

ences, as if they were indifferent to the occurrence of shock. This behavior contrasted sharply with that of animals in the other two groups: every rat easily learned to reverse its choice as the conditions changed.

Since rats are known to have position preferences in many choice situations, a nonreversal control group was added to determine the extent of position preference (fixation) in the present apparatus. Nine rats were given 25 choice sessions corresponding to the 25 reversal days. These rats chose between two equally rewarded levers. They were never exposed to conflict or to shock. Under these conditions, a few rats developed position preferences, but only two rats showed extreme preference; a majority continued to choose both levers. The average fixation for this food-food control group (0.749) was significantly less than the fixation found in the conflict reversal group (0.907) ($t = 2.81$, $P < .02$), and the distributions of scores in these two groups were noticeably different.

Thus, the occurrence of fixated behavior in the conflict-reversal situation is considerably greater than the position preference that would occur without punishment. Further, the extremely fixated behavior must be considered as a direct result of the conflict situation, since other groups reversed normally. Evidence of stereotyped responding was observed in earlier experiments that used the conflict procedure with a single response (9). This latest indication of response fixation is a much more striking instance of strange behavior. Animals choose to endure conflict and punishment when they could easily avoid it by choosing a rewarded alternative, which is always available. This peculiar fixated behavior is not predicted by current reinforcement or conflict theories (10).

EILEEN B. KARSH

Department of Psychology,
Temple University,
Philadelphia, Pennsylvania 19122

References and Notes

1. R. M. Church, *Psychol. Rev.* **70**, 369 (1963).
2. B. F. Skinner, *The Behavior of Organisms* (Appleton-Century, New York, 1938).
3. N. R. F. Maier, *Frustration* (McGraw-Hill, New York, 1949); J. H. Masserman, *Behavior and Neurosis* (Univ. of Chicago Press, Chicago, 1943).
4. R. L. Solomon, *Amer. Psychol.* **19**, 239 (1964).
5. N. H. Azrin and W. C. Holz, in *Operant Behavior: Areas of Research and Application*, W. K. Honig, Ed. (Appleton-Century-Crofts, New York, 1966), pp. 380-447; R. M. Church, in *Punishment and Aversive Behavior*, B. A. Campbell and R. M. Church, Eds. (Appleton-Century-Crofts, New York, 1969).
6. A. J. North, *J. Comp. Physiol. Psychol.* **43**, 442 (1950).

7. E. B. Karsh, *Proc. 76th Annu. Conv. Amer. Psychol. Ass.* (1968), p. 153.
8. J. W. M. Whiting and O. H. Mowrer, *J. Comp. Psychol.* **36**, 229 (1943); H. Fowler and G. J. Wischner in *Punishment and Aversive Behavior*, B. A. Campbell and R. M. Church, Eds. (Appleton-Century-Crofts, New York, 1969).
9. E. B. Karsh, *Science* **140**, 1084 (1963).
10. N. E. Miller, in *Psychology: A Study of a Science*, S. Koch, Ed. (McGraw-Hill, New York, 1959), vol. 2; J. P. Seward in *Punishment and Aversive Behavior*, B. A. Campbell and R. M. Church, Eds. (Appleton-Century-Crofts, New York, 1969).
11. Supported by PHS grant MH 14091 from the National Institute of Mental Health. I thank Barbara J. Granger for experimental assistance and William Roth, Jr., for instrumentation.

22 August 1969; revised 17 February 1970

Brood Care in Halictid Bees

Knerer (1) found that mature larvae of the social halictine bee, *Evylaeus malachurus*, weighed 60 percent more than provisions bearing eggs. He suggested that this weight gain was due to progressive provisioning by the adult bees, although such behavior apparently was not observed.

We report a similar gain in total weight of cell contents during the larval growth of the solitary halictid *Notomia melanderi*, the adults of which have no contact with healthy larvae (2). This weight gain is evidently due to the intake of atmospheric water by the provisions. The hygroscopic nature of honey and of the provisions of several species of wild bees is known (3).

Cell contents of *N. melanderi* changed in total weight with larval development as follows: cell contents, placed in sealed tared vials in the field, after initial weighing were oven-dried at 100°C to a constant weight to determine free water content. Tabulation of results showed:

1) Egg or small larva with provisions: $N = 48$; live weight mean ($\bar{X}$), 0.1369 [range (R), 0.0866 to 0.1777] g; dry weight $\bar{X}$, 0.0829 (R , 0.0606 to 0.0942) g; water content 39.5 percent.

2) Half-grown larva with provisions: $N = 24$; live weight $\bar{X}$, 0.2131 (R , 0.1897 to 0.2548) g; dry weight $\bar{X}$, 0.0724 (R , 0.0615 to 0.0881) g; water content 66.0 percent.

3) Mature larva before defecating, all provisions consumed: $N = 40$; live weight $\bar{X}$, 0.2342 (R , 0.1883 to 0.2695) g; dry weight $\bar{X}$, 0.0661 (R , 0.0442 to 0.0743) g; water content 71.8 percent.

Mature larvae of *N. melanderi* weighed 58.5 percent more than provisions bearing eggs. There was an average gain in live weight of 0.0973 g

during larval growth, but there was a mean loss in dry weight of 0.0168 g, perhaps due to respiration.

Although a species of social halictine has been seen touching provisions bearing eggs with its glossa, this possible provisioning behavior occurred rarely and several other social halictines did not do this (4). The large size of the mature larvae of these and other halictine bees relative to the size of the provisions (5) is probably due to the hygroscopic nature of the provisions as in *N. melanderi* and probably is not due to any significant amount of progressive provisioning.

S. W. T. BATRA

G. E. BOHART

Entomology Research Division,
Agricultural Research Service, and
Utah Agricultural Experiment Station,
Logan 84321

References

1. G. Knerer, *Science* **164**, 429 (1969).
2. S. W. T. Batra and G. E. Bohart, *ibid.* **165**, 607 (1969); S. W. T. Batra, *Ann. Entomol. Soc. Amer.* **63**, 400 (1970).
3. S. I. Malyshev, *Eos* **11**, 249 (1935).
4. S. W. T. Batra, *Insectes Soc.* **11**, 159 (1964); *J. Kansas Entomol. Soc.* **41**, 120 (1968).
5. F. Claude-Joseph, *Ann. Sci. Natur. Zool. Biol. Anim.* **9**, 113 (1926); J. H. Fabre, *Bramble-Bees and Others* (Dodd, Mead, New York, 1915).

9 February 1970

Interaction of Plant Hormones: Absciscic and Gibberellic Acids

Drury has recently proposed that the definition of interaction used by statisticians should be used to describe results of physiological experiments (1) but states it in a restricted form. The statistical definition he quotes confines the term interaction to a numerical value which is the difference between a measurement (R) of the response of a system to the action of two factors (A and B) applied together, when compared with the sum of the measurements of responses (R_A , R_B) to the two factors applied separately; the interaction (I_{AB}) is defined by the equation:

$$R = R_A + R_B + I_{AB} \quad (1)$$

Defined in this way, interaction has a precise meaning for the statistical analysis of received measurements and has been fully discussed by Lockhart (2). Drury's application of this statistical definition of interaction to physiological phenomena is, however, oversimplified. This is because the statistical operations generally work with the data on the scales in which they are pre-

sented. It is often possible, by a suitable transformation of scales, to obtain measurements of response that are additive and lack an interaction term, although the response is not the sum of the two effects applied independently. Until the actions of A and B have been defined in biochemical terms, the selection of an appropriate transformation must remain empirical; if there are sufficient data to define the separate dosage-response curves for A and B, then the equations of the curves indicate suitable transformations. The response of a tissue is a restricted variable because its magnitude cannot exceed a maximum value; as this limit is approached the efficacy of successive increments of a treatment falls. Therefore, unless a tissue with a linear response can be chosen for a bioassay, a spurious interaction between two factors will always appear if the oversimplified definition is used. The more growth is promoted by agent A the less additional effect another growth-promoting agent B can have. For this reason, the analogy of a ball propelled upward at a given velocity from an infinitely adjustable platform (1) is invalid when applied to most physiological responses.

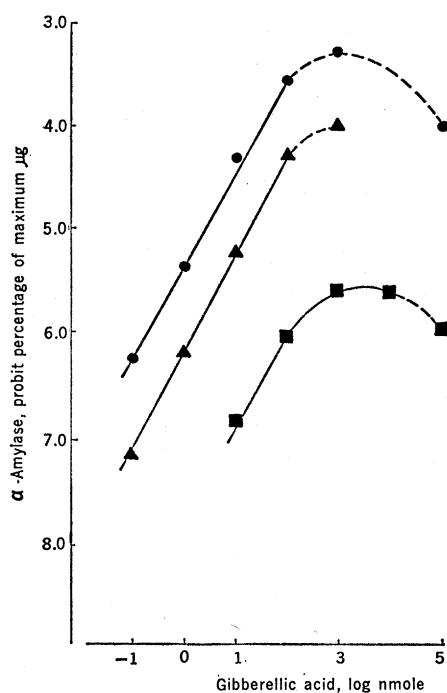


Fig. 1. The effects of abscisic and gibberellic acids, applied simultaneously, on the synthesis of α -amylase by barley aleurone. The data of Chrispeels and Varner (5) were calculated as probit percentages of the maximum value and plotted against log gibberellic acid concentration. Circles, without abscisic acid; triangles, $0.05 \mu M$; squares, $5.0 \mu M$ abscisic acid.

This limiting effect can be clearly seen in both variables in the diagram of Dey and Sircar (1, 3); a change in the concentration of gibberellic acid from 10^{-2} to 10 mg per liter caused the coleoptile sections to increase in length from 10.6 to 12.1 mm (1.5 mm) whereas when 20 units of an inhibitor are present the same change in concentrations of gibberellic acid caused an increase in length from 6.0 to 9.1 mm (3.1 mm). There is a similar disproportion in the effect of the inhibitor.

It seems best to avoid the word "interaction" in describing physiological situations in which the responses are not additive and to keep the term as an exclusively statistical description applied to measurements. When the responses to two factors are directly additive, or can be rendered so by a suitable transformation, the action of the two factors can be described as "independent." For situations in which no transformation can render the responses additive, physiologists already use the term "potentiation," and I suggest that this term should be used, to the exclusion of "interaction." These terms—*independence* and *potentiation*—can be applied whether the two factors produce responses of the same or opposite sign.

Drury examined data of the effects of a growth-stimulating plant hormone, gibberellic acid, and an inhibitory one, abscisic acid (4) but failed to take account of the nature of the experimental material. When the dosage axis of a "limiting factor" type of response curve is transformed to logarithms, the response approaches the control or zero value as the concentration of the reagent approaches zero. Negative values are not obtained, except as experimental errors, or unless caused by the action of another factor, because an initial value is defined when the experiment is begun. Negative values required by Drury's model were omitted from his figure 2 ($0.05 \mu M$ abscisic acid; $10^{-4} \mu M$ gibberellic acid, for example).

Plant tissues can respond in more than one way when treated with a range of concentrations of a growth regulator. Stimulation of growth at low concentrations reaches a maximum and may then be followed by growth inhibition or toxicity as the concentration rises. Two opposing effects of one compound will then produce a quadratic response; it is this dual action of gibberellic acid which causes the curvature of the lines in Drury's figure 2.

The data of Chrispeels and Varner (5) transformed to probit (6) percentages and plotted against log concentration of gibberellic acid fit parallel straight lines, below $0.1 \mu M$, which are displaced laterally by abscisic acid (that is, toward higher concentrations of gibberellic acid) (Fig. 1).

Gibberellic acid has a second, inhibitory action which becomes noticeable above $0.1 \mu M$. If more data show that this "lateral displacement" analysis is justified then the actions of abscisic acid and gibberellic acid are independent. If the plots of probit percentage versus log dosage are parallel and the three maxima occur at the same concentration of gibberellic acid, then it follows that the concentration at which it has a toxic effect is lowered by abscisic acid. This is the reverse of the situation found with oat coleoptiles (7) and mesocotyls (8) where abscisic acid diminishes the toxic effect of supra-optimum concentrations of indoleacetic acid. The "lateral displacement" model is not favored for this reason.

An alternative interpretation is that

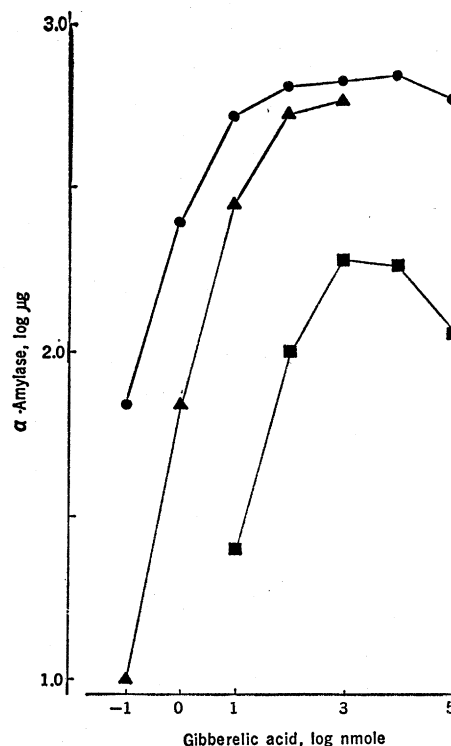


Fig. 2. The same data as in Fig. 1 plotted on log scales. This transformation has the advantage that abscisic and gibberellic acids present in the tissue have little effect on the shape of the curves. The curves are probably not parallel and therefore indicate that the effects of the hormones show slight negative potentiation. Circles, without abscisic acid; triangles, $0.05 \mu M$; squares, $5.0 \mu M$ abscisic acid.

increasing amounts of abscisic acid lower the maximum amounts of α -amylase that the aleurone can make. If this were so then the parts of the curves below the regions of supraoptimum concentrations of gibberellic acids in Fig. 2 should be parallel in the absence of negative potentiation between abscisic and gibberellic acid; unfortunately, there are insufficient data, but the curves are probably not parallel. Work on other tissues (9) has indicated that the inhibitory effects of abscisic acid cannot be completely reversed by large, but nontoxic, amounts of gibberellic acid.

Statistical devices are conceptual tools which can be used to describe results mathematically; the significant factors can then be interpreted in meaningful physiological terms. The aim of physiologists in analyzing simultaneous actions is to obtain insight into the ways in which regulatory agents operate and, eventually, to interpret the responses in terms of the behavior of the enzymes affected. This goal will be reached sooner if the interrelations of several factors are investigated by experiments with a complete factorial design (10), and if the results are described by an algebraic model which takes the characteristics of the test material into account.

B. V. MILBORROW

Shell Research Limited, Milstead
Laboratory of Chemical Enzymology,
Sittingbourne, Kent, England

References and Notes

1. R. E. Drury, *Science* **164**, 564 (1969).
2. J. A. Lockhart, *Annu. Rev. Plant Physiol.* **16**, 37 (1965).
3. B. Dey and S. M. Sircar, *Physiol. Plantarum*, **21**, 1054 (1968).
4. Formerly known as "abscisin II" or "dormin." The new name was proposed by F. T. Addicott, J. L. Lyon, K. Ohkuma, W. E. Thiessen, H. R. Carns, O. E. Smith, J. W. Cornforth, B. V. Milborrow, G. Ryback, P. F. Wareing [*Science* **159**, 1493 (1968)].
5. M. J. Chrispeels and J. E. Varner, *Plant Physiol.* **42**, 1008 (1967).
6. D. J. Finney, *Probit Analysis* (Cambridge Univ. Press, Cambridge, 1952); *Statistical Methods in Biological Assay* (Griffin, London, 1964).
7. H. W. B. Barlow, C. R. Hancock, H. J. Lacy, in *Plant Growth Regulation*, R. M. Klein, Ed. (Univ. of Iowa Press, Ames, 1961), p. 127; J. W. Cornforth, B. V. Milborrow, G. Ryback, *Nature* **210**, 67 (1966).
8. B. V. Milborrow, *Planta* **70**, 155 (1966).
9. D. Aspinall, L. G. Paleg, F. T. Addicott, *Aust. J. Biol. Sci.* **20**, 869 (1967).
10. D. R. Cox, *Planning of Experiments* (Wiley, New York, 1958).

16 January 1970

I did not imply that every useful mathematical correlation of biological phenomena is applicable to the entire region over which it is possible to vary the independent variables involved. This situation is not peculiar to biology. The region of application of the example I gave (1) from classical mechanics is not unlimited. Platform height and initial velocity act independently with respect to peak height only when varied over a region in which the acceleration of gravity is approximately constant.

It may be easier to see why the definition of independent action is adequate and does not need to be revised because of transformations, if one considers the question algebraically rather than geometrically. The set under consideration is the set of functions of x and y ,

$$P = f(x, y) \quad \text{Set F}$$

One subset is that set which can be expressed as a function of x alone plus a function of y alone,

$$P = g(x) + h(y) \quad \text{Set A}$$

This is the algebraic condition for which x and y are said to act independently with respect to P . Let those members of F, which are nonmembers of Set A, be designated Set B. For functions of Set B, x and y interact with respect to P .

Now, of course, it is possible to make up rules of operation or transformation to identify corresponding Subsets, A' and B', of Sets A and B. Let the Subset B', for example, be

$$P = g(x)h(y) \quad \text{Subset B'}$$

where both $g(x)$ and $h(y)$ are positive. By a log operation on this set one identifies the set,

$$\log P = \log g(x) + \log h(y) \quad \text{Subset A'}$$

This set is a subset of A and not of B. There is a one-to-one correspondence between the members of B' and A'. Of each member of A' one can state that x and y act independently with respect to $\log P$. Of each member of B' one can state that x and y interact with respect to P . Of no member of A' or B' can

one state that x and y act independently with respect to P .

Statistics does not define independent action and interaction. However, statistical analysis of variance is such that if its assumptions are met, only data of functions which are members of Set A will result in a declaration of no interaction between x and y . It is sometimes necessary to perform a transformation in order to meet the assumptions of analysis of variance. Nevertheless, one should make it clear whether the original function or the transformed function is the real object of study (2).

Many transformations produce a change in denotation of the sets involved. For example, when a green plant transforms inorganic chemicals into organic chemicals, the molecules cease to be members of the inorganic set and become members of the organic set. Everyone realizes that a change in denotation does not require a change in connotation. However, one might accept such a requirement in a more subtle form by suggesting that a definition be replaced by one which would denote what the old definition denotes plus that which by transformation can become part of what the old definition denotes. But even if this requirement were valid, a mathematical transformation would not require a change in connotation because it does not involve a change in denotation. It merely identifies a correlation between members of different sets. A mathematical transformation is akin to language translation. After being translated into the English word *house* the word *maison* is still French.

On the other hand, one might mistakenly argue that every transformation must produce a change in denotation, either of itself or by means of a revised definition of the sets involved. The concept of transformation of members of sets, however, implies stability of connotation in the sets involved.

ROBERT E. DRURY

New York State Agricultural
Experiment Station, Geneva 14456

References

1. R. E. Drury, *Science* **164**, 564 (1969).
2. D. J. Finney, *Probit Analysis* (Cambridge Univ. Press, Cambridge, 1952), p. 25.

13 March 1970