an obstacle to experimental research only if the detection of deception failed under such conditions. Many studies document the effectiveness of the psychophysiological detection of deception in the laboratory, particularly with the guilty knowledge test.
 11. The subjects were male college students, 18 to 24 years of age, recruited through advertisements and paid \$2 an hour.
 12. "Guilty" subjects were told that the polygrapher would do his best to obtain a confession but that it was possible to "beat the polygraph" by controlling one's emotions. "Innocent" subjects were told that the polygraph examiner would suspect them and that it was often very difficult to prove one's innocence in a lie-detection test. As a test of their "ability to perform under stress," the innocent subjects completed the same timed, interpolated tasks as did the guilty ones, but without learning words.
 13. Meprobamate taken orally reaches its peak plasma concentration in 1 to 2 hours [B. J. Ludwig and J. R. Potterfield, in *Advances in Pharmacology and Chemotherapy*, S. Garattini, A. Goldin, F. Hawking, I. J. Kopin, Eds. (Academic Press, New York, 1971), vol. 9].
 14. Experimenter 2 was a male medical student. Sensors were attached as in field exams, a blood-pressure cuff on the left arm, EDR electrodes on the first phalange of the second and third fingers of the right hand, and a respiration belt around the chest; recordings were made on a Stoelting polygraph.
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 16. Finally, experimenter 3 conducted a postexperimental interview and debriefing and answered the subject's questions about the experiment.
 17. Amplitude of the EDR, suppression of breath amplitude, and amplitude of the cardiovascular response for each stimulus were measured as in Thackray and Orne (20). Detections were scored separately for each channel. A detection was counted if the critical stimulus in a set of four words evoked a larger physiological response than any of the three other items. For innocent subjects one word in each category was randomly designated to be the critical item for purposes of analysis.
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Pheromonal Control of Dealation and Oogenesis in Virgin Queen Fire Ants

Abstract. *In the fire ant Solenopsis invicta, sexually mature virgin females are prevented from shedding their wings and becoming functional egg layers by the presence of the mated queen. Experimental data suggest that this inhibitory effect results from the action of a relatively nonvolatile primer pheromone (or pheromones) produced by the mated queen and distributed by the workers. Target ants are both virgin queens and workers.*

In most species of social insects individual colonies have only one queen (1). Virgin queens are reared seasonally, but these do not become reproductively active until they have either left the parental nest to mate and found colonies of their own, as in ants, wasps, and termites, or until the old queen has left with a swarm, as in honey bees. It has been generally assumed that, among the ants, either the act of shedding the wings (dealation) after a mating flight, or flight itself, initiates the complex physiological and behavioral changes in newly mated queens that permit them to found new colonies (2). One of the most significant of these changes is the development of eggs in the ovaries (oogenesis) with materials from the now defunct flight muscles and from the fat body. In the fire ant, *Solenopsis invicta* Buren, the fundamental processes of dealation and oogenesis are usually prevented from occurring while virgin queens are still in the parental nest by the presence of one or more primer pheromones secreted by the mother queen (3).

During 1979 we collected 151 colonies of *S. invicta* in the state of Georgia, for laboratory study. About 2 weeks after collection, when the ants had moved

from the soil into artificial nests (4), we found a single mated queen in each of 58.3 percent of the colonies. Among the remaining colonies were many that appeared to be polygynous, but dissection of all the queens present showed that none was inseminated, although some had many mature oocytes in their ovarioles. Since these colonies also contained worker pupae, we assumed that they had been orphaned during collection, and we hypothesized that the presence of the mother queen of a colony prevents dealation and oogenesis among sexually mature virgin females (5).

To test the hypothesis, we orphaned colonies containing sexually mature virgin females. Dealates began to appear within 24 hours, and a few days later the workers started to execute some of them (6). Dealation ceased while numerous female alates were still present, but execution of the dealates continued for up to 3 weeks until very few remained. These few had enlarged ovaries containing numerous oocytes. It seemed, therefore, that they had taken over the egg-laying function of the mated queen and that they too could inhibit dealation among sexually mature virgin females. It was also evident that the workers would tol-