INHIBITION AND THE OPERANT

A review of Sensory Inhibition, by G. v. Békésy, and Mach Bands: quantitative studies on neural networks in the retina, by Floyd Ratliff¹

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Inhibition is one of the oldest terms in psychology. It was first used in biology to describe the suppressive action of the vagus nerve upon the heart (Weber and Weber, 1845); in psychology, Sechenov (1863) was apparently first responsible for its use. The concept began to acquire experimental precision through the work of Sherrington (1906) in physiology and the endeavors of Pavlov (1927) and his school in its applications to behavior. Despite this venerable ancestry the term suffered an eclipse in this country with the advent of Watsonian behaviorism and the tacit acceptance of a logical positivist epistemology. Inhibition became one of the "occult qualities" left over from centuries of mentalism, and was disposed of accordingly. A strong attack was made by Skinner (1938) who was concerned both about the inferential nature of inhibition and the difficulty of distinguishing inhibition from absence of excitation (cf. Jenkins, 1965). Skinner was evidently conscious of the weakness of his position, however, for in his original discussion of contrast-the operant phenomenon perhaps most directly related to inhibitionhe was at pains to emphasize the unreliability and relative impermanence of the effect: "Until the conditions which determine whether induction [generalization] or contrast is to occur at a given time have been identified,

the observations of contrast stand simply as exceptions to the Law of Induction. Little is at present known except that contrast is usually a temporary phenomenon appearing at only one stage of a discrimination and apparently not sufficing to abolish it in spite of its opposition to induction. . . . It is doubtful whether contrast is a genuine process comparable with induction." (1938, p. 175.)

A similar scepticism once prevailed in sensory physiology where, as Békésy points out, it was "often assumed that inhibition is a minor side effect, modifying a stimulation pattern only in small degree." (1967, p. 25.) Békésy attributes this view to what he calls the "input-output complex": "Whenever an input is introduced there is an output on the other side. For example, a spot of light on the retina will produce an electrical discharge, which passes through the electrical network of the brain to produce finally a sensation at the cerebral cortex. In a way this is an electrical formulation of the causality principle." (1967, p. 6.) For Békésy, ". . . the euphoria of the input-output concept lasted only a few years".

In recent years two lines have converged to reinstate the concept of inhibition. The first is improvement in experimental techniques, both in sensory physiology and in the experimental analysis of behavior. This has led to anatomical identification of mutually inhibitory neural units (Hartline, 1949) and to direct demonstrations of inhibition in the context of operant behavior (Brown and Jenkins, 1967). The second is an increasing sophistication about the properties of complex systems, which has provided mathematical and computational techniques for dealing with inhibition, and has emphasized its importance to the stability of large neural aggregates.

Within physiology, inhibition was at first only a property of the motor system—the cen-

¹Békésy, G. von. Sensory inhibition. Princeton: Princeton University Press, 1967, 265 pp., \$8.50. Ratliff, F. Mach bands: Quantitative studies on neural networks in the retina. San Francisco: Holden-Day, 1965, 365 pp., \$14.50.

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tral inhibition of Sechenov and Sherrington (Florey, 1961). With few exceptions (the early work of Békésy on tonal contrast was one), the sensory contour effects first identified by Ernst Mach (1865) remained a neglected field for nearly 80 years, until the seminal work of Hartline (Hartline, 1949; Ratliff, 1965) uncovered analogous effects in the compound eye of Limulus. The power of this work lay in its identification of a specific inhibitory mechanism, lateral inhibition, and unequivocal demonstration of the relationship between that mechanism and Mach band-like contour-enhancing effects. The identification of individual inhibitory units disarmed the suspicion many experimenters might otherwise have felt towards an inhibitory interpretation of contrast phenomena; it opened the way to interpretation of a range of contrast effects in these terms, even where physiological identification of the interacting systems is presently difficult or impossible. These findings can be thought of either as making nonsense of the traditional psychophysiological approach in terms of sensory elements and their rules of combination-a legacy of Locke and Mill via Titchener-or as an enrichment of this historically fruitful approach permitting a redefinition of the elements in more precise and powerful terms. Békésy's and Ratliff's books contribute to such a redefinition, both by theoretical explorations and by extensions of the concept to modalities other than vision.

The two books share an appreciation for experimental and conceptual elegance rarely encountered in the present era of "big science" and routinized experiment. In this respect they are reminiscent of some of the classics of Victorian science. In this tradition are the six splendid papers by Mach, translated by Ratliff, that constitute the last third of Ratliff's book. Of the two books, Ratliff's is longer and more scholarly, but also less unified. It is fairly loosely organized around the work and ideas of Mach. Ratliff presents a brief biography of Mach as physicist, philosopher, and psychologist, woven around his concern for epistemology and his related but more concrete interest in sensory processes. The book continues with an account of the psychophysics of Mach bands, followed by an exhaustive account of mathematical models of inhibition in neural networks. A fourth chapter on the functional significance of inhibitory interaction describes the experimental work of Ratliff and his coworkers. The final chapter, "Appearance and reality", is an historical description of some ways in which inhibitory visual processes have entered into practical matters by producing misperceptions of one sort or another. The chapter ends with a discussion on the meaning of objectivity including, as readers of this journal will be happy to hear, an endorsement of animal experiments as aids to the objective study of sensory processes.

Békésy's book is shorter, being derived from the Herbert S. Langfeld lectures he delivered at Princeton in 1965. Békésy aims to demonstrate the involvement of inhibitory processes in all sense modalities, but especially vision, touch, and audition. Phenomena ranging from geometrical illusions (demonstrated on the skin surface as well as the retina) to localization of stimuli (sounds, touches, tastes) in space are all treated from this point of view. The approach is elegant and often dramatic, but also intuitive to a degree that would probably be unacceptable from anyone of lesser stature. For example, the dependent variables (if so crass a term can be applied) in most of Békésy's experiments are freehand sketches by trained subjects of the sensation distributions produced by various patterns of stimulation. No estimate is given of the reliability of this kind of datum, nor, in any detail, of the instructions and training necessary. One is prepared to believe; but the bases for belief bear little relation to current criteria for acceptability in some experimental psychology journals. Whether this reflects more on Békésy or on the journals makes for interesting discussion.

Békésy provides a nice demonstration of sensory inhibition in an experiment on the sense of touch. Subjects were asked to report the sensations produced on the hand by Von-Frey test hairs, thus: "Two test hairs were applied to the palm of the hand of an observer ... and he was asked to describe the distribution of the direct pressure sensation at the point of application and around it. . . . The magnitude and width of the pattern grow greater as the separation of the two points is increased, until at a certain distance two points are perceived. At the same time . . . the magnitude of the sensation decreases sharply. Sometimes, with careful adjustment

of the two stimulus magnitudes, it is possible to cancel the sensation completely, at least for a brief time. At a little larger distance the two stimuli fall apart, there is no more lateral interaction, and the two points feel like two independent sensations. The disappearance of the sensation at a certain distance between the two points seemed to me to be the most striking demonstration of lateral inhibition." (1967, pp. 42-43.) On this basis Békésy concludes that a point stimulus produces two kinds of effect on the receptor mosaic (or its central representation): a central area of sensation (excitation) and a surrounding area of inhibition. He calls this a neural unit; it provides a compact summary of the properties of a sensory surface. It thus serves the same purpose as the transfer function of the engineer; and indeed the two functions are intimately related, as Ratliff indicates. Two differences are that in the neural unit, space takes the place of time (Békésy is not concerned with dynamics) and that more than one dimension may be involved. An extended stimulus is treated as a set of point stimuli of varying intensities, each of which produces a neural unit with a magnitude corresponding to its strength. The net sensation produced by the whole stimulus, be it a visual pattern, a complex tone, or an edge pressed against the skin, is the algebraic súm of all these various excitatory and inhibitory effects. An approximation to this sensation can be produced by graphical methods, by the use of the superposition or convolution integrals or by a variety of iterative techniques.

Ratliff points out that Békésy's neural unit is only one of a number of possible models of Mach band phenomena; indeed Mach himself provided the first such model. Since all the models are about equally effective as gross descriptions of the effects, the only substantial distinction is between those that depend solely upon the stimulus input to predict the sensation pattern (Békésy's is one of these), and those that take more direct account of neurophysiological data and depend upon information about receptor response. The latter models are more powerful because they make dynamic predictions, but are also more restricted because they are not readily applicable in areas where physiological data are lacking. The greater generality of the stimulus-dependent models suggests that this approach is

likely to be more immediately useful for an understanding of behavior.

The potential relevance of this work for the experimental analysis of behavior will be approached from three directions: first by a brief review of recent empirical evidence for inhibitory effects in discrimination learning; second by considering the concept of the operant as a behavioral unit; and third by examining the common features of the various stimulus-dependent models of inhibitory interaction discussed by Ratliff.

Effects apparently related to inhibition are well established in the literature of discrimination learning; spontaneous recovery during extinction, behavioral contrast, and the peak shift of the generalization gradient are three of these. In almost every case an alternative explanation-either in terms of differential stimulus control, simple reduction of excitation, or some other process-has seemed possible. It is only recently that two techniques have unequivocally established the existence, if not the ubiquity, of inhibitory effects. The most important of these is the direct demonstration in a number of experiments (Jenkins and Harrison, 1962; Honig, Boneau, Burstein, and Pennypacker, 1963; Terrace, 1966b) of generalization gradients of inhibition, with minima in the vicinity of the stimulus correlated with extinction. Since the dimensions of the positive and negative stimuli were chosen to be orthogonal, changes in responsiveness with respect to the dimension of the negative stimulus can be attributed to that stimulus and not to the positive stimulus. Thus, the negative stimulus in these experiments inhibited responding to other stimuli on the same dimension in proportion to their distance from it. In this respect the situation is no different from the limulus retina where illumination of one receptor inhibits the firing of adjacent receptors. The second technique is the recent demonstration of conditioned inhibition, using Pavlov's method of differential compound discrimination in an operant situation (Brown and Jenkins, 1967). In this case, responding sustained by one stimulus is suppressed by the concurrent presentation of another.

Both these sets of experiments demonstrate response suppression in the presence of an inhibitory stimulus. A stimulus can also inhibit responding following its offset (or for a time following its onset) after the fashion of Pavlov's inhibition of delay. It is becoming clear that in the steady-state, reinforcement on fixed-interval schedules inhibits responding for some time following its offset; the discriminative stimulus present during the interval may also be inhibitory for some time following its onset. Evidence comes from reinforcement omission experiments (Ferster and Skinner, 1957; Staddon and Innis, 1966; Staddon, 1967a; Innis and Staddon, 1969), from experiments on "disinhibition" of fixed-interval responding (Flanagan and Webb, 1964; Singh and Wickens, 1968; Hinrichs, 1968), and from transient contrast interactions on multiple fixed-interval schedules analogous to the effects of lateral inhibition in sensory systems (Catania and Gill, 1964). Thus, reinforcement omission experiments indicate that response rate is higher if reinforcement is omitted on fixed-interval schedules. "Disinhibition" experiments indicate that in the presence of novel stimuli, response rate is generally higher than during training. A recent study (Hinrichs, 1968) also indicates that if a new stimulus, present throughout the fixed interval, is substituted for the one used in training, response rate is higher at the beginning of each fixed interval, but lower at the end of each interval. This result suggests that if a generalization test were run on FI, presenting a range of stimuli, each present throughout an interval, one might obtain an inhibitory gradient in terms of responding early in the interval, but an excitatory gradient in terms of responding late in the interval. Finally, the contrast results of Catania and Gill are consistent with an inhibitory effect of reinforcement that summates across reinforcements.

Thus, if the term inhibition be restricted to a descriptive level, free of the physiological connotations of Pavlov's original usage, the existence of inhibitory effects in operant conditioning cannot be contested. Uncertainty is only possible concerning the extent of these effects, and their importance for an understanding of operant behavior.

A recent analysis (Staddon, 1967b) emphasized that in the steady state, the fundamental property of the operant as a behavioral unit is its embodiment of a cause-effect relation; the stimulus (an abstract property of the environment, e.g., "red") produces the response (an abstract property of behavior, e.g., the "FI

scallop"). Comparison of this point of view with what Békésy calls the "input-output complex" reveals disconcerting similarities: in both cases causality is emphasized but, more importantly (since it is possible to argue that causality must be central to any scientific description), only the active, excitatory effect of the stimulus is mentioned; no explicit account is taken of the tendency of stimuli to suppress behavior. Thus, on grounds of symmetry, there is reason to be dissatisfied with this concept of the operant. This might be of little consequence except that the same biased emphasis evidently underlies the analytic approach of most behaviorists, even (or perhaps especially) those who consider themselves most free of theoretical presuppositions. It is apparent, for example, in the strenuous attempts that are made to find positive behaviors (e.g., homogenous or heterogeneous chains) to "mediate" spaced-responding and other timerelated behaviors. The major impetus for this search comes from a more or less implicit acseptance of the exclusiveness of excitatory control.

Those who ignore their metaphysical preconceptions are liable to be misled by them. If the operant, as a behavioral unit, is to be taken seriously, some way must be found of incorporating into it both inhibitory and excitatory stimulus control. The models of Mach, Békésy, and Ratliff suggest a new metatheory.

There seem to be three basic properties of the stimulus-dependent models of inhibitory interaction discussed by Ratliff: (1) dimensions along which the inhibitory and excitatory interactions take place, e.g., the two dimensions of the retina or the skin, the one dimension of the basilar membrane; (2) summary of the effects of any and all stimulus configurations by the effect of a point stimulus; (3) excitatory and inhibitory effects, produced by the point stimulus, at specified places along each of the dimensions-this pattern of inhibitory effects is the neural unit, in Békésy's terminology. The magnitude and spread of these effects is a simple (usually linear) function of the intensity of the point stimulus, and the effect of an extended stimulus is the integral of the effects of each point along its extent. These three properties can be translated into a redefinition of the asymptotic operant in a fairly straightforward way. First, a set of dimensions

(which need be neither physical nor metric) is required along which the relevant excitatory and inhibitory interactions can take place. The mapping of this set is a major empirical problem to which much of the work on selective attention, "dimensional acquisition" and so on is relevant. Both response and stimulus dimensions are necessary for a full account, however, because of the reciprocal inhibition of incompatible response topographies, and other relationships within the motor system. In addition, time, which is in many ways intermediate between stimulus and response, must usually be considered as a dimension along which interactions can occur. The second and third characteristics of the "neural unit" approach imply that any stimulus which can be shown to exert stimulus control can be considered as a set of point stimuli, each producing specifiable excitatory and inhibitory effects at different places along these dimensions. All these effects can then be summarized by a "behavior unit", analogous to the neural unit, that specifies the excitatory and inhibitory effects of the multi-dimensional "point stimulus" for that situation. The unit (the asymptotic operant) represents what is invariant in the organism's behavior, and thus should predict the effects of transfer tests in the way that one might expect of any accurate description of "what is learned".

Neither theory nor data have yet developed to the point at which invariances of this sort can be unequivocally demonstrated. Areas of potential applicability are readily apparent, however. For example, behavioral contrast, the higher response rate in the presence of a discriminative stimulus if the stimulus is alternated with another stimulus associated with a less bountiful reinforcement schedule than if it is presented alone, is less puzzling if both inhibitory and excitatory effects are expected concomitants of any reinforcing operation. Thus, reinforcing responding in the presence of stimulus x will to some extent inhibit responding, in the same context, to stimuli \bar{x} ; similarly not reinforcing responding in the presence of stimulus y will tend to potentiate responding to stimuli y. If x but not \bar{x} is correlated with reinforcement, the result, within the common context of the experimental situation, is behavioral contrast. This interpretation, although neither novel nor exact, is perhaps a useful antidote to emphasis on a particular stimulus and its associated response rate. It directs attention towards the effect of reinforcement as a change in the total pattern of responsiveness to a range of stimuli along a number of dimensions. It also emphasizes that change need not always be in the same direction, either with respect to different dimensions or with respect to different values of the same dimension.

Closely related to the problem of contrast are a cluster of phenomena involving the generalization gradient: the peaked form of the gradient and its relation to "similarity" (cf. Shepard, 1958, 1964), the peak shift, effects of multistimulus training and the effects of test stimulus spacing. Inhibition, in a descriptive sense, has been implicated in most of these effects (Terrace, 1966a), although since Spence (1937) few detailed suggestions concerning possible mechanisms of action have been advanced. Spence's theory of transposition required gradients of excitation and inhibition, centered on S+ and S- respectively, of approximately Gaussian form. The algebraic sum of these gradients was to show a maximum displaced from S+ in a direction away from S-, thus describing the related phenomena of transposition and the peak shift. Well and good, except that empirical gradients of excitation (generalization), determined subsequently, often failed to have the smooth form demanded by Spence's theory, being quite sharply peaked (Guttman, 1963; Hanson, 1959). With such excitation gradients, no gradient of inhibition with minimum at S- is sufficient to yield observed peak shifts. Thus, despite recent demonstrations in agreement with Spence's position (Hearst, 1968), the matter in general remains unresolved, with some even doubting whether inhibition is really involved in the peak shift at all (e.g., Jenkins, 1965). The virtues of Spence's model can be retained, and reconciled with observed generalization gradients, with the aid of a hypothesis related to the "neural unit" approach. Suppose that underlying the observed empirical gradient is an excitation gradient of the smooth, concave-downward form suggested by Spence; the empirical gradient being derived from the underlying one by a process of "sharpening" or "funneling" analogous to the sensory processing described by Békésy. This underlying gradient may perhaps embody directly the property of stimulus similarity discussed by

Shepard and others. At the level of individual generalization test stimuli, this sharpening implies that each test stimulus produces an excitatory tendency proportional to the ordinate of the hypothetical underlying gradient and a proportionate inhibitory tendency at adjacent points on the dimension of generalization, i.e., each test stimulus produces both a tendency to respond to that stimulus and a tendency not to respond to other stimuli inversely proportional to their distance from the test stimulus. The observed empirical gradient is then the resultant of the combined excitatory and inhibitory effects of all test stimuli. It will thus be more peaked than the underlying gradient (for an as-yet-to-be-determined range of "inhibitory units" and "similarity" gradients) and will be subject to effects such as increased slope as a function of decreased test stimulus spacing (cf. Marsh, 1957). Results such as the bimodal gradient following equal training to two closely spaced stimuli (Kalish and Guttman, 1957) and three stimuli (Kalish and Guttman, 1959), also become comprehensible in terms of inhibitory interactions among stimuli along the dimension of generalization.

Obviously a great deal more work is necessary before this approach can yield testable predictions, if indeed that is the only aim of theory. Closer to realization is a description satisfying Mach's view of the proper role of theory in psychology: ". . . a formula which represents the facts more concisely and plainly than one can with words, without, however, claiming quantitative exactness." (Ratliff, p. 273.) For the moment it is perhaps sufficient to emphasize the essential properties of the framework or paradigm within which these suggestions are cast. The paradigm has three properties: (1) a recognition of the parity of inhibitory and excitatory forms of stimulus control; (2) the suggestion that these two forms of control, together with the relevant attentional dimensions, are sufficient to describe most if not all operant steady-state behavior; (3) a redefinition of the asymptotic operant in terms of the "behavior unit" characterizing a given steady-state situation. I suggest that this paradigm, or something very like it, may constitute the major contribution of Mach and his successors to the contemporary analysis of learned behavior.

This review has attempted to trace similar-

ities between the two domains of steady-state operant behavior and the steady-state behavior of receptor systems. No uniqueness is claimed for this analysis; it may be that parallels between these two areas can be shown more clearly and directly than I have done. It is certain that applications to problems other than contrast and generalization-frustrative nonreward, displacement behavior, polydipsia, etc.—are possible that have not been explored. Hopefully, the reader has been persuaded of the relevance of the conceptual framework of one area to work in the other, if not of the particular similarities emphasized here. If, in addition, a hint of the liberating virtues of speculative thought has filtered througheven, perhaps, within the hypothesis-free context of the experimental analysis of behavior -then Mach's memory will have been truly served. In his words: "We shall never ascertain what these processes are if, from the very beginning, we conceive of them in too simple a manner."

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