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BRAIN SCIENCE: SPERRY'S CONTRIBUTION. Roger Sperry, Trustee professor emeritus of psychobiology at the California Institute of Technology, is famous for experimental studies of how brain circuits are formed, and for research on mental activities after the connecting tracts between the cerebral hemispheres have been cut. He worked for his doctorate in close association with the biophysicist Paul Weiss, who had developed surgery to analyse how connections between nerves and muscles are patterned, and had demonstrated that the movement patterns of amphibia develop spontaneously in the embryo. By transplanting limb buds and re-routeing motor nerves, Weiss found that salamanders could regain an excellent sequential control of their limb muscles, the nerves making connections that matched, not the locomotor usefulness of the movements, but the embryonic origins of the different muscles. Sperry felt there must be a more specific and refined control of the growth of nerve circuits than any existing theory could explain, and that the intricate networks of the brain must result from a highly differentiated genetic coding for nerve contacts. He transplanted the insertions of extensor and flexor muscles of rats, or cut and re-routed their nerve supply, and then observed their limb movements. He reported that the rats' motor system was almost completely lacking in plasticity: except for some editing out of false moves of the forelimbs, central motor command was inflexible. The rats' wrongly connected nerves or muscles continued to produce maladaptive movements.

In the early 1940s, with Karl *Lashley, Sperry published a paper on the effects of thalamic lesions on olfactory learning in the rat, yet his main endeavour now was to explore the laws that fitted nerves into functional networks in development. He confirmed the finding by Robert Matthey in Switzerland and Leon Stone at Yale that after a newt's eye had been dissected from the head and replaced, retina and optic nerve would re-connect to the brain and normal vision would return. Sperry observed the behaviour of the animals more closely; and he showed that when a transplanted eye had been rotated through 180°, movements to catch food after recovery of vision were precisely as predicted by the theory that cells at each retinal point had re-connected themselves to the same place in the brain as before surgery. All orienting reactions were the reverse of correct, like those of a person who has just put on inverting prisms, though for newts adaptive visuo-motor co-ordination was not regained. This proved that the routeing of nerves, beyond a random tangle in the re-joined optic nerve into the brain centres, was precisely guided by some pathfinding principle in which learning played no part.

Later experiments on amphibia showed that regeneration of links from eye to brain, and from brain to the muscles of the eyes and fins—both of which make intricate movements in these species—obeyed the law of innate specification of connections. With Norma Dupree, a fellow biologist, whom he married in 1949, he carried out an important study at the Lerner Marine Laboratory, Bimini, West Indies, which found evidence suggesting that motor nerves preferred to regenerate connections to their own muscles. This suggested that the salamanders Weiss had studied were atypical. Later Richard Mark, working with Sperry in California, showed this to be the case.

In 1950 Sperry reported that fish and newts with one eye removed and the other either inverted or transposed to the opposite side of the head behaved in a peculiar way. They remained quiet, if not caused to swim, but spun in accelerating circles as soon as they moved. This behaviour was affected only by removal of the midbrain, where the optic nerves terminate, and was unchanged by removal of the labyrinths (organs detecting accelerations and gravity) or severance of the oculomotor muscles. Sperry concluded that the midbrain is the site of a predictive adjustment of visual perception triggered by the impulse to turn. The signal on the retina that the external world was displacing relative to the animal's head, was now reversed along the front/back axis by surgery. It signalled that the world was receding, and the locomotor system then worked harder to catch up, like a kitten chasing the tail of another kitten running twice as fast. Sperry proposed that there is an internal brain signal, which he termed a 'corollary discharge from efference' that matches visual effects normally consequent on each locomotor displacement for its direction and speed. He pointed out that such a 'central kinetic factor' would help explain both perception of self-movement and the constancy of perception of the spatial layout of the world while in motion. He had independently and simultaneously discovered the integrative principle co-ordinating perception with movement that von Holst and Mittelstaedt in Germany had found in the reflex optomotor responses of the praying mantis. They called it the 'reafference principle' and explained it, by the same mechanism as Sperry, under the name of 'efference-copy'.

Sperry then returned to his old idea that many fundamental laws of perception are reflections of inherent and precisely structured mechanisms for patterning movements. In an essay entitled 'Neurology and the Mind-Brain Problem' (1952) he argued that motor output in free behaviour gave better evidence of the neural basis of integrative behaviour than did the enumeration of simple and unnatural reactions by largely inactive subjects to physical variation in imposed stimuli. He also questioned the anticonnectionist views of Lashley and the *Gestaltists, and indicated that associationist *learning theories are to be attacked by examining how patterns of response are co-ordinated, rather than by postulating field-processes in the sensory cortex. He showed prophetic insight with regard to questions now being tackled by systems engineers and cognitive scientists trying to model *intelligence with computational machines, and also to those questions of interest to psychologists who seek to relate categories of perceptual processing to the problems the brain has to solve if it is to initiate movements that use terrain or objects efficiently.

Karl Lashley, Wolfgang *Köhler, and others believed form recognition to be the result of field effects or interference configurations generated in a random cortical net, or of transitory electrical or magnetic fields arising between nerve-cells in the grey matter. To test these ideas, Sperry and his students made minute criss-cross cuts under microscopic control throughout the visual cortex of cats, riddled it with tantalum wires to short-circuit any electrical fields, and implanted leaves of mica to interrupt local transverse currents. Then they subjected the cats to extreme tests of visual form discrimination. They found virtually no losses in vision, and concluded that form perception must depend on the passage of information in and out of small cortical territories, presumably by specific neuronal linkage with cells below the grey matter.

A graduate student, Ronald Myers, invented a delicate operation to cut the cross-over of visual nerves ('optic chiasm') under a cat's brain, so that each eye would lead to only one cerebral hemisphere. In 1953 Myers and Sperry reported not only transfer of the visual pattern memory between the hemispheres in chiasm-sectioned cats, but also that this transfer did not occur when the huge fibre bridge between the hemispheres, the *corpus callosum, was cut. The term *split-brain, with which Sperry's name is associated, refers to this operation and the research to which it has given rise. The operation proved that specific fibre connections could transmit learning, and further challenged Lashley's 'mass action' theory of brain systems.

Sperry and his associates made many experiments on the divided awareness and learning of split-brain cats, confirming the role of the commissural fibres in memory formation, and he also explored systems by which vision or touch controls voluntary limb movements. The investigations were extended to monkeys: like cats, these showed independent learning in the two brain halves after complete section of the corpus callosum, and experiments found that vision and touch crossed in different parts of the commissure. Colwyn Trevarthen showed that split-brain monkeys could learn two conflicting visual discriminations simultaneously; in other words, they could have double consciousness.

In the cat, each disconnected hemisphere directed movements of the whole body, but the motor system of split-brain monkeys was partly divided. They were both less willing to respond with movements of the hand on the same side as the seeing hemisphere and, if forced into action, were clumsy with this combination, as if they became blind each time they moved. Clearly, when the two halves of the cortex were disconnected, only crossed pathways linking each half of the cortex to the opposite hand could guide the fine exploratory and manipulative movements of a monkey's fingers.

Split-brain animals were used to reveal shifts of attention between the two separated halves of the cortex, and the effects on perception of *sets to move in particular ways. Thereby fresh interest was aroused in the global design of the mammalian brain for awareness, learning, and voluntary action. The minimum territory of cortex needed to retain learned control of the hands by touch or vision was determined by progressively removing all other cortex from one hemisphere of a trained split-brain animal around the primary touch or visual area until losses occurred. The other half brain was left intact, so that behaviour could continue as usual outside the training situation where experiences were confined to the operated side.

Between 1950 and the mid-70s Sperry continued to direct research on the formation of nerve circuits in lower vertebrates. He published some twenty articles explaining and defending his theory that most cerebral functions are determined genetically by some chemical or physiochemical coding of pathways and connections. New methods for following nerve growth have revealed competitive epigenetic processes involved in sorting out functional connections while they were growing, but so far every attempt to overthrow the chemoaffinity theory by experiment has reached a point where some such selective principle has to be invoked. Sperry has certainly won his battle against the theories of the 1930s that conceived complex psychological functions to be entirely the result of experiences which impose selective influences on random and infinitely plastic nerve nets.

General articles on experiments with cats and monkeys expressed Sperry's belief that learning itself is the consequence of submicroscopic modification in cerebral circuits whose anatomical design is pre-wired according to genetic instructions. The latter set adaptive goals and give the organism categories of experience as well as intricately co-ordinated forms of action.

Around 1960, a Los Angeles neurosurgeon, Joseph Bogen, observed with Sperry that the behaviour of split-brain monkeys outside test situations indicated that division of the commissures left motivation, consciousness, and voluntary action virtually unimpaired. Bogen pointed out that the operation offered promise of relief from debilitating epileptic fits which involved reverberation of discharges across the corpus callosum. In 1962 Bogen and Philip Vogel performed a total neocortical commissurotomy on a man who suffered frequent epileptic attacks, and Sperry and a graduate student, Michael Gazzaniga, were able to apply systematic psychological tests. After 1965 a growing team of researchers under Sperry's close direction, including Jerre Levy, Robert Nebes, Harold Gordon and Dahlia and Eran Zaidel, explored the state of divided and asymmetric mental activity in a small population of commissurotomy patients. The implications of the findings reached into all areas of human mental life, and excited immense public and scholarly interest. An account of the initial findings was given in Vinken, P. J. and Bruyn, G. W. (eds.) (1969), *Handbook of Clinical Neurology*, vol. 4 (Amsterdam).

From this research came support for concepts of inherent modes of thought and asymmetric involvement of the brain in rational/verbal thinking, non-verbalizable imagery, and conceivably also mystical experience (see SPLIT-BRAIN AND THE MIND). It stimulated studies of patients with lateralized injuries of the brain and research on the perceptual, cognitive, and motor asymmetries of function in normal subjects. Sperry's hypothesis that the hemispheres are so constructed as to display unlike psychological functions—genetic variation in *handedness, or the lateralization of language, being but two manifestations of human hereditary regulation—caused a reappraisal of the reasons for differences in intellectual and educational performance of different individuals.

Reflection on inherent mental processes in the human brain led Sperry to publish, in 1965, the first of a series of philosophical papers entitled 'Mind, Brain and Humanist Values'. He proposed a new monist theory of mind in which consciousness is conceived as an emergent, self-regulatory property of neural networks, which enables them to achieve certain built-in goals. These define requirements of the mind and psychological values which are given detailed form and direction by the rituals and symbols of tradition.

Sperry's philosophical ideas have proved somewhat controversial but derive great force from the range and depth of his experience in the field of psychobiology. Among his publications have been his chapter, Mechanisms of neural maturation, in Stevens, S. S. (ed.), *Handbook of Experimental Psychology* (New York, 1951); Neurology and the mind–brain problem (1952, *American Scientist*, **40**, 291–312); The eye and the brain (1956, *Scientific American*, **194**, 48–52); The great cerebral commissure (1964, *Scientific American*, **210**, 42–52); Embryogenesis of behavioural nerve nets, in Dehaan, R. L. and Ursprung, H. (eds.), *Organogenesis* (New York, 1965); In search of psyche, in Worden, F. G., Swazey, J. P., and Adelman, G. (eds.), *The Neurosciences: paths of discovery* (Cambridge, Massachusetts, 1975); Forebrain commissurotomy and conscious awareness (1977, *Journal of Medicine and Philosophy*, **2**, 101–26); and *Science and Moral Priority* (New York and Oxford, 1982).

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