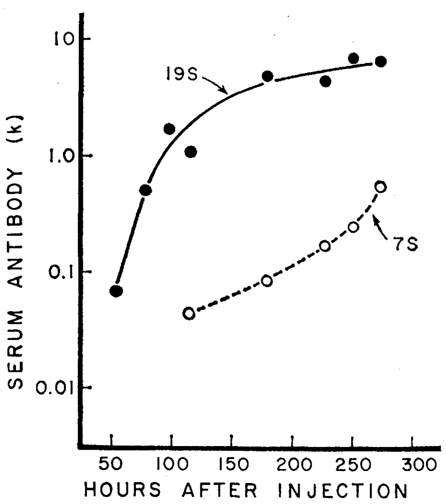

Fig. 3. The sequence of appearance of 19*S* γM and 7*S* γG antibodies in the circulation of a fetal lamb at 131 days gestation, after injection with 3×10^9 plaque-forming units of bacteriophage ϕX174.

lamb *in utero* are qualitatively similar to those reported for premature human newborns and older children (*8*, *9*), for newborn and adult guinea pigs (*5*, *7*), and for adult rabbits (*10*). These features include the initiation of immune elimination of antigen during the 2nd day after immunization, the formation of 19*S* γM antibodies with a rapid initial doubling time unaccompanied by appreciable γG antibody formation when small doses of antigen are used, and subsequent formation of γG antibody in response to larger doses of antigen. Even in its quantitative aspects, moreover, the fetal response appears to be consistent with that observed in more mature individuals, with allowance made for the reported difference in the degree of response (*8*) to different batches of bacteriophage ϕX174 antigen. Thus the initial γM antibody titers in the serums of immunized fetuses increased, the doubling time being about 10 hours, whereas within 1 week of immunization the amount of antibody detectable in the blood was 10^3 to 10^4 times the minimum detectable amount, with continued increase in antibody levels thereafter. A correction of the foregoing values for the rapid growth of the fetus added to a correction for the large volume of extracorporeal blood in the placenta would result in higher estimates of the amount of serum antibodies formed at any given time after immunization. We were, unfortunately, unable to compare the fetal lambs' response with that of adult sheep, owing to the presence of a phage-neutralizing factor, presumably antibody, in the adult serums. The similarity of response in the three different species mentioned above suggests, however, that the aforesaid features of the response are probably typical of the mammalian response to this antigen.

Our data imply that, once the developing fetus is able to respond in any specific manner to antigenic stimulus with the relatively strong immunogens thus far examined, it manifests no significant immaturity in any of the attributes of this response. In this respect, these data are in agreement with those cited above on the earliest manifestation of specific homograft rejection by the fetal lamb, and they agree also with other data (*11*) that the earliest antibody response by the fetal rhesus monkey *in utero* involves the same proportion of its total population of lymphoid cells as is employed by the mature animal (*11*).

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References and Notes

1. Recent reviews include: A. M. Silverstein, *Science* **144**, 1423 (1964); R. A. Good and B. W. Papermaster, *Adv. Immunol.* **4**, 1 (1964); J. Sterzl and A. M. Silverstein, *ibid.*, in press.
2. J. J. Osborn, J. Dancis, J. F. Julia, *Pediatrics* **9**, 736 (1952); B. Vahlquist, U. Murray, N. G. Persson, *Acta Paediatr.* **35**, 130 (1948); R. A. Bridges, R. M. Condie, S. J. Zak, R. L. Good, *J. Lab. Clin. Med.* **53**, 331 (1959).
3. A. M. Silverstein, R. A. Prendergast, K. L. Kraner, *J. Exp. Med.* **119**, 599 (1964).
4. Initial efforts involving catheterization (C. J. Parshall, Jr., and A. M. Silverstein, in preparation) of the proximal jugular vein resulted in frequent early occlusion of the catheter. Use of the proximal carotid artery improved the period of patency of the catheter. Most recently, use of a nonoccluding Y-tube has yielded preparations useful as long as 1 month.
5. J. W. Uhr, M. S. Finkelstein, J. B. Baumann, *J. Exp. Med.* **115**, 655 (1962).
6. M. H. Adams, in *Bacteriophages* (Interscience, New York, 1959).
7. J. W. Uhr and M. S. Finkelstein, *J. Exp. Med.* **117**, 457 (1963).
8. J. W. Uhr, J. Dancis, E. C. Franklin, M. J. Finkelstein, E. W. Lewis, *J. Clin. Invest.* **41**, 1509 (1962).
9. R. T. Smith, in *Cellular Aspects of Immunity*, G. E. W. Wolstenholme and M. O'Connor, Eds. (Churchill, London, 1960), p. 348.
10. J. W. Uhr, in preparation.
11. A. M. Silverstein, R. A. Prendergast, C. J. Parshall, Jr., in preparation.
12. Supported in part by contract No. DA49-193-MD-2640 from the U.S. Army Medical Research and Development Command; by grants from the Alcon Laboratories, Inc.; from USPHS No. A1-01821-9; and from the Commission on Immunization of the Armed Forces Epidemiological Board. We thank S. L. Johnson and W. Dolan for technical assistance.

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Discrimination Learning and Inhibition

Abstract. *Pigeons learned to discriminate between a white vertical line on a dark background (S+) and a monochromatic circle of light (S−) either with or without responses to S− (errors). Gradients of inhibition, which were centered around S−, and which had greater than zero slopes, were obtained only from those subjects who learned to discriminate with errors. The results indicate that the occurrence of errors is a necessary condition for S− to function as an inhibitory stimulus. This finding is consistent with other performance differences in subjects who have learned to discriminate with and without errors.*

During the past decade our knowledge of how a discrimination is acquired has been considerably enhanced by new empirical findings and theoretical analyses. The peak shift and behavioral contrast have both been established as reliable characteristics of discrimination performance. The peak shift, first studied by Hanson (*1*), derives its name from the finding that, after subjects are successively trained to discriminate between a stimulus correlated with reinforcement (S+) and a stimulus not correlated with reinforcement (S−), the peak of a generalization gradient does not occur at S+ but is instead shifted away from S−. Behavioral contrast, a phenomenon studied by Reynolds (*2*), was originally called "induction" by Pavlov (*3*) and was later referred to as "contrast" by Skinner (*4*). The term refers to an increase in the strength of the response to S+ that accompanies a decrease in the strength of the response to S− during discrimination training. Behavioral contrast derives its name from the fact that the rates of responding to S+ and S− diverge. According to classical generalization theory, these rates should converge (*5*).

Recent experiments on "errorless" discrimination learning suggest a possible relationship between the peak shift and contrast (*6*). Errorless discrimination learning is achieved by starting discrimination training immediately after the response to S+ has been conditioned with a large S+-S− difference that is progressively reduced to its final smaller value. These experiments show that a subject can be trained to discriminate without the occurrence of responses to S− (errors), and that many characteristics of discrimination performance usually observed after a subject learns to discriminate with errors are absent after that subject learns to discriminate without errors. Neither behavioral contrast nor the peak shift, for example, occur after the subject learns to discriminate without errors (*6*, *7*). Other characteristics of performance that were absent after a subject learns to discriminate without errors are gross emotional responses (*8*) and the occurrence of errors that are typically observed after the administration of certain tranquilizers (*9*). These differences suggested that S— functions differently after a subject learns to discriminate with and without errors. After a subject has learned to discriminate with errors, S— appears to function as an inhibitory stimulus; after discrimination is learned without errors, S— appears to function as a neutral stimulus.

A theoretical analysis by Jenkins (*10*) of inhibition in discrimination learning suggested a way of directly observing the inhibitory function of S—. Jenkins argued that an inhibitory stimulus can be considered to control the tendency not to respond in a manner analogous to the way that an excitatory stimulus controls responding. The existence of both types of control is determined by varying S+ and S— in a generalization test. Just as the control of excitation is determined by varying S+ and observing to what extent the tendency to respond decreases as the distance between a test stimulus and S+ is increased, the control of inhibition may be determined by varying S— and observing to what extent the tendency not to respond increases as the distance between a test stimulus and S— increases.

In a generalization test in which gradients around both S+ and S— are obtained, Jenkins also points out that S+ and S— should be varied independently of each other so that a change in the distance between a test stimulus and S— does not affect the distance between that test stimulus and S+. This can be done by selecting S+ and S— from different continua. If S+ and and S— were from the same continuum, a change in response frequency could be attributed either to a change in the distance between the test stimulus and S+ or to a change in the distance between the test stimulus and S—. Jenkins and Harrison (*11*) and Honig *et al.* (*12*) have obtained empirical gradients of inhibition from individual subjects, after they were trained to distinguish between stimuli from different continua. These gradients serve as an effective answer to Skinner's position on inhibition, which holds that inhibition is merely another name for a decrement of excitation and that changes in response frequency can be entirely accounted for in terms of different magnitudes of excitation.

The present experiment is an attempt to test the hypothesis that S— does not function as an inhibitory stimulus after a subject has learned to discriminate without errors. Subjects were trained to discriminate, with and without errors, between stimuli from two different continua; the shapes of the gradients centered around S— were then examined. A U-shaped gradient, with a minimum at S—, would indicate that S— was an inhibitory stimulus, while a flat gradient would indicate the absence of any inhibitory function.

The experiment was performed in a standard operant conditioning apparatus (*13*) which contained a single circular key, 2.54 cm in diameter, 10.16 cm above the opening to the food hopper. An optical system, consisting of a high-intensity point source, a collimating lens, and a solenoid-operated dual filter box, could project onto the back of the key any one of 15 uniformly-bright monochromatic stimuli, or a 32-cm white diameter on a black background in any one of nine equally spaced orientations. The half-widths of the monochromatic stimuli were each less than 15 nanometers (nm).

The subjects were eight white Carneaux male pigeons that were maintained at 80 percent of their free-feeding weight throughout the experiment. None had been used in previous experiments.

During the conditioning sessions and the 14 subsequent sessions of nondifferential training, the stimulus on the response key was a white vertical (0°) line on a dark background (S+). At the end of each minute the key was darkened for 2 seconds. These 2-second time-out periods were later used during the discrimination and generalization sessions to change the value of the discriminative stimuli. Responses were never reinforced during the time-out periods. During discrimination training, which began after 14 sessions of nondifferential training, S+ was alternated with S— in a random sequence. For six subjects (birds 131, 138, 140, 141, 142, and 144) the value of S— was 580 nm; for the remaining two subjects (birds 122 and 123) the value of S— was 550 nm. Responses to S+ during both the nondifferential and the differential reinforcement sessions were reinforced on a 1-minute variable-interval schedule, a schedule that reinforced the first response that occurred after an interval whose average value was 1 minute (*13*). Each session was terminated after 25 reinforcements.

During discrimination training each presentation of S+ lasted 1 minute. The duration of S— was also 1 minute, unless the subject responded to S—. Each response to S— delayed the termination of S— for 30 seconds. This procedure insured that responses to S— would not be reinforced by the subsequent appearance of S+.

Since a pilot study indicated that the discrimination between a white vertical line and a circle of monochromatic light can be acquired without errors with no special training, no explicit attempt was made to train the discrimination without errors by progressively reducing the difference between S+ and S—. After the fifth discrimination session, a generalization gradient of wavelength was obtained from each subject. No reinforcements occurred during the generalization test. The stimuli during the wavelength generalization test were 490, 510, 520, 530, 540, 550, 560, 570, 580, 590, 600, 610, 630, 650, and 670 nm. S+ was also presented during the generalization test. The 16 test stimuli were presented in four different random sequences, each time for a duration of 1 minute (*14*). After the first generalization test each subject received four more sessions of discrimination training, after which a generalization gradient of line orientation was obtained. No reinforcements were given during the generalization test. The test stimuli consisted of lines whose orientations were ± 90°, ± 67.5°, ± 45°, ± 22.5°, and 0°. In addition, S— (550 or 580 nm) was also included in the generalization test, which consisted of four random sequences of the test stimuli, each presented for 1 minute. After the second generalization test each subject received three additional sessions of discrimination training. Each subject was then exposed to six sessions of nondifferential training during which only S+ was presented. Each of the these procedures was carried out on successive days of experimentation.

Half of the subjects learned the discrimination with few or no errors (birds

123, 138, 140, and 141), while the remaining four subjects (birds 122, 131, 142, and 144) made many responses to S—. The range of the number of responses to S— of the group which was considered to have learned the discrimination without errors was 0 to 19, while the range of errors of the group which was considered to have learned the discrimination with errors was 171 to 1551.

The rate of responding to S+ for all of the subjects who learned the discrimination with errors increased at the start of discrimination training. In three instances (birds 122, 142, and 144) the rate of responding to S+ reached a value that was double the value of the prediscrimination rate of responding to S+. After nondifferential training was resumed, the rate of responding to S+ of each subject decreased and approached the prediscrimination value. The rate of responding to S+ of each of the subjects who learned to discriminate without errors remained unchanged throughout the experiment. The results confirm the findings of earlier experiments (*6*) which showed that contrast develops only when discrimination learning takes place with errors.

The wavelength generalization gradients of each subject who learned to discriminate with errors were U-shaped functions centered around S— (Fig. 1). Each of these gradients was asymmetrical with the longer tail occurring at the short end of the spectrum; the reason for this was not understood. In other respects these gradients confirm the findings of earlier experiments (*11, 12*) which have shown that the tendency not to respond is maximal at S— and decreases as the distance between S— and the test stimulus increases.

The wavelength generalization gradients of the subjects who learned to discriminate without errors (Fig. 2) were in each case flat, indicating that for these subjects the value of S— did not affect the tendency to respond.

No systematic differences in the shapes of the gradients of excitation were observed as a function of whether or not the subjects learned to discriminate with or without errors. In most cases the gradients of excitation were peaked around S+. A peak shift would not be expected from the subjects who learned to discriminate with errors, since S— was on a continuum orthogonal to the S+ continuum.

The difference between the shapes of the gradients of inhibition obtained from those subjects who learned to discriminate with and without errors clearly indicates that S— functions differently in each case. After a subject learns to discriminate with errors, S— comes to control the tendency not to respond in a manner that is in most respects analogous but not identical to the control S+ exerts over responding.

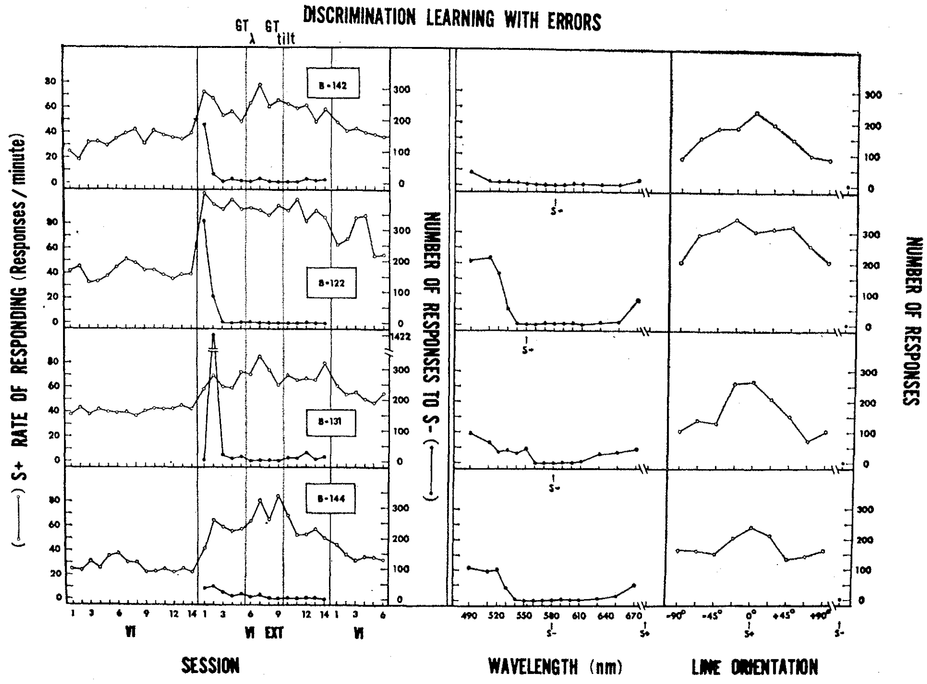
DISCRIMINATION LEARNING WITH ERRORS

Fig. 1. (Left) Rate of responding to S+ (open circles) of subjects who learned to discriminate with errors during nondifferential and differential reinforcement sessions, and number of responses to S— (closed circles) during each differential reinforcement session. The vertical lines indicate when discrimination training began and ended and when the wavelength and line-orientation generalization gradients were obtained. GT_λ and GT_{tilt} refer to the wavelength and line orientation generalization tests, respectively. *VI* and *VI EXT* refer to the nondifferential and differential reinforcement sessions, respectively. (Right) Wavelength and line-orientation generalization gradients.

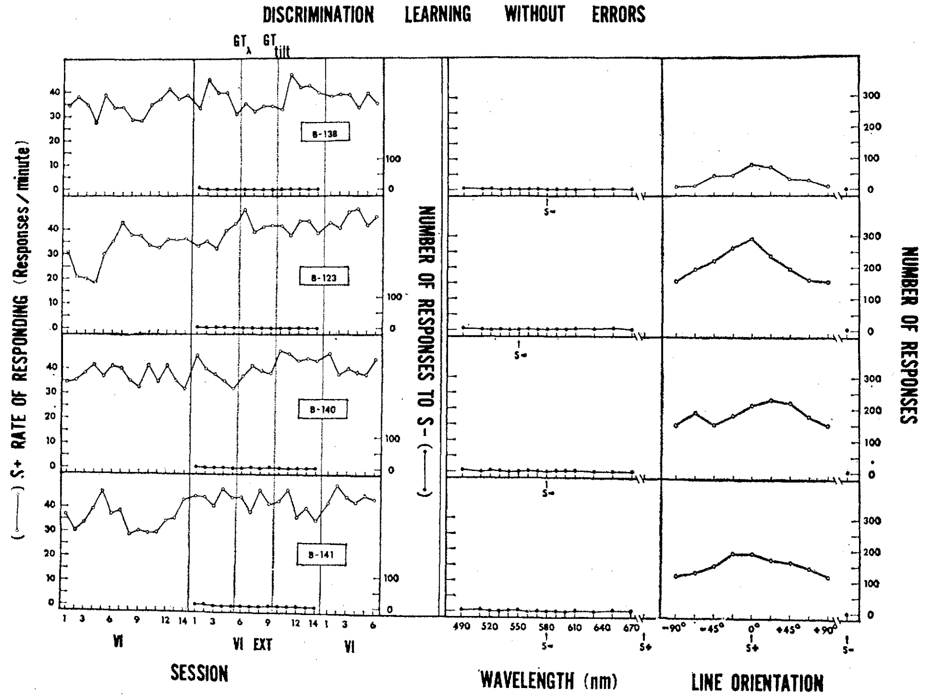
DISCRIMINATION LEARNING WITHOUT ERRORS

Fig. 2. (Left) Rate of responding to S+ of subjects who learned to discriminate without errors during nondifferential and differential reinforcement sessions, and number of responses to S— during each differential reinforcement session. Abbreviations are the same as in Fig. 1. (Right) Wavelength and line-orientation generalization gradients.

The flat gradients obtained from the subjects who learned to discriminate without errors indicate that S− did not acquire any differential control over the tendency not to respond. However, responding and other behavior cannot be considered as symmetrical opposites. The generalization gradients shown in Fig. 1 clearly indicate that the number of responses to the wavelength test stimuli was generally much lower than the number of responses that occurred to S+, and that the gradients of inhibition were not as steep as the gradients of excitation. Jenkins (*10*) has suggested that this asymmetry between responding and other behavior stems from two different ways of classifying other behavior. The first class includes responses antagonistic to key-pecking, for example, turning away from the key or jerking back the head after the onset of S−. The second class of other behavior includes "anything else" or what Skinner would refer to as the absence of excitation, for example, grooming, brooding, or pecking at objects on the floor of the experimental chamber. This second type of nonresponse is controlled by the absence of S+, rather than by a specific value of S−. In testing for the generalization of the tendency not to respond, the experimenter is only able to record when responses occur, but there is no way to determine which type of nonresponse was involved. Only when the responses which define a gradient of inhibition are entirely transferred from the first type of nonresponse (antagonistic) will the gradients of excitation and inhibition be symmetrically opposite. The gradients of inhibition shown in Fig. 1 indicate that this was not the case. These gradients were presumably flattened by the prevalence of the second type of nonresponse.

Although it is not possible to differentiate between the two types of nonresponse, it is nonetheless clear that S− controls the tendency not to respond, that is, it functions as an inhibitory stimulus only after a subject has learned to discriminate with errors. Thus, different things are learned after a subject learns to discriminate with and without errors. After learning to discriminate with errors, the subject learns to respond to S+ and not to respond to S−. This finding was demonstrated by gradients of excitation and inhibition, each of which had a slope greater than zero. After learning to discriminate without errors, the subject learns to respond to S+ and not to its absence. S− does not specifically control the tendency not to respond.

The differences between the gradients of inhibition of those subjects who learned to discriminate with errors and those who learned to do so without errors are consistent with the finding that a peak shift occurs only after a subject has learned to discriminate with errors. As Spence's model of discrimination learning suggests (*5*), if an inverted U-shaped gradient of inhibition centered around S− is subtracted from a larger gradient of excitation centered around S+, then the peak of the gradient of excitation will be displaced away from S−. Since discrimination learning without errors results in a flat gradient of inhibition, no peak shift would result when the gradient of inhibition is subtracted from the gradient of excitation.

The occurrence of contrast, however, cannot be accounted for in terms of interacting gradients of excitation and inhibition. An algebraic combination of peaked gradients of excitation and inhibition would result in a divergence rather than a convergence of the rates of response to S+ and S−. The occurrence of contrast after a subject has been trained to discriminate between stimuli from two different continua suggests, however, that responses which are not reinforced may have an effect that is uniformly distributed over all stimuli. According to this view, elaborated by Amsel (*15*) and Lawson (*16*), a nonreinforced response to S− results in a general elevation of the gradient of excitation. Subtracting a U-shaped gradient of inhibition from this elevated gradient of excitation would still displace the peak away from S−. This appears to be the simplest way to account for the fact that the peak shift, contrast, and U-shaped gradients of inhibition occur only after a subject has learned to discriminate with errors.

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References and Notes

1. H. M. Hanson, *J. Exp. Psychol.* **58**, 321 (1959).
→ G. S. Reynolds, *J. Exp. Analysis Behav.* **4**, 57 (1961).
3. I. P. Pavlov, *Conditioned Reflexes* (Oxford Univ. Press, London, 1927).
4. B. F. Skinner, *The Behavior of Organisms* (Appleton, New York, 1938).
→ K. W. Spence, *Psychol. Rev.* **44**, 430 (1937);
→ C. L. Hull, *ibid.* **57**, 303 (1950).
6. H. S. Terrace, *J. Exp. Analysis Behav.* **6**, 1 (1963).
7. ———, *Science* **144**, 78 (1964).
8. ———, in *Operant Behavior: Areas of Research and Application,* W. K. Honig, Ed. (Appleton, New York, 1966).
9. ———, *Science* **140**, 318 (1963).
10. H. M. Jenkins, in *Stimulus Generalization,* D. I. Mostofsky, Ed. (Stanford Univ. Press, Stanford, 1965).
11. H. M. Jenkins, *J. Exp. Analysis Behav.* **5**, 435 (1962).
12. W. K. Honig, C. A. Boneau, K. R. Burstein, H. S. Pennypacker, *J. Comp. Physiol. Psychol.* **56**, 111 (1963).
13. C. B. Ferster and B. F. Skinner, *Schedules of Reinforcement* (Appleton, New York, 1957).
14. The correction procedure was not used during the generalization tests.
→ A. Amsel, *Psychol. Rev.* **69**, 306 (1962).
16. R. Lawson, *Frustration: The Development of a Scientific Concept* (Macmillan, New York, 1965).
17. Research supported by NIH grant HD-0930-05 and NSF grant GB-4686.

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Curiosity and Play: Basic Factors in the Development of Life

The article on "Curiosity and Exploration" by Berlyne (*1*) contains observations on curiosity and exploratory behavior in animals which appeal to anyone who has observed young animals at play. I believe that this topic and the questions connected with it ("Why do animals play and explore?" and "What do they gain by it?") will take on an interesting perspective if we begin with the assumption that play is a basic feature of life and a main factor in its evolution.

Play involves the recognition that there is a possibility for making choices. The current picture of physics does not admit subjective feelings, and has no place for deliberate choice. The physical laws concerning molecular processes leave open alternatives at each step; the quantum theory makes possible the calculation of statistical weights, but it does not predict the outcome of an individual experiment. To have an instrument for exploring what supplemental relations may be introduced, it is suggested that in living systems there is active a faculty not recognized in the current physical picture, which induces decisions or choices between the alternatives. Such a hypothesis will enable us to construct a link with mental activities if we assume that the decisive faculty is the carrier of subjective aspects such as we find in the activities of the mind. In view of the continuity of all forms of life, we assume that forms of these activities are also present in other living beings. Within ourselves, we notice that not all these processes penetrate the "master mind;" evidently processes go on at various levels, and it is appropriate to