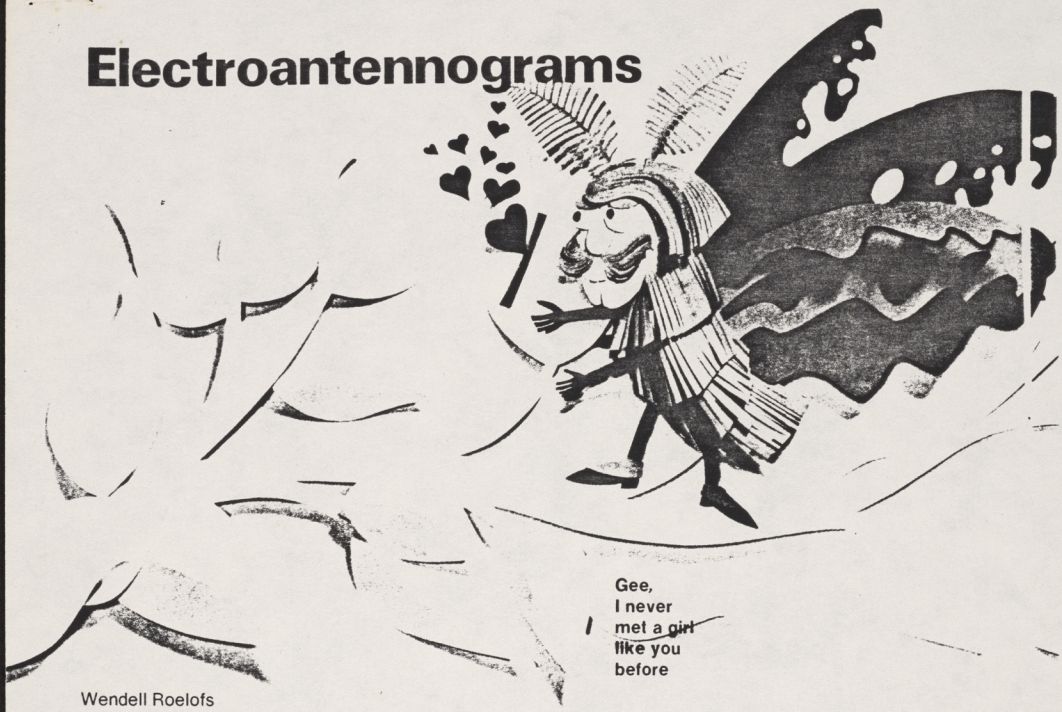
Electroantennograms



Wendell Roelofs

Did you know that insects smell with their antennae; that males find their loves by detecting their ladies' pheromones from afar and then following their antennae? What's most interesting about this concept is that understanding it enables us to control insect populations quite safely. When we spread sex attractants in fields and orchards, the males get so confused that they cannot find females with whom they can mate. One way to spread the sex attractant, the pheromone, is placing it in open-ended capillaries and having an airplane drop them about the field. Moreover, when we put some of these chemicals into traps we can follow the course of insect infestations. It is therefore important to identify such sex pheromones, and I will report here on a method that allows us to do so quickly and unambiguously.

Electroantennogram technique (*1*) measures the response of receptor cells in male insect antennae to biologically active compounds. We have used EAG with good success since the early seventies. I will illustrate the method first with the discovery of a sex attractant for the tentiform leaf miner, a moth which has experienced an upsurge and has presented a serious problem to orchards in the eastern United States and Canada.

How it's done

The moths of this particular species are extremely small—5 mm long—and thus have very small antennae. Nevertheless, it was no problem to remove the head of a male moth and position it in a piece of wax partially covered with saline solution (Figure 1). The distal end of one antenna was snipped and brought in contact with the tip of a disposable pipette containing a silver chloride-coated piece of silver wire and saline solution. An indifferent Ag/AgCl electrode was in the dish of saline solution to complete the "hook-up" of the antenna between the 2 electrodes. The high impedance signals from the antenna were fed into a 100× amplifier and then into a storage oscilloscope to observe any polarization changes of the antenna. Everything was ready to record electroantennograms.

A male moth's antenna can be a tremendous specialized instrument for detecting biologically active compounds. No other sophisticated instrument available to a chemist can duplicate the sensitivity and specificity of the male's antenna for its sex pheromone compounds. Male moth's antennae possess thousands of specialized olfactory hairs that efficiently filter chemicals from the air and respond quite specifically to those compounds that are used in their own mating communication system. This is generally true for male moths since they have short lifetimes (ca. two weeks) and their primary function is to locate a female moth to mate. Over half of the antennal receptors usually are specialized to respond to sex pheromones. For example, the male giant silkworm, *Antherea polyphemus*, antenna has more than 60 000 sensilla with 150 000 receptor cells, and over 60% of these are specialized for the pheromone components. This specificity enables a chemist to interpret antennal responses to various chemicals in relationship to the actual pheromone structures.



After positioning the male tentiform leaf miner antenna between the electrodes, we directed a stream of air across it, and puffed test chemicals into the air stream. Monounsaturated 14-carbon and 16-carbon acetates, alcohols and aldehydes did not elicit large responses from the antennal receptors, but 12-carbon acetates caused huge responses. The responses increased as the double bond was moved further from the acetate group. (*E*)-10-dodecenyl acetate (E10-12:Ac) gave a surprising 16 millivolt response (Figure 2). This was the largest response of all compounds tested and suggested that its structure was similar to that of the natural pheromone. It was an unusually large response, since responses to pheromone compounds in other moth species are usually in the 3–6 mV range.

The next step was to verify the natural pheromone structure by working with gland extracts or airborne collections from female moths. Usually extract from 10–20 females is sufficient to obtain GLC retention time data for the active components on polar and non-polar columns. Female abdominal tips are clipped into a small volume of methylene chloride and about half of it injected onto a non-polar column (OV-1). Glass capillary tubes are used to collect the column effluent in 1-min fractions. Then air is puffed through each tube onto the antenna to determine the retention time of active compounds. Most 1-min fractions will elicit responses of less than 1 mV, whereas fractions containing the major pheromone components will evoke responses of up to 6–7 mV. Responses of 1–3 mV in other fractions can indicate the presence of minor pheromone components or some related precursors. Although individual compounds elicit antennal responses, many times precise mixtures are needed for behavioral responses.

The contents of capillaries eliciting activity are injected onto a polar column (e.g., 50% cyanoethyl methyl silicone). Effluent again is collected in 1-min fractions and analyzed by EAG to obtain retention times for active components. Tubes containing activity are rinsed and the

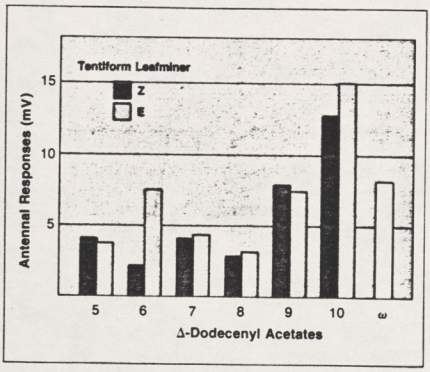


Figure 1. Male tentiform leaf miner antennal responses to a series of monounsaturated 12-carbon acetates. The greatest response was obtained with E10-12:Ac

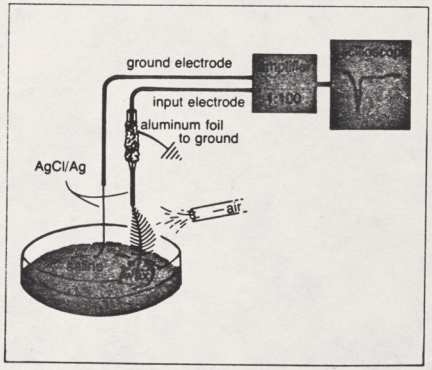


Figure 2. Diagram of an EAG setup
Test compounds are puffed into the continuous airstream from either capillary tubes containing GLC-collected material or disposable pipets with synthetic compound on filter paper strips

twice-purified compounds used for further analyses. Micro-reactions, such as saponifications, acetylations, ozonolysis, hydrogenations, can be carried out in addition to physical determinations, such as mass spectra, NMR spectra or exact GLC retention times relative to standards. If purified compounds are not needed precise retention times can be obtained by connecting the EAG directly to the GLC (*2, 3*).

The tentiform leaf miner females are extremely small and only a few individuals were available for analysis of the pheromone gland extract. Collection of extract effluent from OV-1 did not reveal any EAG-active compounds, and so we could not complete the characterization of the sex pheromone. Since the E10-12:Ac was so active on the EAG, however, it was tested in apple orchards for attractancy and luckily it turned out to be a potent lure for tentiform leaf miner males (*4*). In several weeks over 16 000 males were trapped in 5 traps, and in the next year it was used in many eastern states and Canada to monitor the presence of this pest in apple orchards. A report from Canada showed that 4 traps baited with E10-12:Ac captured 32 000 tentiform leaf miner males in two weeks. This compound is classified as a sex attractant, but not a sex pheromone since its presence in female moths was not proved.

How it started

The above story illustrates the potential of EAG analyses when only a few specimens of a species are available. It can be even more useful when a pheromone component possesses two sites of unsaturation. This was the case for our first EAG identification in 1971. We had initiated a project on the codling moth pheromone in spite of the fact that others had been working on it for several years with the availability of hundreds of thousands of female moths. Female extract of several thousand moths seemed to produce less than a nanogram of active compound, so any classical characterization approach was dependent on a huge moth rearing program. At this time, however, a graduate student, Andre Comeau, and I had become interested in the electrophysiology studies by Dietrich Schneider and his colleagues in Germany (*5*). It seemed that the EAG was as simple as an undergraduate student experiment and was easy to set up. Schneider used it to study the antennal responses of the domestic silkworm moth, *Bombyx mori*, to natural and synthetic pheromone and several analogs. Unfortunately, Comeau's background in entomology and mine in chemistry did not provide us enough confidence to put together an EAG apparatus. Finally Comeau took an electronics course and put together the essential pieces for EAG recordings.

We tested it on the redbanded leafroller moth, *Argyrotaenia velutinana*, a species for which we had identified the major pheromone component to be (*Z*)-11-tetradecenyl acetate (Z11-14:Ac). (*Editor's Note:* For those whose organic chemistry goes back a few years let it be said that Z stands for *zusammen* and in substituted ethylenes is identical to *cis*. E stands for *entgegen* and corresponds to *trans*. The value of these new notations lies in their more universal applicability to unsaturated compounds of the type



For further information see Naming and Indexing of Chemical Substances for Chemical Abstracts during the Ninth Collective Period (1972–1976), paragraph 203f.)

In playing around with the technique and the antennal responses to various materials, we found that the Z11-14:Ac compound elicited the largest response of all analogs and isomers, and that the responses to monounsaturated 14-carbon acetates became larger as the double bond position approached the 11-position from either end. Other series of compounds, such as monounsaturated 12- and 16-carbon acetates, and 12-, 14- and 16-carbon alcohols, produced substantially lower responses, although the largest response within each series was with the Δ-11 compounds. We became convinced of the predictive value of the technique.

We connected a codling moth antenna and rapidly puffed across every monounsaturated compound we had on hand. Many of the series of compounds were not complete, but the 12-carbon alcohols definitely produced the maximum responses. Within that series, the most active compounds were E8-, E9- and E10-12:OH. This did not follow the profile of responses centered on a single position as obtained with the redbanded leafroller moth, and suggested that either a diunsaturated compound or a mixture of monounsaturated compounds was involved.

We injected the extract of fifty female codling moth abdominal tips onto polar and non-polar GLC columns and assayed 1-min fractions by EAG. There was a single area of activity (5 mV) on each column with retention times relative to dodecyl alcohol of 1.15 to 1 on the non-polar column and 2.3 to 1 on the polar column. The long retention time on the polar column relative to the saturated alcohol indicated a conjugated diunsaturated compound, most likely (E,E)-8,10-12:OH. We synthesized and bioassayed this compound and its geometric isomers. The E,E-isomer produced the largest EAG response of all synthetics, it had identical retention times to the natural pheromone on GLC columns, and it was the only isomer that attracted male codling moths in the field. This strong evidence—that (E,E)-8,10-12:OH was the codling moth sex pheromone—had to await confirmation (*7*). Until that time it was only classified as a sex attractant (*6*). The compound has been used worldwide in pest management programs as a potent monitoring tool and in air permeation mating disruption programs for insect control. Similarly we were able to identify the sex pheromone of the European grape vine moth (*8*).

Normally, people send pupae to this laboratory so that



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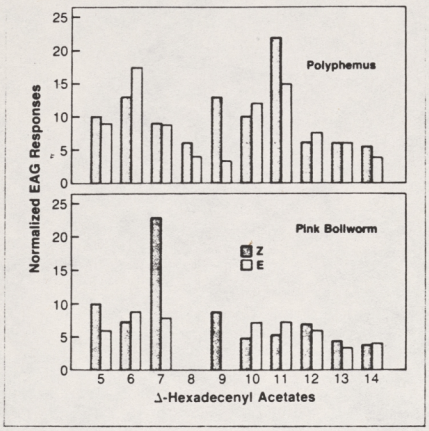


Figure 3. Male antennal responses of *A. polyphemus* (*top*) and pink bollworm (*bottom*) to a series of monounsaturated 16-carbon acetates

The *polyphemus* histogram indicates both E6 and Z11 unsaturation in the pheromone, whereas the pink bollworm does not reflect activity at the Δ11 position as found in the pheromone

we can separate the sexes and handle the moths under whatever environmental regime is appropriate. In one case, however, carpenterworm moths, *Prionoxystus robiniae*, were captured live in the forests of Mississippi and shipped to our laboratories in New York for EAG analysis. At first we got only two females and one male. EAG analysis showed that the active material was either a 14-carbon acetate or a 16-carbon aldehyde. A supply of additional male moths allowed us to test monounsaturated standards, and we found that Z3-, E4- and E5-14:Ac's elicited the best EAG responses. These data suggested that the main pheromone component could be (Z,E)-3,5-14:Ac. This compound was synthesized and several seasons of field tests in Mississippi showed that it was indeed a good attractant for carpenterworm males (*9*).

The use of monounsaturated compounds to predict the position and configuration of double bonds in a diunsaturated pheromone can sometimes be inadequate. In particular, monounsaturated standards do not always elicit good responses if their double bond represents one in the pheromone compound that is separated by several carbons from a central Z double bond. Note, for example, the results obtained with the giant silkworm, *Antheraea polyphemus*, and the pink bollworm, *Pectinophora gossypiella* (Figure 3). EAG responses with male *polyphemus* antennae showed strong responses to E6-16:Ac and to Z11-16:Ac standards. The main pheromone component as expected is (E,Z)-6,11-16:Ac compound (*10*). With pink bollworm, however, EAG standards only revealed good activity for Z7-16:Ac. The monounsaturated E11- and Z11-16:Ac compounds were no better than the other positional isomers, even though the pheromone is a mixture of (Z,E)- and (Z,Z)-7,11-16:Ac's (*11*). In this case chain distortion, owing to the Z7 double bond, modifies the juxtaposition of acceptor molecule active sites so that the monounsaturated Δ11 compounds cannot interact strongly with the corresponding Δ11 active site.

Pheromone mixtures

An extension of the above phenomenon plagued us in the identification of the potato tuberworm moth, *Phthorimaea operculella*, pheromone. A GLC-EAG analysis (Figure 4) immediately revealed one area of activity on a non-polar column close to the retention times of 13-carbon acetates. This material produced two areas of activity on a polar column at much larger retention times than saturated tridecyl acetate, indicating the presence of either conjugated or homo-conjugated double bonds. EAG responses to standards immediately revealed that the monounsaturated 13-carbon standards were very active, and that the E4- and Z7-13:Ac standards were the most active ones. Research with natural material, synthesis of (E,Z)-4,7-13:Ac and subsequent bioassays in the laboratory and field proved that this compound was identical to the first active area on the polar column (*12*). Enough natural material was collected from the second area to obtain a mass spectrum, which revealed that it was a trisubstituted 13-carbon acetate. Assuming that the second compound is related to the first, and taking into account the longer GLC retention times, we could predict that the trisubstituted pheromone component has the E4,Z7 system along with either a Δ10 or a Δ11 double bond. The monounsaturated 13-carbon acetate standards were of no use in this situation because there was little EAG activity from all isomers with the double bond positioned further out than Δ7. Without a large supply of female moths, we could only speculate as to which isomer is the correct one. Both the potato tuberworm and the pink bollworm are in the family Gelechiidae, and since the pink bollworm utilizes the 7,11 system in a 16-carbon acetate, we felt that the potato tuberworm could use the 4,7,11 system. Scientists at Zoecon synthesized the isomers of 4,7,11-13:Ac. These compounds were attractive

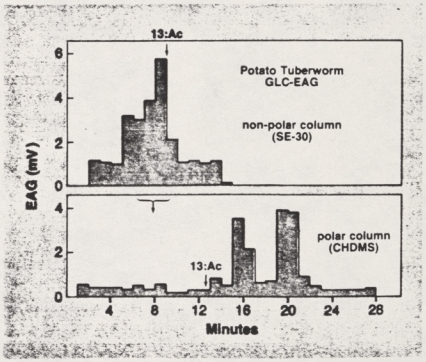


Figure 4. Male antennal responses of potato tuberworm to crude pheromone extract collected from non-polar and polar GLC columns. The activity area on the non-polar column produced two active materials when collected from a polar column

in the field to male potato tuberworm moths, but their GLC retention times were slightly different from the natural. Synthesis of the 4,7,10 system was not carried out, but research groups in Japan (*13*) and The Netherlands (*14*) solved the problem by analyzing natural material and synthesizing the (E,Z,Z)-4,7,10-13:Ac pheromone component.

Mixtures

Many species of Lepidoptera use monounsaturated compounds that are easy to identify and synthesize, but problems arise in determining the exact blend of 2–4 compounds that are utilized in each unique pheromone system. The predominant components can be identified rapidly, but some of the minor components (sometimes 1% or less) are difficult to detect. The GLC-EAG analysis can indicate the presence of some of these components, but a complete study includes laborious laboratory and field bioassays and in-depth ethological analyses of male moth behavioral responses to various pheromone extract fractions and synthetic mixtures to determine the total pheromone blend. Instead of producing a unique complex chemical for a pheromone, many moth species produce a unique blend of simple compounds (*15*). In the late 60's, we cooperated with scientists from Sault Ste. Marie, Canada, on a major forest pest, the spruce budworm, *Choristoneura fumiferana*. It is a tortricid species and we expected it to utilize a 14-carbon compound as its main pheromone component. EAG analysis with standard acetate and alcohol chemicals showed that the 14-carbon compounds elicited the greatest responses and that E11-14:OH produced the best response of all monounsaturated standards. A GLC-EAG run with pheromone gland extract revealed activity on non-polar and polar columns at retention times different from E11-14:OH and all other available standards. The retention times were different from any pheromone components previously encountered. The project was temporarily halted until we finally realized that insects also could utilize aldehydes as pheromones. It then took only a few hours to show that the retention times were identical to E11-14:ALD and a rapidly synthesized standard produced antennal responses much greater than any previously obtained. Analyses of female-produced pheromone confirmed that the main component is E11-14:ALD (*16*), but it took further capillary GLC analyses of the pheromone and field tests to unveil the importance of 3% Z-isomer (*17*).

In the case of a California grape test we found that Z11-14:Ac was active in a GLC-EAG run but inactive in field tests. Mixtures of the acetate and Z11-14:ALD were active in field tests. It turned out that the pheromone gland did not store the free aldehyde, but airborne collections of calling female effluent recovered the aldehyde in greater amounts than the acetate (*18*).

The EAG technique also played an important role in defining the pheromone for the threelined leafroller, *Pandemis limitata*. This apple-feeder was becoming increasingly abundant in New York apple orchards in the early 70's and entomologists requested an attractant monitoring trap. To accommodate this request we picked larvae from apple trees in the Hudson Valley, which is south of our laboratories and usually is two weeks ahead of our season. The larvae were brought rapidly through to the adult stage in 78 °C rearing rooms. Female pheromone extract was used in the GLC-EAG technique and we located one area of activity at the retention time of

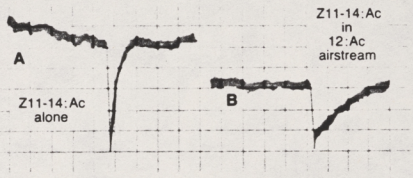


Figure 5. EAG responses of male redbanded leafroller moths to the main pheromone component, Z11-14:Ac (A), and to this compound when the antenna was continuously exposed to a secondary pheromone component, 12:Ac (B)

Z11-14:Ac. The EAG standards also showed that this compound produced the greatest EAG response of all standards. This compound, as well as various mixtures with the E-11 isomer, had been field tested during previous summers, but no males had been captured. Therefore, there must be some additional component necessary for field attractancy. A histogram of the EAG responses to all monounsaturated 14-carbon acetates showed something different in the profile of responses. The responses did not gradually increase as the double bond position approached Δ11, but rather the Z9-isomer elicited a greater response than E9, Z10 and E10. This suggested that the Z9 isomer interacted with some receptor cells more strongly than witnessed with other leafroller species that we had investigated. We searched the female pheromone gland extract and by microozonolysis were able to prove that the Z9-isomer was present in a 9:91 ratio to Z11-14:Ac. Both compounds then were fully characterized by chemical and physical means (*19*).

Another trip to the Hudson Valley at the initiation of moth flight was successful in optimizing the release rate and ratio of these two chemicals for attracting male moths to traps. With moth flight coming two weeks later in our area, we were able to provide entomologists with a good monitoring trap for the threelined leafroller before the first moth flight occurred.

Differential saturation

The EAG has proved to be a tremendous tool in pheromone identifications. Studies on the interaction of pheromone components with antennal olfactory acceptors are best conducted by single sensillum electrophysiological studies, but even here the EAG can provide some information. A differential saturation (adaptation) technique can help elucidate the olfactory receptor system (*20–22*). In this technique an antenna is exposed continuously to one pheromone component at a concentration that saturates receptors for that component and no further response is observed when that same compound is puffed across the antenna. Another pheromone component will still elicit an EAG response if it interacts with other receptors. Thus, with redbanded leafroller males, single sensillum studies (*23*) showed that there were two pheromone olfactory cells, one more responsive to Z11-14:Ac and another one more responsive to E11-14:Ac. EAG differential saturation studies (*24*) supported the presence of two functionally different

receptor sites for the Z11 and E11 isomers, and in addition it provided information on a third pheromone component, dodecyl acetate (12:Ac). Antennae continuously exposed to Z11-14:Ac still gave EAG responses to E11-14:Ac, but not to Z11, and *vice versa*. Exposure of the antenna to 12:Ac significantly slowed the response recovery rate of antennal receptors to the Z11 isomer (Figure 5), but not to the E11 isomer, suggesting that this component could function by temporal modulation of the Z11 receptors.

Although single sensillum studies (*25*) only produced evidence for one pheromone olfactory cell, differential saturation studies (*26*) with the gypsy moth, *Lymantria dispar*, gave evidence for one receptor type having greater affinity for the pheromone, (+)-disparlure [(7*R*,8*S*)-*cis*-7,8-epoxy-2-methyloctadecane] and another type having greater affinity for (−)-disparlure and the corresponding olefin, which decrease the male moth responses to (+)-disparlure.

EAG information has been used extensively for lepidopteran species. It is also used in various degrees with beetles, cockroaches, maggot flies, bees, weevils, etc., to assist in studies involving antennal responses to volatiles affecting oviposition, host attraction, mating, and other behaviorial responses. It is a simple tool, but we must remember that the information can be misleading if not interpreted correctly and not used in conjunction with proper behavioral studies.

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A socieconomic decision

What follows relates to the article which starts on p 284
read it before you read this

"Reichhold Chemicals decided to shut down permanently its phenol production facilities at its Tuscaloosa, Ala., complex. The 150 million lbs/year plant had been on a standby status (for nearly a year). The company cited changes in process technology and raw materials markets, and rising energy costs, as reasons for its decision. The closing will result in a fourth-quarter charge against income of $4.6 million and will cut 1978 per-share earnings 40¢, to less than the $1.70/share earned in 1977. Reichhold had expected 1978 earnings to be "modestly in excess" of 1977 earnings. The company said it has made long-term purchasing arrangements for its phenol requirements."

***Chem. Week*, 12/20/78**

"Reichhold Chemicals will abandon its phenol production facility at its Tuscaloosa, Ala., chemical complex. Parts of the facility have been redesigned for production of synthetic sodium sulfite, octyl phenol, and benzene sulfonic acid. The phenol produced at the plant had been used internally. The facility was something of a relic. It was the last major plant producing phenol via sulfonation of benzene, a process that has been replaced by newer techniques."

***Chem. Eng. News*, 12/18/78**