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POST-PAVLOVIAN DEVELOPMENT IN CONDITIONAL REFLEXES

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Liddell: It is appropriate that Dr. Gantt and I are making our brief presentations at the same session of this conference. Both of us represent post-Pavlovian conditioning in a very specific sense. As a result of direct contact with Pavlov, his laboratory, and his publications we both were motivated to embark upon, and to continue throughout our professional careers, the investigation of conditional reflexes. In a genetic sense, we belong to the first generation of post-Pavlovians.

When I equipped my first conditioning laboratory in 1924 for the study of behavior in sheep and goats, Dr. Gantt was already an experienced co-worker in Pavlov's laboratory and in daily personal contact with him. Since then both of us, independently, have reproduced all the major phenomena of conditional reflex action in the dog as described by Pavlov. Moreover, in our laboratories at Ithaca we have been able to demonstrate in detail these same conditioning phenomena in sheep, goat, and pig with surprisingly little differences from species to species. Salivary conditioning was limited to the pig and dog but conditioning of motor responses to electric shock has been employed with all four species.

This tedious but also exciting labor of validation extending over 30 years has been completed. It was necessary, however, in order that neurophysiologists may now base their precise experiments upon reliably

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reproducible conditioned responses, the dynamics of which are firmly established. The time seems to have arrived for the formulation of a sound neurophysiological theory of conditioning and perhaps of experimental neurosis.

Pavlov's physiological theory of conditional reflex action was based upon careful observations of the dog's behavior in the Pavlov frame under conditions of self-imposed restraint. Unfortunately, in those early days, from 1900 to 1926, his experimental tools were too few and too blunt. Modern electrophysiological techniques for direct examination of brain function were not available and hence Pavlov's theory of higher nervous activity was, of necessity, an exercise in speculative neurology. Thus, this monumental edifice of precise and quantitatively verifiable behavioral data was erected many years before it could be of direct experimental significance for the neurophysiologist.

Since the last portion of our conference is to be devoted to most exciting developments in post-Pavlovian conditioning, namely, precise electrophysiological studies of conditioning, I shall confine my brief remarks to other developments in this field and their impact upon psychosomatic medicine, psychiatry, and pediatrics.

In the first place, I think that Dr. Gantt and I have gone farther than the Pavlov workers in persisting in the observation of a single animal. Dr. Gantt, for example, kept his experimentally neurotic dog Nick under observation for 13 years, spanning almost a quarter of a scientific career. Nick died in his fifteenth year and it is this long-term observation of the behavior of a single animal which I have not discovered in the published work from the Pavlov laboratories.

There is no field of biological science, unless it be genetics, that is less rewarding to the investigator who is accustomed to a hit-and-run type of research. In our field, subtle changes in conditioned behavior occur very slowly, and are only to be detected by unremitting observation.

As a consequence of Dr. Gantt's study of experimental neurosis in the dog and our work with experimentally neurotic sheep, goats, and pigs (and later, Jules Masserman's extensive investigation of experimental neurosis in the cat), a progressively more intimate liaison with psychiatry is being established.

Due to the encouragement of Dr. Frank Fremont-Smith, my colleague Dr. George F. Sutherland was enabled to divide his time between studies of conditioning and experimental neurosis in the pig in our laboratory and experiments with the salivary conditioning of psychoneurotic patients in collaboration with Dr. Jacob Finesinger in Dr. Stanley Cobb's department at the Massachusetts General Hospital. Then it was Dr.

Gantt's good fortune to be invited by Adolph Meyer in 1929 to establish his Pavlovian Laboratory at the Phipps Clinic. Still more fortunately for the liaison with psychiatry that we are trying to maintain and strengthen, Dr. John Whitehorn was chosen as director of the Phipps Clinic upon Meyer's retirement. Whitehorn had spent 17 years as an experimental biologist at McLean Hospital as a consequence of the inspiration of his medical teachers Cannon and Folin. At Phipps, Dr. Gantt works with Whitehorn at the clinical level and recently they have been collaborating in conditioning studies with dogs. What could be a happier association?

Two medically important events that resulted from Pavlov's work on experimental neurosis must be briefly mentioned. In 1936 a Macy Conference similar to the present one, on the topic of neurosis, was held in Ithaca. It was a most eclectic meeting including as participants psychoanalyists, neuropsychiatrists, physiologists and investigators of animal conditioning. It goes almost without saying that no agreement was reached in answer to the question, "What is neurosis?"

The second event has been almost completely forgotten. I have never seen it mentioned as it should be in connection with the history of American psychosomatic medicine. It came about as follows:

In 1937 the late Walter Hunter of Brown University was chairman of the Division of Psychology and Anthropology in the National Research Council. He organized an interdivisional conference of the Council which met at Washington in the spring of 1937 and included the divisions of psychology and anthropology, zoology, agriculture, and medicine. The topic of the conference was "Experimental Neuroses and Allied Problems." Lawrence K. Frank and Frank Fremont-Smith attended as representatives of the Josiah Macy, Jr. Foundation.

On the third day, the conference dissolved into a small group of committees and all agreed that a new journal should be founded. This is how the journal *Psychosomatic Medicine* originated. A grant from the Josiah Macy, Jr. Foundation made possible its prompt publication.

Brief mention should be made of another development in post-Pavlovian conditioning as it relates to pediatrics. In the sheep and goat, parturition may occur in the pasture or on the range. The newborn, if it is to survive, must struggle to its feet within 15 or 20 minutes in order to suckle and to follow its mother with the flock. Thus, Pavlovian conditioning to electric shock is possible within 4 hours of birth. This conditioning is severely traumatic, even with the mildest shock to the foreleg, if the newborn is separated from its mother during this brief and seemingly innocuous conditioning routine. *In the mother's presence, however, the conditioning of the newborn is quite harmless.* But separatas I previously described, is now being employed with lambs and kids from 4 hours to 2 weeks of age. The procedure seems quite innocuous. The room is darkened for 10 seconds followed by a mild shock to the foreleg. Twenty of these darkness signals are given spaced exactly 2 minutes apart. The young animal thus conditioned *in the absence of its mother* (although it rejoins her immediately after the test) invariably dies within the year. Usually death occurs before 6 months of age.

Fremont-Smith: Do you keep it up until they die, or just for a certain time and then they later die?

Liddell: We have had them die after not more than 4 weeks of conditioning with three sessions a week They die sometimes during the training period and sometimes months afterward. They do not thrive. They are sluggish in growth as well as in behavior. Social behavior is also affected. If twin lambs are being conditioned, one alone and the other with its mother present, and then, after a few weeks of training, the mother is led toward the laboratory, the twin trained in her presence will follow her; the one trained in isolation lags behind and may not even follow the mother and other twin.

Yakovlev: I would like to ask Dr. Gantt or Dr. Liddell to comment on the development of the concept of the "first" and "second signal systems" which is much discussed in post-Pavlovian literature on conditional reflex theory, especially in the current Russian literature.

Gantt: In his later years, at the age of 80, when he started working especially with the human material, Pavlov laid great stress on the function of the human being in performing these secondary conditional reflexes—what he called the secondary signaling system, represented by language function. He considered that this was of a different order of conditional reflex from what he called the primary signal conditional reflex which the sub-human animal has.

A great deal is being done in Russia now with this concept of Pavlov's, in different methods of recording speech and studying the development of speech in infants. Some of this work is being done by Krasnogorsky, and some by Ivanov-Smolensky.

Galambos: I would like to point out that in 1885, Ebbinghaus (1), using nonsense syllables, did the first systematic studies on learning and conditioning in man.

Olds: I would like to pay a debt of gratitude in the post-Pavlovian phase of our meeting, before we begin discussion on the modern work. The debt of gratitude and recognition is to Professor Konorski (2,3), who has recently visited our country and who is certainly a post-Pavlovian. He is also in some sense a contemporary of Pavlov. Konorski is very important, both for a theoretical revision and for a methodological revision. On the theoretical side, Konorski examined Pavlov's concept of the spread of fields from point to point, in some way making junctions and channels, and he felt that this was too far outside the mainstream of neurophysiology to make sense; and so, basing himself on a Sherringtonian view, and a sort of neurobiotactic connectionism, Konorski began to revise Pavlov's rationalization of his findings and began to interpret conditioning in terms of changes of synaptic facilitation and inhibition rather than spread of fields of excitation and inhibition.

Slightly more important, perhaps immensely more important, than such a theoretical revision was his contribution to methodology. Konorski introduced in preliminary form the main psychological technique which is used today in the United States in psychology. He introduced instrumental conditioning as opposed to what is called classical conditioning.

Liddell: What year did he begin—about 1929 or 1928?

Olds: He began two years before he went to visit Pavlov's laboratory. He was invited there because of his work on instrumental conditioning of reflexes.

In the classical conditional reflex, a conditioning stimulus is applied, and then, whatever the animal does, eventually, an unconditioned stimulus follows. This means that the animal has no means of escape if the unconditioned stimulus is a punishing stimulus. It means that the animal does not have to do anything to gain the reward if the unconditioned stimulus is a positive stimulus.

In the instrumental conditioning paradigm, the animal is presented with a similar situation, but his response determines what follows. Given the conditioning stimulus, the animal will not get the unconditioned stimulus at all unless he makes a particular response which the experimenter has planned for the experiment.

Fremont-Smith: Would you just illustrate by two actual examples?

Olds: Yes. In the classical experiment, one presents a noise and gives food on the tongue. Eventually, to the noise, there comes salivation before the food reaches the tongue. In the instrumental paradigm we might arrange a situation where a noise is presented, but only if the animal lifts a forepaw is he given food on the tongue. I shall not take time to elaborate a further point of interest (though I rather hope someone else will) namely, that there is a whole school of psychology in this country who maintain that these are not two paradigms, but that one is a special case of the other; that of Pavlov being a special case of Konorski's. A reasonable case can be made for this possibility. I might almost say that the main stream of psychology in this country for the last 20 years, though many of us here would prefer to forget this, has been based on the assumption that Pavlovian conditioning is a special case of instrumental conditioning.

May I add one further comment. When you take Pavlov's theory of the formation of connections (Figure 89), on the one hand, and Konorski's theory of the formation of connections, on the other, you end up, on the Pavlov side, with the notion that if you could obstruct these fields in some way, you might be able to obstruct the memory process, and on the Konorski side, with a notion that you might be able to scoop out the engram with a spatula.

I believe that Dr. Sperry has done some experiments along this line.

Sperry: I think perhaps Dr. Olds was referring to some work that we did a few years ago in an effort to test the possible functional role of intracortical transmission as postulated in Pavlov's scheme. Briefly, the experiments consisted of placing in the cortex numerous intersecting knife cuts, inserts of tantalum wire, or dielectric plates of mica in such a way as to block, or at least to distort grossly, the patterning of any tangential intracortical transmission. Although we were not aiming particularly at Pavlov's concept of irradiation, I think that the absence of any significant functional disorganization as a result of these measures is difficult to reconcile with such a concept. We never emphasized this specific point, because, I had supposed that the idea of cortical irradiation had already been generally abandoned for other reasons.

Now that we are approaching the new work with implanted electrodes, I wonder if it would not be helpful, particularly for those of us not working on conditioning, to summarize briefly some of those conditioning phenomena that have seemed particularly relevant to brain theory. I can start by mentioning a few that come to mind and probably others here can add to the list.

First, I think we have not yet mentioned conditioning under curare. Apparently the process goes perfectly well in the absence of any motor response. The motor response has been eliminated also, I believe, by crushing of the nerves, and further, by local anesthetization of the motor cortex, which, of course, blots out the—Dr. Doty says "No." Well, you correct me on that.

Doty: There are a lot of objections that can be raised to the latter experiment.

Sperry: In any case, there have been experiments in which ablation of the motor cortex has failed to abolish learned responses (4). This should eliminate as a necessary part of the brain mechanism the dominant focus of attraction in the cortex that according to Pavlov was supposed to funnel the conditioning stimulus excitation down into the reflex motor pathways.

The effect of random reinforcement is particularly critical for any brain theory. We estimate the strength of the conditional reflex in part by its duration and the difficulty of extinguishing it. It has been shown (5) that with an equal number of trials in the conditioning procedure, aperiodic, rather than regular, reinforcement produces a conditioned response that is much more difficult to extinguish than one formed with reinforcement at every trial. According to most physiological explanations you would expect to get a much stronger connection between the brain centers involved if you pair the unconditioned with the conditioning stimulus on every trial.

The effect of alternate reinforcement and extinction has already been mentioned. If you establish a conditioned response, then extinguish it thoroughly, then reestablish it, and then extinguish it again, it has been found that, after so many repetitions of this, the learned response can be reestablished with a single trial (6). This too has important implications for the underlying brain process.

The phenomenon of delayed conditioning is also interesting. Generally, the signal stimulus precedes the natural reflex by a short period, from, say, ½ sec.—which is about optimal for the eyelid response in man—on up, depending on the situation and species. It is possible to set this signal stimulus as far forward as ½ hour or perhaps even longer. This poses some nice physiological problems as to the nature of the trace effects of the stimulus and how they operate at the end of the delay. The animal somehow has to hold the effect and to respond at the proper time. It is one kind of "timing behavior."

Even the simple absence of reversed conditioning is something to keep in mind in formulating a brain theory. That is, that the signal stimulus has to precede the reflex that it is to be tied to. I wouldn't be surprised if there exists in the vertebrate brain in general some kind of built-in tendency to perceive "what-follows-what," "what-leads-to-what." Appropriate central nervous adjustment in this respect is fundamental not only to our cause-effect thinking, but to the behavior of all vertebrates from the lowest forms to the highest.

In particular, we should not forget the examples of rapid conditioning. In conditioning, we have one problem in the initial acquisition of the conditional reflex, and another associated with its prolonged retention. Generally it is not easy to distinguish the two because in most laboratory conditioning the time span is great enough so that the acquisition proceeds in part on the basis of traces retained from earlier conditioning trials. However, a great deal of rapid conditioning and learning can and does occur in a single trial or two, not only in the laboratory but also under natural conditions. With human subjects, it is not difficult to establish a conditional reflex and extinguish it, all within a 20-minute session. The point is that a lot of learning and conditioning is so rapid that you don't have to deal with the permanent-type memory traces at all. The establishment of the "temporary connection" becomes a problem primarily of dynamic reorganization. In time the reorganization becomes consolidated through lasting tissue changes. It is often convenient in considering the brain processes, to separate these two phases of the problem.

The effect of electroconvulsive shock is of interest in this regard in that electroconvulsive storms wipe out temporary or recent learning, *i.e.*, of trials made up to ½ hour or so before the shock, but do not eradicate the more permanent trace systems.

Fremont-Smith: When you say "more permanent," you mean those that have resided longer in the brain?

Sperry: Yes.

Fremont-Smith: This is a very general phenomenon, that all recent memory is more vulnerable than memory that has resided a longer time. In a disease process, excepting psychological blocking, it is always the most recent memories which are wiped out and the long-established ones, the memories of childhood, that are the most persistent. There is a very fundamental aspect there that needs to be touched on.

Sperry: Yes, it is particularly relevant to the problem of the engram and its nature. Another point here will illustrate the rapid dynamic reorganization occurring independently of trace formation. Experiments with human subjects (7) have shown that a conditioned response that required some fifteen to twenty trials to be established under the usual conditions, will be performed on the very first trial with no training when the subjects are given a full understanding of what to expect in the conditioning procedure.

Fremont-Smith: This was in man?

Sperry: Yes, this was in man. I believe that we have not discussed motor equivalence as seen in instrumental conditioning. This also is difficult to account for with any theory that postulates the wearing in of connections between conditioning stimulus and conditioned response centers. The observation in this case is that an animal will easily and spontaneously substitute for the conditioned response a quite different response if the situation is changed to demand it, or if the goal is perceived to be more readily achieved thereby. There is, of course, continuous motor readjustment of this kind in the learning of new motor skills.

With respect to decorticate conditioning, it is worth noting that fishes have been reported to show excellent learning and retention after removal of the entire forebrain, and Dr. Arora in our laboratory has recently confirmed this. We find also that a visual discrimination can be retained in fishes after complete section and regeneration of the optic nerve. This shows that the memory traces or engrams are not rigidly or directly connected to the sensory input channels. There probably is a certain amount of reshuffling of optic fiber connections in the brain as a result of regeneration. We infer that the regenerated fibers get back quite close to the same cells, but suppose that probably they do not reestablish exactly the same synaptic terminals. Whatever the degree of synaptic rearrangement, it does not disturb reactivation of the engram.

White: They change without variation in response?

Sperry: Yes. These are color and also acuity discrimination habits. The findings show not only that memory for the habit is retained, but also that color perception is restored in its original form after regeneration. Accordingly we must infer the existence of another dimension of specificity in the optic system associated with color. This presumably is superimposed upon the topical specificity demonstrated earlier and associated with directionality (8). The restored visual acuity also approximates closely that of the normal fish suggesting that most of the severed optic axons must succeed in reestablishing functional connections.

Some of the work on the corpus callosum that Myers and I (9) did shows that the memory trace system established with unilateral input is set up not only in one hemisphere, but that there is a duplicate set of traces set up in the opposite hemisphere via the corpus callosum. You can cut out the cortex on the trained side, or section the callosum (10) after training, and you find that the memory survives in the opposite hemisphere.

I think it is fair to say that so far we know of no irrelevant or external agent that can wipe out long-established engrams. Temperature changes, magnetic fields, concussion, electric currents, drugs, etc., are ineffective. Normal nerve impulses can put them in and possibly can wipe them out. (This latter remains a question as already indicated, *i.e.*, whether or not impulses can actively wipe out the memory trace.) One may wonder here whether the impulses generated in electroconvulsive shock are not as effective in establishing traces as are impulses generated in organized activity. It is entirely possible that shock treatment, if repeated frequently enough, does gradually wear blankness and confusion into the brain, the traces for which in time begin to compete in stability with all but the long-established engram systems. In this regard I like to picture two factors at work in engram formation: first, a transient disturbance or shift or excitatory threshold that tends to recover within a ½ hour more or less, and second, a metabolic-type factor that is constantly at work and tends to maintain and to reduplicate or freeze the existing threshold. A slower process, this latter has little effect over intervals of less than 20 minutes or so. The nearly perfect replication within the engram structure that is achieved in the metabolic turnover throughout a human lifetime is always a source of amazement to me and may be indicative of the kind of physicochemical change to look for. An alternative would be trace systems stabilized, like the nucleic acids of the genes, which are said to be subject to little or no metabolic turnover.

A modification of Pavlov's theory has been proposed by Konorski (10), in which he suggests that stimuli have both a gnostic, high-level effect and a lower affective component, and that the new connections are formed between the gnostic center of the conditioning stimulus and the affective center of the natural reflex. Dr. Liddell has mentioned that no really adequate brain theory has been brought forward to replace Pavlov's. At most we have only some vague thinking about the possible nature and location of the new connections laid down between conditioning stimulus and response centers, *i.e.*, that they must be more complex than the direct transcortical linkages proposed by Pavlov, that they probably involve subcortical centers, and that some kind of reverberatory activity may be important in the earlier stages (11). Some years ago I was bold enough to suggest that the conditional reflex does not necessarily depend upon the establishment of traces or connections of any type between the centers for conditioning stimulus and conditioned response. The neural association between conditioning stimulus and conditioned response was conceived to be a purely functional one and effected in quite a different way (12)—but this probably is too long a story to go into now.

Briefly, the suggestion is that the engrams support the arousal of a perception or "expectancy" of what is to come in the conditioning situation. Having learned what to expect, the animal prepares, through a "cerebral facilitatory set," to make the appropriate response. The excitations of the conditioning stimulus are routed into the new pathways of the conditioned response, not by left-over traces, but by an active pattern of facilitation and inhibition imposed on the neural circuits by the transient facilitatory set. With this scheme, there is no need to search for the "new connections" established between conditioning stimulus and conditioned response centers, as almost universally assumed, because there is none there. There is only an evanescent opening or facilitation of these (preexistent) pathways within the conditioning situation. The permanent traces that lead to arousal of the expectancy and preparatory set may be extremely complex and diffused and are not tied particularly to the specific conditioning stimulus, but to countless stimuli associated with the conditioning experience.

I am sure others can think of further background material and issues relevant to brain mechanisms, *i.e.*, things that it would be well for us to have in the back of our minds as we begin to try to interpret the new data from the studies with implanted electrodes.

Liddell: I knew of Konorski's and Miller's work before they joined Pavlov, but I also remember that in the Pavlovian context, P. S. Kupalov, as early as 1929, formulated the notion of conditional reflexes without initiation, and he got into difficulties at the Stalin session for this concept of reflexes without initiation.

What he meant was this: He watched a dog in Pavlov's laboratory which had a battery of conditioning signals. The observer watching his manometer saw secretion begin. He looked at the dog. The dog was looking under the edge of the table where the bell-tapper was, and was wagging his tail and salivating. Later, the dog looked forward toward the light and salivated. In other words, he was going through his repertoire of possible signals that might come, and this was what Kupalov called "reflexes without initiation."

We have observed these conditional reflexes without initiation in the sheep, goat, and pig. The pig conditioned to electric shock sometimes stages a real show in the absence of the conditioning stimulus—squealing and shaking the foreleg as if in real pain.

I don't think that any of us who study conditioning across species lines fails to realize that Skinner has benefited us very much and so has Pavlov. Their observations form a continuum in a dynamic sense.

Galambos: I rather like the distinction Dr. Olds has emphasized between the classical Pavlovian or Type I conditioning and the instrumental, operant or Type II conditioning. It might be well for experimental physiologists, with their electrodes in the brain, to maintain this distinction, just on the chance that there might be different central correlates for the two.

In the Type I situation, the animal is unable to modify its environment by anything that it does. In the Type II situation, by contrast, the response serves to change the animal's environment. There is just enough suggestion in the material available on what goes on within the brain during learning to make us think that the obvious differences of behavior in the two situations have corresponding brain correlates that differ.

Liddell: I am very much in favor of what you are saying. I believe that we have a spectrum or continuum in conditioned behavior. Instead of the concept of collision of the active and opposed processes of excitation and inhibition as postulated by Pavlov, or the psychiatrist's notion of conflict, I agree with Konorski's idea of two limits or extremes in conditioning. We have plasticity with many degrees of freedom in behavior at one pole, and we have rigidity of behavior at the opposite pole. In our animals, conditioned to a rigid time schedule, rigidity in the sheep's behavior manifests itself as complete passivity; in the goat it is expressed as tonic rigidity of posture with stiff extension of the trained forelimb at the signal.

Pribram: I want to be sure that we don't sell Skinner short. I think that he has made tremendous contributions, both in technique and in theory. Though he does not admit to theory, the notion of operant conditioning implies that the consequences of behavior modify subsequent behavior. This notion is of course not entirely original with Skinner (13), but he and his pupils have certainly developed it to a greater extent than has anyone else. I think that this body of knowledge and the influence it has had on young people in the field should not be ignored. Operant conditioning fits right into the work we are discussing and is an extremely important contribution.

Olds: The aspect of Skinner's (13) work that I wanted to point out is that there is something very important and very different that Skinner first gave us. Skinner took us out of the Pavlovian situation and gave us a totally new one, by putting the animal in what we might call the continuous operant environment, where we could count the frequency of a response as a measure of many things. We don't give ten trials a day in a Skinner box, and we don't have to present any stimuli to get behavior started. Instead we put the animal in a free environment, and then count the number of times he does something. We can count frequency as the measure of learning; we can count frequency as the measure of drive; and I have recently thought that we can count it as some measure of pleasure. In any event, I wanted to say one other thing, and this is also relevant to what Dr. Galambos and Dr. Pribram have just said, about classical versus instrumental conditioning.

It is important to keep in mind the fact that the animal even in the classical conditioning situation, is not totally at a loss to modify some component of the stimulus input. The animal can, perhaps, make the acid have less effect by secreting a certain kind of saliva, so there is a contingent and an uncontingent component of the stimulus in the classical conditioning paradigm. The animal, by hunching his shoulders or tightening up muscles, can perhaps make the shock feel a little different. I think that we have to keep this in mind when we think of distinguishing two mechanisms. I wouldn't go so far as to say let us not look for two mechanisms; but I would say, let us be open-minded to the possibility that there may be only one.

Gantt: Dr. Olds, I understand in general what you mean, but I don't understand specifically the significance of, or what you have in mind, when you say that the type of conditioning which you call classical is a species of the other.

Olds: I would say that if what I have just said is true—and, admittedly, it may not be—then, classical conditioning is the situation where the animal has very little control over the unconditioned stimulus, whereas in operant conditioning the animal has a great deal of command over the unconditioned stimulus.

Liddell: What do you mean by "paradigm?"

Olds: By "paradigm," I mean what the experimenter does to the animal; that is, when I say "classical conditioning paradigm," I am talking about the situation in which the experimenter himself determines the conditioning stimulus, the unconditioned stimulus, when these are to occur, and the total time order of the experiment. That is what I mean by the "classical conditioning paradigm."

Fremont-Smith: The paradigm is a design, really.

Mirsky: A model.

Olds: A plan of the experiment. When I speak of the instrumental conditioning paradigm, I mean that the experimenter decides when to give the conditioning stimulus, but some response of the animal determines the time when the unconditioned stimulus will be given.

Gantt: Do you mean that the classical conditioning is only part of the instrumental? Do you mean that the instrumental is a bigger, more complex conditioning, and that it includes the classical?

Olds: The basic set of events in any conditioning experiment is that we apply a stimulus and the animal produces some responses, and we apply another stimulus. If we don't care what that intervening response is, that is, if the animal may do anything at all and still get the unconditioned stimulus, this is classical conditioning. If we decide beforehand that the animal must make a very specific response in order to get the unconditioned stimulus, then we have the instrumental type of conditioning.

Sperry: Dr. Gantt, if you record heart rate and respiratory rate, don't these appear in both instrumental and in classical conditioning, and don't they appear prior to the specific conditioned response, such as salivation or leg flexion?

Gantt: Yes, they appear before. I started studying the cardiac conditional reflex with the method of not reinforcing, except when the dog does not make the movement. I don't know whether or not you call that instrumental. Then, I went over to constant reinforcement. As far as the cardiac component goes, it is better when constant reinforcement is used, but the point that you brought up is that the cardiac conditional reflex is formed in general after the first reinforcement. You mentioned earlier the fact that the conditional reflex can be formed much more rapidly than has been recognized in the ordinary classical Pavlovian type of measurement.

Sperry: Yes, and I was thinking here that these early visceral effects may indicate a common basis for both types of conditioning. It may be that the classical is somewhat simpler than the instrumental, because, in the instrumental, the animal has to learn, not only what to expect from the signal stimulus, but also what kind of reaction to make to handle the situation in the best way; whereas under the conditions of classical conditioning, the animal needs only to learn what the signal stimulus brings and the anticipatory response comes automatically.

EDITOR'S NOTE: Dr. Olds would like to add the following "afterthought" to his remarks at the conference:

> The argument that makes classical a special case of instrumental goes like this: (*a*) Classical conditioning is supposed to involve a pairing of two stimuli, a conditioning stimulus first, an unconditioned stimulus second, with the response to the unconditioned stimulus eventually occurring (partially at least) to the conditioning stimulus. (*b*) Instrumental conditioning is supposed to involve a conditioning stimulus, an arbitrary response on the part of the animal, and an unconditioned stimulus contingent on the intervening response (or, in avoidance learning, on its absence). The response eventually learned in this case is the arbitrary response that produces or avoids the unconditioned stimulus. (*c*) In fact, in classical conditioning, the animal does arbitrary things between the conditioning stimulus and the unconditioned stimulus. (*d*) The response learned in classical conditioning is not really a component of the response to the unconditioned stimulus, but rather some arbitrary response that produces some more reward from, or avoids some punishment from, the unconditioned response. (*e*) Therefore, since the learning in classical conditioning is not the learning of the unconditioned response to the conditioning stimulus, but rather of an instrumental response, classical is just a special case of instrumental.

Leake: In considering the post-Pavlovian development in Russia itself, it is important to call attention to two lines of development, in addition to the further intensive investigation of the classical Pavlovian conditioning.

These two are: first, the extension of the picture to the evolutionary factors that may be involved in the conditioning process. I think this was first undertaken by Orbeli, and he is approaching phylogenetic factors in relation to conditioning from the standpoint of adaptations. The second rather important line of development is the increasing interest in comparative studies on conditioning, particularly with invertebrates. Three-fourths of a new volume on the comparative physiology of the nervous system by Konstantin Kostoyantz at Moscow are devoted to invertebrates, and this is a book of about 600 pages. There are a couple of specific types of studies of this sort to which I would like to call attention. First, at Koltushi, we were shown conditioning with bees; that is, individual bees are conditioned to both sight and smell, with reward from sugar water. This conditioning seems to be transferred to other bees by contact with the one rewarded. The dance of the bees seems to have an inverse relation to delay in getting food to which a stimulus has been given. The conditioning is said to depend on the integrity of a mushroom-like protuberance on the antennae of the bee. Attempts are being made to obtain action currents from implanted electrodes in the neural ganglia of the bees. Similar studies of this sort are going forward on earthworms, where implanted electrodes are being placed in ganglia. Other studies are being made in silkworms. Related experiments of this type on bees are reported by von Frisch in Germany.

Fremont-Smith: You say "related." Didn't von Frisch anticipate or do the first work on the bees' dancing?

Leake: On the bees' dancing, yes, but I'm not sure about these conditional reflexes.

Teuber: It was 1913, I believe (14-17).

Leake: As early as that?

Teuber: Yes.

Leake: One other interesting observation in connection with bees was this. If one bee is injected with acetylcholine, it is attacked on returning to the swarm, and then those who attack it are attacked by others, until the swarm is very nearly destroyed.

Another study of a comparative nature on vertebrates has to do with birds. Anokhin, studying crows, finds a response to characteristic sounds at birth. Young crows respond only to the "caw" sound, but gradually will learn to respond to other sounds, and there seems to be a correlation, then, with the growth and development of cells in the organ of Corti.

Then, finally, in comparative studies on conditional reflexes, Professor Kostoyants, who has been studying various aspects of this matter, is, with his group, studying silkworms. Here he has obtained action current records from microelectrodes in the ganglia of cocoons, and has shown types of responses to variations in air currents, and the initiation in the adult silkworm of the weaving process under the influence or stimulus of air currents. He describes a simple action current occurring in the ganglia of butterflies from the stimuli produced by light. He finds that stimuli of this sort, or action currents of this sort, are blocked by mercury bichloride but are restored by glutathione. This has to do with the general study that he is making on factors concerned in acetylcholine transfer, which I have not time to comment upon now.

It is interesting that one of the characteristic features of post-Pavlovian conditioning studies in Russia is the extension, rather widely now, to invertebrates.

Purpura: While we are on the subject of comparative physiological psychology, I would like to mention that there have recently appeared in *Science* (18) two or more papers dealing with the rather controversial subject of "learning in paramecia." Dr. Gelber apparently claims that food-deprived *Paramecium aurelia* can be induced to cling to the sides of a clean and sterile platinum wire after having been exposed to the wire when it was baited with food. I suspect that she believes that this represents some form of learning process which the protozoa have acquired. On the other hand, in the same issue (19), Dr. Jensen claims that the results reported by Dr. Gelber may be alternatively explained in terms of the development of acid zones which tend to trap the paramecia. Now I bring this up for the purpose of discussion as to whether or not one can apply the kind of concepts developed with higher metazoan animals to the protozoa. Dr. Jensen believes that Dr. Gelber has overestimated the sensory and motor capabilities of the protozoa. Maybe paramecia do "learn" without an elaborate central nervous system. I don't know, but I would like to get some information on this subject from this group.

Teuber: The issue was whether the enduring change was in the Paramecia or in the fluid around them.

Sperry: Perhaps it is worth emphasizing that literally thousands of studies have been made since the first demonstration of the conditional reflex in attempts to solve this seemingly simple phenomenon, and that it has turned out to be worse than a Chinese puzzle, the solution to which we still are not even close, a good half century later. In this short meeting, I suspect we can't hope to achieve an effective encyclopedic coverage but will have to be selective, trying to pick out those things that really bear on the brain problem, and trying especially to point up some of the more critical issues that have come out of the work to date, and on which data from studies with implanted electrodes may soon shed new light.

Teuber: Dr. Sperry mentioned the various directions the work has taken since Pavlov. It could perhaps be put this way: For one thing there has been a tremendous effort by many people to show that conditioning is an important phenomenon occurring in many species, orders, and even phyla. But this may not be the most important aspect of the more recent work; there are two or three other issues that have arisen.

There is, first, the attempt to find out what goes on in the brain during conditioning, whatever conditioning may be. I agree with Dr. Sperry. We don't know, at least not yet, what it is, nor can we expect to find out during this conference.

A second issue, and one that is probably just as important as the first, is this: How do we analyze what goes on in conditioning, on the behavioral side? Are we dealing with a unitary process, or are there two or more processes? An answer to this question would bear on the way in which we might be looking for neurophysiological correlates of conditioning in the brain. It is clear that our discussion went back and forth on this point and that we don't know whether we are dealing with one or several processes.

There is a final point and one we have slighted thus far; we might have to continue to slight it in this context, but it is far from trivial: Is conditioning a paradigm of all learning, *i.e.*, is it the most representative form of learning we might find for study, or is it only a very special, and perhaps restricted, way of modifying behavior? On this third point one could assemble a good deal of evidence; in work with perceptual processes one encounters a great many phenomena that are exceedingly difficult to subsume under the categories of conditioning, whether Pavlovian or post-Pavlovian (20-23).

These then are the three issues: What are the brain correlates of conditioning (whatever conditioning might be)? What constitutes the process of conditioning, or its processes, on the behavioral side? And, lastly, is conditioning the example *par excellence* of learning, or is it only a very special case?

Olds: There are two people who ought to be mentioned at this time, because they have done so much work on two of the topics which Dr. Teuber mentioned. One is Lashley, who has not been mentioned explicitly yet.

Teuber: Implicitly, just now (20).

Liddell: I meant to mention him previously. His whole career was spent in trying to find these temporary connections. That is the way he got into behavioral studies.

Teuber: And into analyzing behavior by making cerebral lesions, with results quite different from what Pavlov would have predicted.

Olds: And I think that the one other person we ought to mention is Tolman (24), who spent a long time on a series of latent learning experiments. He demonstrated that an animal which performs a set of responses that might eventually become instrumental but are not so at the time of learning, will learn something from accidental responses, such that if the outcome of one of them becomes valuable to the animal later, he will demonstrate that he already knows how to perform to get it.

Lilly: I think it is time we discussed a few of the actual conditions under which these experiments are done or at least mention them. It seems to me that the Pavlovian conditioning and Skinnerian operant conditioning have one other set of conditions in common: isolation and restraint of the animal. This is selection from the environment of those aspects for control which will generate the result you are looking for.

If you take an animal in a natural situation, it is very hard to show this kind of learning because of the background racket. Therefore, you try to cut this background noise of stimulation and opportunities for action down to the very minimum. I must also emphasize here the experimenter's relationship to the animal, which Dr. Liddell brought up. In the case of animals with larger nervous systems, as you go up the scale from the Paramecium to the human being and the porpoise, you find—

Purpura: Thank you, then the paramecium is included.

Lilly: When you work with dogs, monkeys, porpoises, or man, you find that the relationship to the experimenter becomes an increasingly important determinant of the result. If you isolate a monkey in a room and feed him through a slot, he becomes apathetic, withdrawn, and refuses to work for anything. However, by developing a close relationship with him, if you are going to keep him away from other monkeys, you can keep him in good spirits for many months. There are species differences, obviously, between the pigeons of Skinner and the dogs of Pavlov, which it is rather redundant to point out, especially the species difference with regard to isolation and restraint and the relationship to the experimenter that I was mentioning.

I would like to finish with a series of questions: Who started and who has taboos on the words, "reward," and "punishment"? What does this have to do with the Pavlovian unconditioned stimulus? Who discards the word, motive, and who uses it?

Liddell: Speaking personally and with prejudice, I discard motivation and reward and punishment in my intellectual frame of reference, without any prejudice to the data.

Pribram: I don't think we should discard the words, "reward," or "punishment." On the other hand, when we use the Skinner box or a conditioning setup we must be very careful to determine what we are to call "reward" and "punishment." This is especially so when we try to identify these terms as referring to the same thing that we subjectively and intuitively feel. The two universes of discourse can be brought together only by a whole series of experiments. Until we ourselves are fairly sure that these particular experiments demonstrate what we have labeled them to demonstrate, can we safely use the words "reward" and "punishment" to denote the effects of neural self-stimulation?

Liddell: We should not load our procedures with value terms.

Pribram: I don't agree to that either. We are not interested in trivialities. We are interested in "reward" and "punishment," so let us use the terms but with care.

Fremont-Smith: I think that we should simply define our terms and load them all we want to, provided we make our use of them very clear, as it may be quite different from someone else's use of them.

Leake: I think that it is very striking that the Russian physiologists use none of these terms. I think that they avoid them deliberately on the ground that they are value-loaded.

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Here, there would be circumstances to be kept in mind also, not only from the neuromuscular and the neurovisceral afferent feedback that may be involved in connection with the behavioral aspects of the conditioning process, but, in the second place, the chemical or chemico-metabolic factors that may come in as a result of the influence of the limbic-midbrain circuit on the endocrine system itself. From this chemico-metabolic factor, may come a servo return also of a chemical nature, through the over-all metabolic reaction in the body. There is then, the possibility that this may alter the metabolic condition of the nerve cells themselves. It is this alteration of the metabolic condition of the brain cells which may, in part, encompass the factor, referred to so often by the Russians as developed from Wedensky and Ukhtomsky, of the functional lability of the central nervous system cells. That this may be influenced by endocrine or other chemical factors is quite clear.

Magoun: In a recent paper Efron (14) describes the therapeutic use of conditioning procedures for the control of seizure discharge. If I may take just a moment, I think this is fascinating enough to epitomize.

Efron had a patient in whom uncinate seizures began with an olfactory aura. He found that an intense olfactory stimulus, presented during the aural phase of the seizure, was able to block its subsequent development, as has previously been recognized in the case of other modalities. He was then able to undertake conditioning procedures, so that the patient ultimately found it possible, when she experienced the aural stage of the seizure, simply to think of an intense odor, which had been conditioned by numerous trials and, by so doing, to abort the progress of the seizure. Entry into the course of the seizure discharge would appear, in such an instance, to occur somewhere centrally in this woman's brain, where we describe events as mental or subjective.

I wanted to mention, too, that F. Worden,* James T. Marsh, and William J. Hockaday have, over the past 2 years, been engaged in a program of conditioning studies which employ auditory signals and electrical recording from the animal brain, with results much like those which Dr. Galambos has described. The auditory signal evokes discharge more widely in the brain, and responses become of higher amplitude, when it is first paired with situations that can be called rewarding or punishing. The amplitude of the evoked responses diminishes and their distribution shrinks again when the animal has learned to manage the situation so as to avoid punishment.

Sperry: I have one or two points that I can cover quite briefly. The first concerns a subject to which Dr. Doty referred in passing but to

*Worden, F.: Personal communication, 1958.

which otherwise we have given little attention, namely, the problem of the location in the brain of the "new connections" or engrams. As Dr. Doty mentioned, the engram has proven to be a rather elusive will-o'-the-wisp and is considered to be diffuse and nonlocalizable.

I was surprised to find that in the cat we could attain the degree of localization illustrated in Figure 157 *A*. The engrams for various kinds of touch discriminations performed by the left forepaw appear to have been localized in the remnant of cortex left in the right hemisphere. Preoperatively trained discriminations survived the surgical isolation shown and new ones were learned almost as well as with the whole hemisphere. This brain, incidentally, was previously divided down the middle by section of the corpus callosum and hippocampal commissures. For short, we call it a "split-brain" preparation. The neocortical portion of the anterior commissure is degenerate. (Usually we section the anterior commissure and also the optic chiasm if vision is to be involved.) In an earlier study (15) it was found that the normal contralateral transfer of somesthetic discriminations from left to right forepaw is prevented by

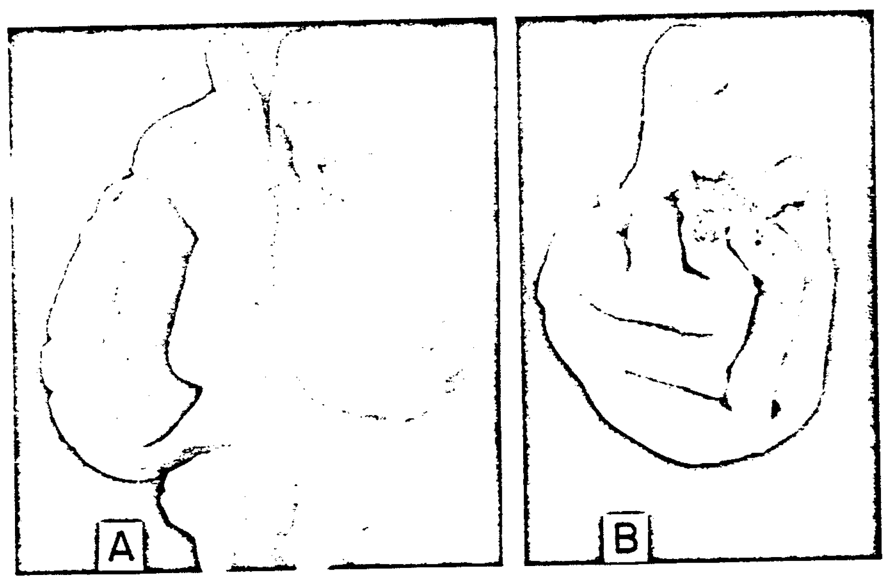

FIGURE 157. Cat split-brain preparation showing cortical remnant in right hemisphere: (*A*) that mediated retention and new learning of somesthetic discriminations performed by the left paw. Subsequent reciprocal lesion made on left, shown better in lateral view (*B*), abolished all but a bare trace of discriminatory performance with right paw without impairing that of left paw. Reprinted, by permission, from Sperry, R. W.: Preservation of high-order function in isolated somatic cortex in callosum-section cat. *J. Neurophysiol.* 22 (In press).

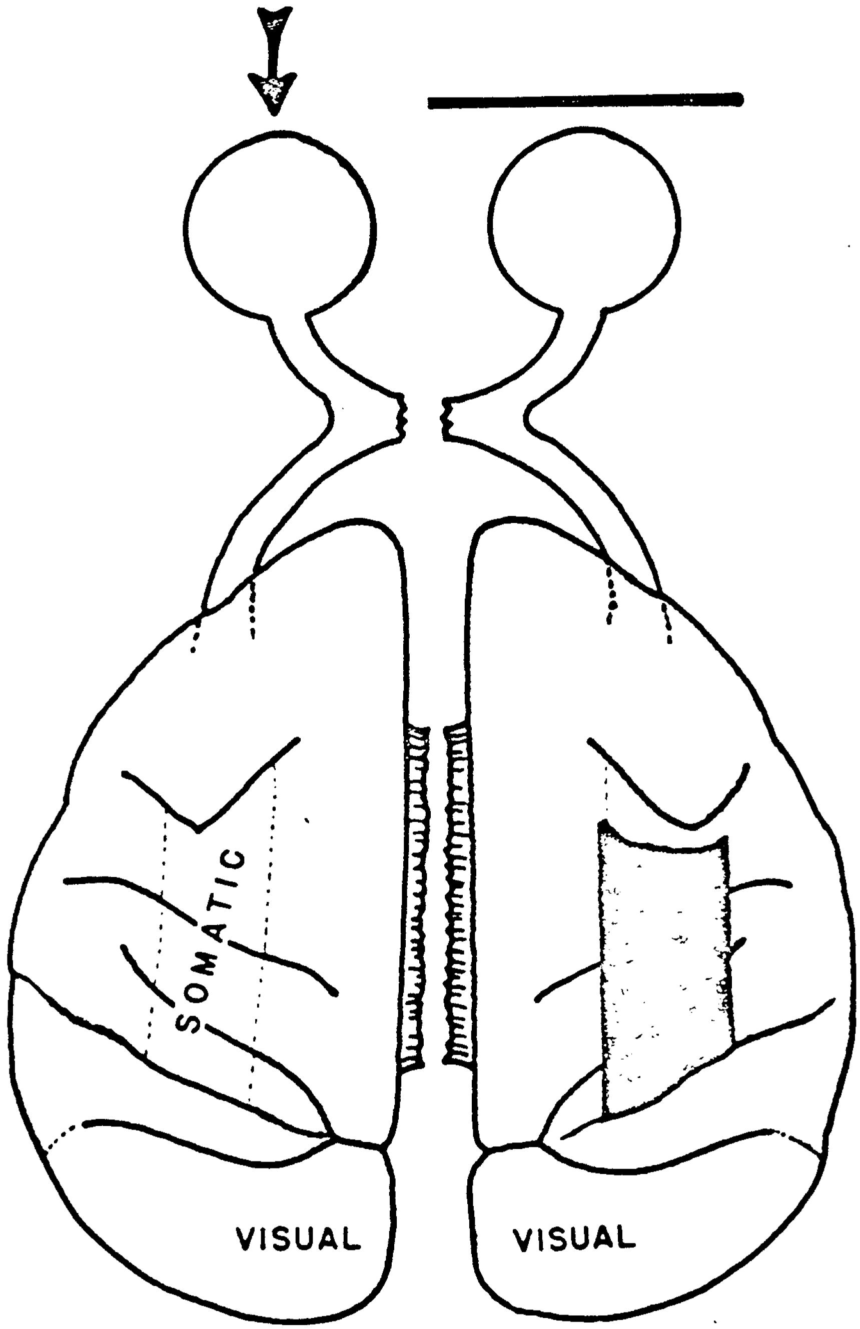

FIGURE 158. Sensori-sensory integration. Use of split-brain preparation to study perceptual integration between vision and somesthesis in monkey.

section of the callosum. That the engrams are not partly in the intact hemisphere is further indicated by the fact that relatively small lesions centered in the forelimb area of the left cortex; *i.e.*, small reciprocal lesions on the opposite side severely impaired the discriminative performance of the right paw while that of the left paw was not affected. The lesion in the left hemisphere, barely visible in Figure 157 *A*, shows better in the lateral view in *B*. This lesion left a bare trace of discriminative performance with the right paw without impairing that of the left. I suspect that the cortical island on the right could be pared down somewhat farther provided the somatic cortex and its projection fibers were preserved. Additional removal of the amygdaloid complex and the bulk of the hippocampus on the side of the cortical isolation, in current work with Dr. Schrier, has produced little, if any, additional impairment of the retention and new learning mediated through the cortical island.

In regard to this rather circumscribed localization, it should be emphasized perhaps that the discrimination habits were well stabilized by overtraining, and that they were of a highly specialized nature. All the cat was obliged to do was to stand upright and to push on one or another pedal depending on its surface texture or contour. Both the input and output specific to the performance were thus narrowly restricted within the somatic sphere.

One further point here regarding methodology. We are told that Pavlov used to say that he took for science the salivary duct and its output on one side, leaving the one on the other side for the dog. In somewhat similar manner we here take one hemisphere for science and leave the other for the use of the animal. The cat gets along fairly well, as do similar and lower forms, with the cortex of only one hemisphere. Restricting the cortical ablations and the learning and behavior tests to a single hemisphere makes it possible to extend greatly the scope of the ablation and lesion techniques, mainly because one can thereby avoid the severe paralyses and other deficits in background function that are produced when the lesions must be bilateral.

Figure 158 illustrates a somewhat different use of the split-brain preparation. Conditioning typically involves a functional association of some kind between two sensations produced respectively by the conditioning and unconditioned stimuli. So-called sensori-sensory conditioning poses still more specifically a problem in the central association of two sensory stimuli. We are currently running a study aimed at the mechanism of sensori-sensory integration involving visual and somesthetic sensibility in the monkey. The monkey is shown two round plaques, one of which is heavier than the other. Four of these plaques are employed, a black pair and a yellow pair, the two pairs being similar in appearance except for color. The monkey is taught to select the heavier one of the black pair and the lighter of the yellow pair. The black and yellow pairs are switched at random so that in any given choice the correct proprioceptive cue is conditional on the visual cue and vice versa (the term *conditional* being used here in a rather different sense than elsewhere in the Conference).

Before going deeper here, let me fill in some necessary background. Earlier studies (16) have shown that visual discriminations transfer readily from one to the other eye in the unoperated monkey and also in the monkey with midline section of optic chiasma, anterior commissure, and anterior half of the corpus callosum. Section, in addition, of the remaining posterior part of the callosum along with the hippocampal commissure abolishes the interocular transfer of visual discriminations involving brightness, size, color, three-dimensional shape, and flat pattern. Opposing discriminations can be learned *seriatim* or concurrently through the separate eyes without interference, *i.e.*, with five or ten trials to one eye, then as many to the other, and so on, alternately. It was interesting to note in one animal, which developed a sulking response to a particular problem presented to the second eye, that this response remained restricted not only to the given problem, but also to the one side. The monkey would perform the same problem very nicely, if we switched back to the first eye, and would perform without sulking with the second eye on any of the several other problems it had already mastered.

Unlike the visual tasks, somesthetic discriminations for softness, roughness, weight, and three-dimensional forms were found to transfer at a fairly high level from the trained to the untrained hand, as did the correlated motor learning.

Fremont-Smith: Even in the split-brain?

Sperry: Yes, this is contradictory to the results which Dr. Stamm and I found in the cat. Perhaps it is correlated with a more highly developed bilateral representation of the somesthetic system in the monkey, and/or the integrative relations of the ipsilateral system at the cortical level.

If we keep in mind here the presence of somesthetic transfer and the absence of visual transfer, we are ready to return to the question dealing with sensori-sensory integration. After the monkey had mastered the conditional visuo-tactile problem described above using the right eye and left hand combination, the same problem was switched to the left eye and right hand. The training on the second combination started from a level of pure chance and showed little, if any, significant saving. When the right eye, right hand and the left eye, left hand combinations were then tested, we found high level transfer in both cases with only a little hesitancy during the first several trials.

An additional new tactile problem was then trained with the left hand, after which I removed the somatic arm area from the right cortex as indicated in Figure 158. The lesion extended from about the anterior edge of 4 back to the superior temporal fissure with an additional ablation from the anterior bank of the Sylvian fissure, not shown in the figure, aimed at the arm portion of Somatic II. On the 13th day after operation while the left hand was still severely paralyzed, tests for transfer of the newly learned tactile problem to the untrained hand yielded scores no better than chance and relearning required over 200 trials. Learning with the first hand had taken about 600 trials, but had been delayed by a pre-existing preference for the negative pattern. Also we find considerable variation in the learning curves of the two separated hemispheres for a given problem in the monkey, in contrast to the amazing similarity observed in the cat (15,17,18). Possibly this reflects a true species difference correlated with greater perceptual insight in the primate. In any case the result here would seem to indicate that somesthetic transfer depends in part upon ipsilateral input from the untrained hand into a dominant engram system laid down in the cortex contralateral to the trained hand. We're still checking to determine whether there may also be a subsidiary engram system laid down in the other hemisphere.

Postoperative tests on the visuo-somesthetic discrimination showed the performance with left eye and right hand to be unaffected as anticipated. It was a surprise, however, to find that the discrimination could also be performed with the right eye and right hand. When this was first tested on the 20th postoperative day, the score reverted to chance in the first 20 trials but quickly rose to criterion by the 50th trial and to 90 per cent correct by 100 trials.

It was possible to test the left (paralyzed) hand in combination with either eye by the 6th week where the hand had recovered enough to indicate a choice by reaching and contact. Tactile discrimination depending on cutaneous cues from the hand had not recovered, but weight discrimination, depending on proprioceptive cues from arm and shoulder, was restored. The visuo-somesthetic, as well as pure visual discriminations were performed at preoperative levels, above 90 per cent correct, with the left hand and right eye.

When we switched to the final combination involving left eye with left hand, the score on the visuo-somesthetic problem dropped abruptly to chance. With purely visual tasks, the performance was on-off, being perfectly good in one testing session then lapsing to chance on the next. When it was off, the monkey acted as though disoriented, almost blind, but performed perfectly well when shifted to the other eye or when using the same eye with the other hand. On the 4th day of this peculiar performance, there occurred an abrupt change after which both the visuo-somesthetic and visual discriminations were performed at high level with the left hand paired with either eye. These latter observations are based on one case only and are not rigidly controlled as yet. I mention them here mainly to illustrate some of the possibilities of this approach.

The monkey uses either hand to perform visual discriminations even though the visual input is restricted to one side. Work in progress by Dr. Schrier shows this to be true also in the cat after training has been confined throughout to a single paw. In earlier unpublished studies of Myers and Miner it was found that removal of most of the neocortex except somatic area in one hemisphere and occipital area in the other in the chiasm-sectioned, split-brain cat does not eliminate eye-paw coordination.

I mention these to indicate some of the kinds of combinations and numerous possibilities which the split-brain approach offers for working out functional interrelations between different cortical areas and between cortical and subcortical centers. We have only just started to apply this kind of analysis to conditioned response mechanisms, and we hope to combine the method before long with recording from implanted electrodes.

Lilly: Is the anterior commissure cut here, too?

Sperry: Yes, it is cut.

Purpura: This is all very interesting and brings up some important factors relating to apparent discrepancies between electrophysiological and behavioral data. There is a considerable body of electrophysiological data indicating that in the cat stimulation of all four limbs evokes unit activity in thalamic projection nuclei, although some workers dispute these claims. Assuming for the moment that somesthetic activity from contralateral and ipsilateral limbs evoked activity in thalamic nuclei on one side, from Dr. Sperry's experiments we must conclude, that ipsilateral activity apparently does not register in behavioral terms. If the data indicate that an animal cannot transfer somesthetic information from one side to the other with a split corpus callosum, then I think that we must re-examine some of the interpretations based exclusively on electrophysiological experiments. However, there must be some basis for the contralateral paralyses and sensory deficits comthe pattern of time-space ordination by the experimenter. More recently, a choice available to the animal of its own programming during the experiments has been introduced by a few investigators. The elaboration of ways of central as well as peripheral approach and avoidance procedures is involved here, too. Finally, the recent achievement of chronic microelectrode recording in waking animals represents an experimental triumph.

Areas that we have not discussed much—I think that Dr. Purpura and Dr. John were the only ones who talked to any degree about them—are neuropharmacology and neurochemistry. Undoubtedly, these represent fields of equal significance although as yet less exploited than the physiological ones under consideration at this first meeting.

The third subject that I want to bring up relates to trends in concepts. It seems to me that there has been, although it has sometimes been derided, great usefulness in the confidence expressed by Sechenov that behavior can be studied scientifically by objective measurement.

I believe it to be extremely useful to pursue the intention of continually locating our conceptual models within the brain. There are groups of scientists who locate such models on blackboards or entirely separately from the brain. Even though Pavlov may have been incorrect in the degree of responsibility he assigned to cortex, I think that it has been eminently useful, nevertheless, that he intended to locate the functions under consideration within the brain.

Sperry: I have never been entirely satisfied with the materialistic or behavioristic thesis that a complete explanation of brain function is possible in purely objective terms with no reference whatever to subjective experience, *i.e.*, that in scientific analysis we can confidently, and advantageously, disregard the subjective properties of the brain process. I do not mean we should abandon the objective approach or repeat the errors of the earlier introspective era. It is just that I find it difficult to believe that the sensations and other subjective experiences *per se* serve no function, have no operational value and no place in our working models of the brain, whether blackboard or otherwise. The materialistic dialectic advanced by Bechterev, Pavlov, Watson, and others is still not 100 per cent foolproof: There remains a weak link, deep centrally between input and output, perhaps about where the impulses hit those positive and negative (self) reinforcement centers that Dr. Olds and Dr. Lilly and others are mapping. Perhaps it is true that the "pain" and the "purple glow" effects of the self-activated electrode can be ignored in our explanatory neural models, but in my book the point is not satisfactorily settled.

Livingston: This calls for further explication, Dr. Sperry. The fact that I was stressing the utility of objective measurement in the study of behavior does not mean that I ignore or reject subjective phenomena. On the contrary, I think that the exclusive study of one or the other is an unnecessary deformation of a total scientific approach. I do not consider objective and subjective phenomena as opposites so that the advocacy of one implies the rejection of the other. They are as complementary as the odd halves of a pair of scissors. It is quite essential that we consider the subjective; in fact, I would like vastly to extend our experimental approach in this area. I repeat my suggestion that there appears to be an entirely unexplored domain of perceptual conditioning. We know that perception is affected by experience, but we do not know any of the laws which might relate to the possible conditioning of perceptions. Instead of inducing conditioned motor responses exclusively, we could induce conditioned subjective experiences.

Sperry: With reference to the conditioned response, specifically, I suspect that a good case can be made for the contention that in most or all conditioning, the stimuli used, in order to be effective, must register as sensation or feeling in the neural stream of subjective awareness. In other words the animal must feel the pain from the shock, must smell or taste the meat juice, and so on. Most of us proceed on the familiar and generally accepted thesis that these subjective phenomena play no part in the causal sequence of neural events. Our picture of how the brain excitations are generated and transmitted seems to have no place in it where a sensation, that is, the subjective property, could get into the act.

On the other side of this old argument we have the reasoning that the pain *per se*, and subjective awareness in general, emerged in central nervous evolution and could only have been maintained and differentiated because it does serve a real use, *i.e.*, by virtue of its operational value in the causal sequence. On these terms one wonders if any physiological model of the conditioned response that fails to include the subjective properties is not bound to end up with some kind of gap in the chain of cerebral events. My point is merely that we may have gone a bit far in the past several decades with our behavioristic postulate that neurophysiological science can confidently assume that a full understanding of cerebral events is possible in theory from the purely objective approach that excludes and ignores the emergent properties of subjective awareness.

Livingston: I agree completely. I would only like to say that there have been a number of times when disproportionate emphasis has been placed on one or the other approach.

My final point refers to the advantages of an historical approach.