The following are my corrections and references through page 150. The remainder will follow shortly.

R. W. Sperry

p. 19, line 35:

SPERRY: It's very likely that I'm here in part for just the opposite reason that Dr. Olds stressed; namely, that I'm not associated with Dr. Magoun.

p. 20, line 6:

SPERRY: That's right. One of his colleagues stopped by a few days ago and indicated how much he would have liked to come. Knowing some of the very interesting and excellent work this man is doing in conditioning, I am sure he would be here had Dr. Magoun not felt that his own laboratory already was modestly well represented. (Laughter). As for the conditioned reflex, I can at least say that I have published on the subject from the vantage point of not having done any real research in the field. Our work has been concerned largely with the unconditioned reflexes, particularly with problems concerning the developmental patterning and organization of the "natural reflexes," as Pavlov called them. Nonetheless I have always had a special interest in the neural basis of conditioning and I am delighted to have the opportunity to participate.

p. 108, line 28:

SPERRY: I would guess that once a reflex is strongly extinguished, it is extinguished for life, in the same sense and to the same extent that once a conditioned response is established, it cannot be erased. I say this on the supposition that the conditioning and the extinction process are basically the same mechanism, i.e., a learning and an unlearning, or re-learning, and that the positive-negative difference resides essentially in the kind of response effects to which they lead. This is important with reference also to problems concerning the nature of the memory trace. If the trace changes are located at the synapse, then presumably the change can be made in one direction only, whether it be facilitory or inhibitory. That is, impulses can be directed over the synapse or withheld, but so far as we know, the effects of previous transmission cannot be actively wiped out by reversing the synaptic activity from facilitation to inhibition or vice-versa. Active reversal of this sort, i.e., erasure of previous traces, could be obtained, however, at the cellular level. For example, a lasting decrease of a neuron's excitatory threshold established in conditioning could be wiped out and reversed by active inhibition of the same cell through other synapses. But I presume these are questions that we'll be getting into in more detail later on in the conference.

p. 109, line 10:.

SPERRY: This is demonstrated in various experiments in which conditioning and extinction have been repeatedly alternated (1). If you continue the alternation, you reach a point where a single trial is sufficient to reestablish or to extinguish the conditioned response. In this case, at least, it is clear that even strong extinction does not wipe out the traces of previous conditioning. Without question the previous history is there in some form.

p. 119, line 33:

SPERRY: May I go back to Dr. Teuber's comment? I am not entirely ~~satisfied~~ happy to let the impression stand that Pavlov's use of the terms, "inhibition," and "excitation," did not refer to physiological entities. He was thinking here of brain processes, was he not? He even makes reference to their chemical bases. It was my impression he implies definite physiological brain processes.

p. 150, line 6:

SPERRY: Back in the middle and late 30's Anokhin and his coworkers published a number of papers along with a book (8) covering his extensive nerve-cross and muscle-transplantation studies. His conclusions therein were in full accord with those of the leading German, English, American, and other authorities of the time. Specifically, it was inferred that the pathways of the brain and cord are not regidly specified in their function but are instead highly plastic and readily readjusted under the conditions of nerve and muscle transplantation. That is, any dysfunction produced by surgical rearrangement of the normal innervation pattern is corrected through central readaptation and normal function is restored. Even the phylogenetically old reflex pathways of the spinal cord were inferred to be thoroughly plastic and readaptable in this respect.

¶ When we attempted back in 1938 to determine the level of the CNS at which these readjustments take place, it was a complete surprise to find that no readjustment occurred. Rats with crossed nerves and transplanted muscles continued indefinitely to move their feet in reverse in a thoroughly machine-like fashion (C). Further experiments with a variety of sensory and motor nerves in rats and later in monkeys (D) yielded similar results and led us to conclude that the earlier claims of extreme plasticity of the nerve centers were incorrect. Our findings suggested that the basic sensory and motor coordination patterns of the nervous system are rather rigidly organized: that the organization is laid down in the beginning by the growth process, and that the extent to which it is subsequently modifiable by learning is extremely limited.

As I vaguely recall it, some of the observations Anokhin included in his book seemed to support better our own conclusions than they did his. In line with this, it is interesting now that the account which Dr. Leake has just read us mentions only the dysfunctions that result from abnormal nerve connections. There is no reference to any readaptation or restoration of normal function. Although I no longer attempt to follow this literature closely, I have the impression that the work of the past 10 years has in the main confirmed our earlier contention that the kind of extreme plasticity generally imputed to the mammalian central nervous system up through the 30's simply does not exist.

References

A) Cole, L. E.: Human Behavior. Yonkers-on-Hudson, N. Y., World Book Co., 1953.

B) Anokhin, P.: Reports on the Problem of Centre and Periphery in the Physiology of Nervous Activity. Gorky, U.S.S.R., Gorky State Publishing House, 1935.

C) Sperry, R. W.: The Problem of Central Nervous Reorganization after Nerve Regeneration and Muscle Transposition. Quart. Rev. Biol. 20, 311 (1945).

D) Sperry, R. W.: Effect of Crossing Nerves to Antagonistic Limb Muscles in the Monkey. Arch. Neurol. Psychiat. 58, 452-473.

1. 26 SPERRY: I have one or two points that I can cover more briefly with the help of slides. The first concerns a subject to which Bob Doty referred in passing but which otherwise we have given little attention, namely, the problem of the location in the brain of the 'new connections' or engrams. As Bob mentioned, the engram has proven to be a rather elusive will-o-the wisp and is considered to be diffused and non-localizable.

I was surprised to find that in the cat we could attain the degree of localization illustrated in Figure (1A). 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 (N) it was found that the normal contralateral transfer of somesthetic discriminations from left to right forepaw is prevented by 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 Fig. (14) shows better in the lateral view in Fig. (10). This 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 thehippocampus on the side of the cortical isolation appears to produce little, if any, additional impairment of the retention and new learning mediated through the cortical island, according to current work with Dr. Schrier.

In regard to this rather circumscribed localization, it should be emphasized perhaps that the discrimination habits tested for retention were well stabilized by overtraining, particularly that they were of a highly specialized nature, i.e., 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 comment here regarding methodology. Pavlov is supposed to have stated that he used the salivary duct and its output on one side for science, leaving the rest 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.

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1. 21. SPERRY: Let's turn to the next slide which 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 conditioned and unconditioned stimuli. So-called sensori-sensory conditioning poses even more specifically a problem in the central association of two sensory stimuli. We have come across some interesting data lately in a study aimed at the mechanism of sensori-sensory integration involving visual and tactile sensibility in the monkey. The monkey is shown 2 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 tactile cue is conditional on the visual cue and vice versa (the term 'conditional' is used here in a rather different sense than has been used in the conference).

Before going deeper into this problem, let me fill in some necessary background. Earlier studies (0) 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, 3-D shape, and flat pattern. Opposing discriminations can be learned concurrently through the separate eyes without interference, i.e., with 5 or 10 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, i.e., would perform the same problem very nicely, if we switched back to the first eye, and without sulking, with the second eye would perform on any of the several other problems it had already mastered; nor was there sulking on subsequent new problems.

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.

p. 444

1. 7 SPERRY: Yes, this is contradictory to the results which Dr. Stamm and I (N) 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 now the presence of somesthetic transfer and the absence of visual transfer, we are ready to return to the initial 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. We next tested the right eye, right hand and the left eye, left hand combinations, and, in both cases found high level transfer with only a little hesitancy during the first several trials.

A new tactile problem was then trained with the left hand, after which I removed the somatic arm area from the right cortex. 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 aimed at removal of the arm portion of Somatic II. On the 13th day after operation, the left hand being still severely paralyzed, we tested for transfer of the newly-learned tactile problem to the untrained hand. Lack of transfer would indicate a unilateral engram system underlying somesthetic transfer. In this case the score reverted to chance and relearning with the second hand required over 200 trials compared to about 600 with the 1st hand. Learning with the first hand had been delayed by a pre-existing preference for the negative pattern. Also there is considerable variation in the learning curves of the two separated hemispheres for a given problem in the monkey. (This is in contrast to the amazing similarity we have seen in these curves in the cat (N, P), and possibly reflects a species difference correlated with greater perceptual insight in the primate). One can infer that the somesthetic transfer depends in part upon ipsilateral input feeding into a dominant engram system formed from experience with the first hand and laid down in the cortex contralateral to the trained hand. We're now checking to determine whether there is also a subsidiary engram system laid down in the other hemisphere via ipsilateral input from the trained hand.

Postoperative tests on the visuo-tactile discrimination showed the performance with left eye and right hand to be unaffected as anticipated (see Figure). It was a surprise, however, to find that the monkey could also perform the discrimination with the right eye and right hand. When this was first tested the 20th day post-op, the score reverted to chance in the first 20 trials but quickly rose to criterion by the 50th trial and to 90% correct by 100 trials.

Tests combining left and right eye with the left (paralyzed) hand were possible by the 6th week. Recovery had proceeded to where the hand could be used 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 proprioreceptive cues throughout arm and shoulder, was possible. The visuo-tactile and pure visual discriminations were performed at preoperative levels, above 90% correct, with the right eye, left hand combination.

When we switched to the final combination involving left eye with left hand the score on the visuotactile problem dropped abruptly to chance. With the purely visual problem, the performance was on-off, being perfectly good one day then lapsing to chance on the next session. When it was off, the monkey acted disoriented, almost as if it couldn't see, but it performed perfectly well as soon as it was shifted to the other eye. On the 4th day of this peculiar performance, something seemed to click and thereafter both the visuotactile and visual discrimination were performed at high level with either eye and left hand.

You will note that the monkey is able to use either hand to perform visual discriminations even though the visual input is restricted to one side. Schrier (Q) finds this to be true also in the cat after training has been confined throughout to one paw. In earlier studies with 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 the inherent