

This may be of practical value in the study of specific drug and surgical treatments.

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References and Notes

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- 8**, 135 (1958); F. A. Mettler, *Trans. Amer. Neurol. Ass.* **91**, 304 (1966).
 3. S. L. Liles and G. D. Davis, *Fed. Proc.* **27**, 387 (1968).
 4. Three animals were discarded from this series. One developed pneumonia postoperatively, another had a totally misplaced lesion, and one cat's cerebral cortex was noted to be grossly malformed at autopsy.
 5. H. A. Smith, *Rhubarb* (Doubleday, New York, 1946), pp. 149-151.
 6. A more extensive account of this work will be published by the NIH in the proceedings of a workshop on Psychotropic Drugs and Dysfunctions of the Basal Ganglia, which was held 31 October to 2 November 1968 in Bethesda, Md.
 7. S.L.L. was an NIH predoctoral fellow (5-F1-GM-28, 258-04) during this work, which represents part of the research toward his Ph.D.
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The "Co-" in Coevolution

In a report describing the selective pressure of grazing by butterfly larvae on flowering time of *Lupinus amplus* through control of seed production, Breedlove and Ehrlich (1) introduced the quite correct but largely irrelevant information that "also discounted is the primary role of plant biochemicals as herbivore poisons." In this connection they quoted me, again quite correctly, as considering the toxic compounds of plants to be "primarily metabolic wastes." I appreciate their publicizing my viewpoint on this basic evolutionary question, but I feel that the isolation of this reference in a report on a subject so slightly related must necessarily have left most readers wondering why it was included at all.

Opposing viewpoints have developed largely as a consequence of the antecedent interests of the proponents of each. Students of plant-animal interactions have been greatly impressed by the impact of animals upon plant evolution. Students of plant evolution have been equally impressed by the influence of the total environment upon the diversification of plants. Many have failed to give full consideration to the inherent qualities of evolving plant systems as these determine the limits of potential plant evolution. Thus, Ehrlich (2) has expressed the view that selective pressure of animal depredation has determined the qualities of chemical production by plants, focusing his attention particularly upon those plant products which repel animals and relieve from animal depredation the plants that produce them. In expressing this view, furthermore, he has rejected my position that these, as well as the toxic products of plants that inhibit potential

competing plants, are "primarily metabolic wastes." In this difference of opinion he expresses the common view of a large number of students of coevolution (of plant and animal species pairs) whereas my view is shared by many students of allelopathy (biochemical inhibition) among plants.

In allelopathic studies it is commonplace to encounter clear evidence of autointoxication traceable to the accumulation of toxic products released into the plants' own environment. The "fairy ring" effect of mushrooms is reflected in the behavior of *Helianthus rigidus*, *Hieracium pilosella*, *Salvia leucophylla*, *Artemisia californica*, and numerous other plants which inhibit chemically the growth of adjacent species but eventually suffer similar suppression when their chemical products become too concentrated in the environment (3). Were these toxic products to be retained in the protoplasm that produces them, the effects would be even more spectacular. It is therefore clear that excretion of these toxins by any means whatever is of immediate benefit to the plant that produces them. Such elimination may involve volatilization of terpenes in arid climates (4), leaching of phenols in humid climates (5), isolation in deciduous organs, or being rendered innocuous by chemical bonding as in the formation of glycosides. In any event, the primary result (in the sense of the first or most immediate) is relief from the deleterious consequence of autointoxication. There has been reported no respiring system, either plant or animal, that can long sustain its metabolic activity without production of some noxious products. Such metabolic inefficiency is estheti-

cally difficult for most biologists to accept, but this fails to alter the facts.

The retention of some toxic plant products is made possible by their isolation within the plant body or by temporary blockage of their toxic potential through chemical bonding. Plant tissues laced with such materials are often rendered immune to attack by animals or infection by pathogens to which these compounds are toxic. Such protection constitutes a secondary benefit (in the dual sense of arising later in evolutionary time and of being less immediate a necessity to survival). However, the advantage thus attained may well be the basis of selective pressure resulting in the development of high concentrations of protective toxins, providing that these are so contained as to render them innocuous to the tissues that produce them. The secondary or protective role of these toxins may well be their principal role in the present ecology of a particular species. They remain, however, primarily metabolic wastes capable of destroying the system that produces them unless they are loosed into the environment or sequestered harmlessly within the plant.

It is clear that failure to make the distinction between *primary* and *principal* might easily cloud our understanding of the origin and functions of plant-produced toxins. To regard such plant products as primarily animal toxins renders impossible the explanation of how these products came to be. Associated animals are possessed of no mechanism by means of which they can call forth *de novo* the evolution of a specific metabolic mechanism in plants. To credit them with this role in the absence of such a mechanism constitutes a teleological (almost mystical) explanation which I am sure Breedlove and Ehrlich did not intend. If, however, a plant species has several alternative and simultaneous metabolic pathways already in operation, producing varying quantities of the numerous by-products characteristic of plants, selective pressure might well increase the proportion of one of these. Thus, the toxicity to animals of these metabolic wastes, no matter how important eventually, is subsequent and secondary to their elimination from protoplasm. No useful purpose is served by simplifying this explanation beyond the limits of reality.

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6. The investigations basic to this position statement were supported by grants GB-149, GB-4058, and GB-6814 from the National Science Foundation.

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Discriminative Control of "Attention"

Heinemann *et al.* (1) suggest that discriminative control by an auditory frequency dimension over the key-pecking of pigeons may be under the discriminative control of another dimension. They concluded that the auditory dimension controlled the distribution of pecks between two keys when the keys were one color and not when the keys were another color. Their procedure was designed to provide two conditions for the pigeons—tone relevant and tone not relevant—with a different key-color associated with each condition. Because the pigeons behaved as though the tone were relevant when the keys were one color and not when the keys were the other color, one might assume that there was discriminative control by some visual dimension, presumably wavelength, throughout the generalization tests.

The experimental procedure was symmetrical with regard to color and tone frequency, except that color differences were introduced before tone differences and generalization functions were gained with respect to tone frequency alone. The same procedure could also have been formulated to provide two other conditions for the pigeons (color relevant and color irrelevant), and similar generalization functions (for wavelength) could have been obtained with equal facility. Had this been done, one might conclude that control by wavelength was conditional on tone frequency, and hence, that control by tone frequency was evident throughout the generalization tests.

Thus, although the auditory dimension may not have controlled the distribution of pecks when the keys were one color, the conclusion that the auditory dimension was completely without influence during some generalization test trials must be treated with reservation. Goldiamond (2) has made a useful distinction between dimensional stimulus control (control by a dimension over behavior) and instructional stimulus control (environmental control over which dimension controls behavior). To

rephrase the conclusion of Heinemann *et al.*, in their experimental situation wavelength exerted instructional control over whether the tone frequency had dimensional control. Because of the symmetry of the procedure with respect to wavelength and tone frequency, one must presume that each dimension exerted instructional and dimensional control during the generalization tests, with the instructional control continuously available and the dimensional control evident only when appropriate.

Such an analysis of the gaining of control by two features of a compound stimulus may not be justified. Nevertheless, the possibility of two kinds of stimulus control remains intriguing and, as Heinemann *et al.* suggest, raises problems for current theories of stimulus generalization. It is probably difficult to provide a demonstration of exclusively instructional control by one dimension over a single other dimension. It might be possible, however, to place a pigeon's pecking under the control of either the intensity or the wavelength characteristics of a transilluminated key, depending on the value of an auditory dimension which has only instructional control.

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In a more complete experiment that included the conditions discussed by Gilbert, we followed our procedure (1), except that the two stimulus continua were the radiance of white light and the intensity of white noise. Generalization curves for each dimension were obtained in the presence of each of a large number of stimuli from the other dimension. The results are as surmised by Gilbert; the steepness of the noise curves varies

as a function of the radiance of the light, and the steepness of the light curves varies as a function of noise intensity. In particular, the generalization functions for noise and light that were obtained in the presence, respectively, of the radiance associated with condition "noise not relevant" and the noise intensity associated with condition "light not relevant" are horizontal lines.

Provided that control by a stimulus dimension is defined in terms of observed variations in behavior there appears to be no room for argument: in the presence of the stimulus quantity associated with the "not relevant" condition the "irrelevant" dimension has no control over behavior. This conception of control, however, leads to a paradox. When a pigeon is presented with the combination of stimuli consisting of the radiance associated with condition "noise not relevant" and the noise intensity associated with condition "light not relevant", neither dimension can be said to control the behavior; yet the pigeon responds to the disk that is appropriate when these dimensions do control his behavior. One way to avoid this paradox is not to assume that each dimension exercises instructional control over the other. It should be noted that although the symmetrical formulation proposed by Gilbert adequately describes the data, it involves a redundancy. All that is required for a full description of the data is an expression showing how the form of the generalization curves for one of the dimensions varies with stimulus values from the other dimension. This means that a theory which assumes instructional control by only one dimension is compatible with the data. To avoid the paradox it is necessary only to assume that on a given trial only one of the dimensions exerted instructional control. The dimension which exerts instructional control might change from trial to trial. Whether this is what happened or whether one dimension exerted instructional control throughout cannot be decided on the basis of our experiments.

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