age frequency or total area of the neural activity.

Typical frequency meter and summator responses are presented in Fig. 2. The frequency meter traces show the average frequency response on the lateral nerve (L) and the medial nerve (M) for four different chemicals. The ratio of the maximum response of the lateral nerve to the maximum response of the medial nerve increases in the following order: geraniol, citral, *d*-limonene, octane.

Each frog was presented with the series of chemicals four times, and the average lateral-nerve-to-medial-nerve ratio was computed for each chemical. These ratios for the four chemicals were ranked in order of magnitude with "1" being the lowest and "4" being the highest. This procedure was followed for ten animals, and the ranks for each chemical were compared across animals to determine whether there was any consistency in the order into which the ratios fell. Figure 3 gives a graphical representation of these data. Although no chemical gave ratios confined solely to a single rank, there is a definite trend for orderliness. Statistical testing for this orderliness across the ten animals showed it to be significant ($p < .01$) (*6*).

Further statistical testing of differences between each chemical and every other chemical revealed that the differences in rank were all significant with the exception of that between octane and *d*-limonene (*7*).

Tests were conducted with four additional animals, the summators rather than the frequency meters being used (Fig. 2). During these tests two more chemicals were added, and the data were analyzed in the same manner as before. The lateral-to-medial nerve discharge ratios showed the same order noted: geraniol, citral, *d*-limonene, and octane. In addition, phenyl ether had the smallest ratio, whereas the naphthalene ratio was much like that of geraniol. The order across animals was again statistically significant ($p < .01$) (*6*).

For both the frequency meter and summator records a temporal measure was also taken, namely, the average time that elapsed between the onset of the stimulus and the point when the response reached 70 percent of the maximum. This measure of latency showed that the lateral nerve responses for all chemicals occurred later than the medial nerve responses a statistically significant number of times ($p < .01$) (*8*). The average difference between the lateral nerve response and the medial nerve response for each chemical was computed and ranked. The ranks were then compared across animals. They increased in the following order: octane, *d*-limonene, citral, and geraniol. Again, statistical testing of order across animals yielded significance ($p < .01$) (*6*). Likewise, all the average temporal differences between chemicals were significantly different from each other except that of geraniol and citral (*7*).

These data strongly suggest that the input to the central nervous system from the olfactory peripheral system differs in temporal and spatial discharge pattern for different chemicals. It is possible to explain these different response levels of the two nerve branches either by unequal distribution of selectively sensitive receptors or by a mechanism such as the separation of the vapors by adsorption. It is more difficult to ascribe the temporal differences to the unequal distribution of selectively sensitive receptors. It should be noted again that the effect of concentration on the results described here is yet to be determined. At any rate there appears to be a time-space encoding of the mucosal analysis of incoming vapors.

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References and Notes

1. E. D. Adrian, *Brit. Med. J.* **1954-I**, 287; R. C. Gesteland, J. Y. Lettvin, W. H. Pitts, A. Rojas, in *Olfaction and Taste*, Y. Zotterman, Ed. (Pergamon, New York, 1963), p. 19.
2. E. D. Adrian, *Anneé Psychol.* **50**, 107 (1950); M. M. Mozell, *J. Neurophysiol.* **21**, 183 (1958).
3. W. E. LeGros Clark, *Nature* **165**, 452 (1950).
4. M. M. Mozell, *Am. J. Physiol* **203**, 353 (1962).
5. L. M. Beidler, *J. Neurophysiol.* **16**, 595 (1953).
6. As tested by the Kendall coefficient of concordance described in S. Siegal, *Nonparametric Statistics* (McGraw-Hill, New York, 1956), pp. 229–239.
7. As tested by the Wilcoxon matched-pairs signed ranks test described in S. Siegal, *ibid.*, pp. 75–83.
8. As tested by the sign test described in S. Siegal, *ibid.*, pp. 68–75.
9. Supported by NIH grant NB 03904–02.

2 December 1963

Variation in the Monoterpenes of Pinus Ponderosa Laws

Abstract. *Wide differences from tree to tree were found in the monoterpene composition of the wood oleoresin of ponderosa pines located in the same geographic area in California. Differences attributable to variation within the tree, to the season of sampling, to the year of sampling, and to methods of analysis by gas chromatography were only slight. There may be an inverse relation between the amounts of* Δ_3*-carene and* β*-pinene in a given tree.*

Few data are available on the extent to which the terpene composition of the wood oleoresin of pines varies within the species. Hagen-Smit *et al.* (*1*) analyzed the resin of 19 samples of *Pinus washoensis* and found variation in the density, index of refraction, and specific rotation of their turpentines. Specific rotation varied from plus 10 to minus 9 degrees, and the difference was attributed to varying quantities of Δ_3-carene and β-pinene. Bannister *et al.* (*2*) observed only slight differences between trees of *P. radiata* and *P. attenuata.* In ten trees of *P. maritima* and three trees of *P. pinaster* Sandermann (*3*) found differences in the percentage of α-pinene and β-pinene. Mirov's (*4*) comprehensive review of pine turpentines contains much data on the interspecies differences in terpene composition, but only limited data on intra-

Table 1. Percentage of monoterpenes in the volatile oils of selected ponderosa pines.

α-Pinene	β-Pinene	Δ_3-Carene	Myrcene	Limonene	β-Phellandrene	Unknown
7.7	8.9	65.9	8.5*	5.0	0.9	3.1
4.5	17.2	29.6	15.2	30.7*	1.8	0.8
11.5	55.3*	0.4	15.5	15.5	1.8	0.0
8.7	21.4	28.8	14.4	23.2	2.4	1.1
4.0	14.4	27.3	24.9*	26.5	1.8	1.1
4.0	16.5	52.6	10.3	12.3	1.9	2.4
6.2	16.7	59.2	15.5	†	0.3	2.1
1.5*	0.1*	82.5	11.1	1.5	1.4	1.9
13.3*	57.5*	†	8.2	12.0	1.8	1.7

* Extremes indicated. † Trace.

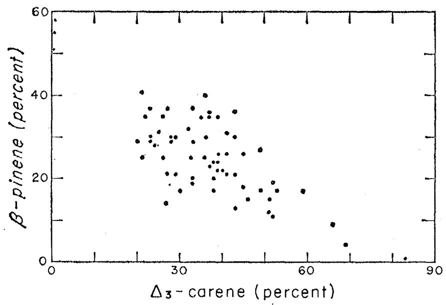

Fig. 1. Relationship of β-pinene and Δ_3-carene in the oleoresin of 64 ponderosa pines.

Table 2. Range in amount (percentages) of monoterpenes in the oleoresin of 64 ponderosa pines.

Terpene	Average	Minimum	Maximum
Δ_3-Carene	36.2	*	82.5
β-Pinene	26.4	*	57.5
Limonene	14.5	*	30.7
Myrcene	13.3	4.6	27.5
α-Pinene	6.3	1.5	13.3
β-Phellandrene	1.8	0.3	3.7
Unknown	1.5	0.0	3.1
Camphene and heptane	*	0.0	*

* Trace.

specific differences, most of which is expressed by optical rotation.

During studies on the relation of resin to the resistance of pines to bark beetles (*5*), large differences were found among ponderosa pine trees (*Pinus ponderosa* Laws.) in the monoterpene composition of their wood oleoresin. This tree is economically the most important and ecologically one of the most widespread pines in western North America. The 64 trees examined were located in several plots in the central Sierra Nevada in California from Lake Tahoe to Placerville and in one plot in the Warner Mountains north of Alturas. All resin was collected with a closed-face microtap (*6*). The freshly collected resin was processed for gas chromatographic analysis either by (i) petroleum ether extraction or (ii) molecular distillation with a Hickman still at 40°C for 24 hours at atmospheric pressure. There was essentially no difference in the terpene composition of the extract and the distillate.

The analyses were made with a thermal conductivity detector and a stainless-steel column (2.5 m by 0.6 cm) packed with 10-percent or 20-percent oxydipropionitrile on 60- to 80-mesh acid-washed chromosorb W (*7*). The conditions of operation were temperatures of 120° to 130°C on the injector, 55° to 60°C on the column, and 145° to 151°C on the detector; filament current, 200 ma; helium flow, 90 or 60 ml per minute at the outlet port; and sample size, 0.2 to 4.0 μl.

Qualitative determinations were made by comparing relative retention times for the oxydipropionitrile columns and for a LAC-446 column (*8*) with data from the literature, with known compounds, and by internal standardization with known compounds. Quantitative determinations were made by internal normalization of disk integrator values. The two columns agreed in both qualitative and quantitative analyses.

No qualitative and practically no quantitative differences in monoterpene composition could be associated with the way in which the sample was prepared, the variations of column and the instruments used within the stated limits, the time of the flow of resin after wounding the tree, circumferential and vertical position of the source of the resin within a tree, the time of sampling within and between seasons of the year, and the year of sampling. No differences were found in 60 duplicate sets of samples representing changes in time or place within trees.

There was, on the other hand, great variation in the quantitative terpene composition of the wood oleoresin between individual trees (Table 1) and a wide range of difference within the 64-tree sample (Table 2). Several of the values for the extremes were greater than those obtained by Mirov (*4*) in his analysis of bulk samples from 12 widely separated areas in western United States. There was a tendency for inverse relationship between the amounts of Δ_3-carene and β-pinene (Fig. 1).

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References and Notes

1. A. J. Hagen-Smit, C. T. Redemann, T. H. Wang, N. T. Mirov, *J. Pharm. Sci.* **39**, 260 (1950).
2. M. H. Bannister, H. V. Brewerton, I. R. C. MacDonald, *Svensk. Papperstidning* **62**, 567 (1959).
3. W. Sandermann, *Holzforschung* **16**, 65 (1962).
4. N. T. Mirov, *U.S. Dept. Agr. Tech. Bull. 1239* (1960).
5. R. H. Smith, *J. Econ. Entomol.* **54**, 365 (1961).
6. ———, *ibid.*, p. 359.
7. M. H. Klouwen and R. ter Heide, *J. Chromatog.* **7**, 297 (1962).
8. R. A. Bernhard and B. Scrubis, *ibid.* **5**, 137 (1961).

28 October 1963

Dissociation of Olfactory Neural Response and Mucosal Potential

Abstract. *The olfactory mucosal slow potential decreased remarkably or disappeared when part of the mucus on the olfactory epithelium was removed with absorbent paper. In contrast, the neural response was not changed much, while unitary spikes in response to odor also appeared in the epithelium. The paper reduced the thickness of the mucus by about half, but olfactory cilia were still present. This evidence suggests that the slow potential is not the generator potential.*

Slow potentials in the olfactory mucosa in response to odors have been recorded by several investigators (*1–6*). Ottoson (*1*) proposed the name electro-olfactogram for the record of change in electrical potential led from the surface of the olfactory mucosa. This phenomenon is naturally expected to bear some causal relation to the initiation of olfactory neural activity, perhaps quite directly related to the generalized concept of a generator potential responsible for initiation of propagated action potentials which are conducted to the central nervous system by sensory nerve fibers (*7*). Indeed, Ottoson (*8*) recently interpreted the electro-olfactogram as a mass response due to contributions from many individual receptors, and he stated that it is "the generator potential of the olfactory organ." However, a few workers occasionally observed that the slow potential did not coincide with the neural discharge or the response of the olfactory bulb (*2, 4*).

Experiments to ascertain the influence of mucus thickness over the olfactory receptors on their response parameters yielded the unexpected result that the electro-olfactogram can be practically abolished without significantly affecting the neural activity. The tortoise (*Gopherus polyphemus*) preparation described by Tucker (*9, 10*) was used. The small area of the sensory epithelium to which the nerve twig projected was detected by means of mechanical stimulation (probing with a human hair) of the epithelium or by antidromic electrical stimulation of the nerve twig (*10*). To record slow potentials a macroelectrode (glass pipette with tip diameter of about 200 μ filled with Ringer's solution) and a microelectrode (less than 1 μ in tip